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Abiotic plant stress mitigation by *Trichoderma* species

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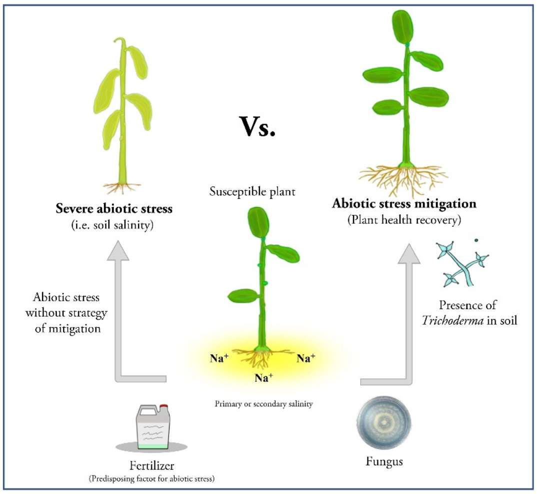
ABSTRACT

- Ascomycetes of the genus *Trichoderma* are beneficial fungi that promote plant growth.
- Several fungal species can mitigate abiotic stress in plants.
- *Trichoderma* spp. induce salt stress tolerance and drought protection in plants.
- Soil contamination by heavy metals can be bioremediated by *Trichoderma*.
- *Trichoderma* can detoxify pesticides and other pollutants in soils.



Plants drive both carbon and nitrogen cycling and mediate complex biotic interactions with soil microorganisms. Climate change and the resulting temperature variations, altered precipitation, and water shortages in soils, affect the performance of plants. Negative effects of abiotic stress are reflected in changes of plant morphology associated with biochemical alterations and inadequate adaptation to rapid ecological change. Accumulation of chemical agents, derived from pesticides, salinity due to chemical fertilization, and accumulation of heavy metals, are recurrent problems in agricultural soils. *Trichoderma* spp. are soil fungi interacting with roots and in this way helping plants to cope with abiotic stresses by increasing root branching, shoot growth and productivity. In part, such fungal effects on the host plant are consequences of the activation of fine-tuned molecular mechanisms mediated by phytohormones, by profound biochemical changes that include production of osmolytes, by the activity of the redox-enzymatic machinery, as well by as complex processes of detoxification. Here, we summarize the most recent advances regarding the beneficial effects of *Trichoderma* in mitigating the negative effects on plant performance caused by different environmental and chemical factors associated with global change and agricultural practices that provoke abiotic stress. Additionally, we present new perspectives and propose further research directions in the field of *Trichoderma*-plant interactions when the two types of organism cooperate.

Keywords *Trichoderma*, abiotic stress tolerance, salinity, drought, pollution, beneficial fungi

1 Introduction

Climate change, caused by emissions of greenhouse gases from anthropogenic activities, results in changes in temperature and precipitation, which strongly affect plant functioning whether in their native or managed ecosystems (Allen et al., 2010). In addition, the excessive use of agrochemicals in agroecosystems is leading not only to further climate gas emissions but also to soil eutrophication and salinity, and to adverse effects on soil biota function and diversity (Butterbach-Bahl and Dannenmann, 2011; de Almeida Silva et al., 2019; Cavicchioli et al., 2019; Menegat et al., 2022).

Complex communities of plant-beneficial soil microorganisms are of valuable biotechnological importance, especially in terms of plant stress mitigation from biotic and abiotic stress factors (Kolandasamy et al., 2023). Among the myriad of rhizosphere microorganisms there are some beneficial species of microscopic filamentous fungi, among which *Trichoderma* spp. stand out (Woo et al., 2023; Yao et al., 2023). Due to their ability to promote plant growth, alleviating

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plant stress and degrading toxic substances, selected *Trichoderma* spp. represent a sustainable alternative and/or complement to minimizing the use of agrochemicals (Contreras-Cornejo et al., 2020a, 2020b; Cardarelli et al., 2022).

A growing body of literature, detailed below, reveals an important role for *Trichoderma* spp. as key microorganisms under field, greenhouse or *in vitro* laboratory conditions. In this review we present and discuss novel information on the mechanisms of *Trichoderma* in supporting plant health.

2 *Trichoderma* in the rhizosphere

The fungal genus *Trichoderma* belongs to the phylum *Ascomycota*. Currently, at least 325 species are known (Macías-Rodríguez et al., 2018). Soil population density of *Trichoderma* spp. is estimated to be in the range of 10^1–10^3 propagules g^{-1} soil in tropical soils (Harman et al., 2004). At species level, the population density of *Trichoderma atroviride* has been shown to be approximately 10^3 propagules g^{-1} soil (Cordier et al., 2007). Some species show saprotrophic behavior, growing on decomposing plant organic matter. Other species have a great capacity to compete with other soil microorganisms for space and nutrients and to modulate plant interactions at different trophic levels (Contreras-Cornejo et al., 2018, 2020b; Macías-Rodríguez et al., 2020). Moreover, endophytic growth has been reported for some *Trichoderma* spp. (Bae et al., 2011; Chaverri et al., 2015).

The effect of *Trichoderma* on microbial communities can be negative (repressor), neutral (no apparent effect), and positive (stimulator of specific microbial communities). In this context, it is important to investigate the environmental and ecological conditions that modulate the activity of *Trichoderma*, especially when some of the species are used as bioinoculants and introduced into agricultural soils, where they represent exotic species under new environmental conditions.

Commonly, many *Trichoderma* species are associated with plant roots, in the rhizosphere, on the root surface or endophytically (Evans et al., 2003; Bae et al., 2011; Rosmana et al., 2016; Harman et al., 2021), most often resulting in symbioses with plants (Harman, 2011). In situations with different abiotic stress factors such as extreme temperatures, water deficit and the presence of toxic substances (Björkman et al., 1998; Govarthanan et al., 2019; Cristaldi et al., 2020), *Trichoderma* spp. can promote plant adaptation, tolerance and/or resistance to adverse environmental conditions (Table 1).

3 *Trichoderma*-plant interactions

Trichoderma is a common soil fungus forming part of the plant holobiont (Contreras-Cornejo et al., 2016; TariqJaveed et al., 2021). The interaction of *Trichoderma* with plants can happen without physical interaction between the mycelium of the fungus and the tissue, commonly with the roots

Table 1 Mitigation of abiotic stress by *Trichoderma* on plants under different stresses.

Type of stress	Fungal species	Beneficial effect	Reference
Oxidative stress	*T. harzianum* 1295-22	Induction of shoot biomass accumulation in maize (*Zea mays* L.)	Björkman et al., 1998
Thermic stress by low temperatures	*T. harzianum* 1295-22	Root biomass formation in maize (*Zea mays* L.)	Björkman et al., 1998
Cadmium tolerance	*T. virens*	*TvGST*, a fungal glutathione transferase expressed in *Nicotiana tabacum* enhances Cd in the transgenic plant	Dixit et al., 2011a
Contamination by anthracene	*T. virens*	*TvGST*, expressed in *N. tabacum* enhanced anthracene tolerance and degradation of hydrocarbonated compounds	Dixit et al., 2011b
Salinity	*T. atroviride* IMI 206040; *T. longibrachiatum* TG1; *T. atroviride* HN082102.1; *T. viride* RA1	Na^+ detoxification through enhanced ion root exudation in *Arabidopsis thaliana*. TG1 promotes wheat tolerance to salinity and resistance to the plant pathogen *Fusarium pseudograminearum*. The marine isolate HN082102.1 alleviates salt stress in cucumber (*Cucumis sativus* L.). In tomato plants, *T. viride* increased the concentration of proline and the activities of CAT, PPO and APX.	Contreras-Cornejo et al., 2014; Boamah et al., 2021; Zhang et al., 2022; Metwally and Soliman 2023
Drought	*Trichoderma* spp.	Several fungal species increase plant tolerance to water deficit. Particularly, *T. parareesei* has a chorismate mutase that is involved in tolerance to water deficit in rapeseed (*Brassica napus* L.) and *T. asperellum* NT33 promoted biomass accumulation of tomato (*Solanum lycopersicum*) under drought conditions	Poveda, 2020; Rawal et al., 2022; Hoseini et al., 2022
Elevated soil pH	*Trichoderma* spp.	Plant adaptation and growth promotion under alkaline soil pH	Cabral-Miramontes et al., 2022
Aluminum tolerance	*T. asperelloides*	The fungal inoculation reduces Al stress-induced damages by improving growth, photosynthetic pigments and organic solutes in maize	do Rego Meneses et al., 2022
Heat stress	*T. longibrachiatum* SMF2	This fungal strain produces trichokonins that enhance heat stress resistance in *Lilium davidii* var. unicolor by the up-regulation of the heat-protective genes *LzDREB2B*, *LzHsfA2a*, *LzMBF1c*, *LzHsp90*, and *LzHsp70*	Cao et al., 2023

(Martínez-Medina et al., 2017; Poveda et al., 2023). Roots exude monosaccharaides and sucrose that function as a nutritional source for *Trichoderma*. In this scenario, the fungus grows towards the source of carbohydrate emission, encountering the root which it subsequently colonizes, initiating further physical interaction (Macías-Rodríguez et al., 2018). *Trichoderma* also releases substances, including auxins and ACCase that stimulate plants and have biological activity related to plant growth (Gravel et al., 2007; Ou et al., 2023). Table 2 indicates the main signaling pathways activated by *Trichoderma* species in plants under different abiotic stress conditions (Fig. 1).

There is experimental evidence for the communication of plants with *Trichoderma* when the environmental conditions are a challenge for plant growth. For example, tomato roots of stressed plants release oxylipins, including 10-hydroxy-8*Z*,12*Z*-octadecadienoic acid, 12,13 epoxy-9*Z*-octadecenoic acid and 9,10-epoxy-12*Z*-octadecenoic acid into the rhizosphere; under high salinity these substances attract *Trichoderma* and promote the interaction (Lombardi et al., 2018).

4 Influence of *Trichoderma* on plant growth under stress conditions

Abiotic stress can compromise plant health and performance (Waadt et al., 2022). Several *Trichoderma* species have been shown to promote plant growth under abiotic stress and reduce the negative effects of abiotic factors that delay or alter plant growth (Bae et al., 2009; Shukla et al., 2012; Contreras-Cornejo et al., 2014; Metwally and Soliman, 2023; Fig. 2). Under abiotic stress the phytohormone-like

Table 2 Molecular mechanisms by which *Trichoderma* promotes abiotic stress tolerance in plants.

Phytohormone	Gene	Product	Function	Reference
ABA	*ABI4*	Encodes a transcription factor, which belongs to the family of APETALA 2	Under abiotic stress ABA signaling is activated and ABI4 is required in salt responses	Arroyo et al., 2003
	ABI1 and *ABI2*	The *Arabidopsis* ABI1 and ABI2 encode two protein phosphatases 2C (PP2C)	In adverse conditions that promote plant dehydration, ABI1 and ABI2 promote stomatic closure to reduce rate of water lost and improve water-use efficiency	Contreras-Cornejo et al., 2015
IAA	*NIT1* and *NIT2***	Protein nitrilases	Saline stress induces nitrilases that are involved in IAA production	Bao and Li, 2002; Liu et al., 2021
	ARF7 and *ARF19*	Transcription factors in IAA response	An intact auxin signaling pathway has a critical role to salt tolerance in modulating the root branching and consequently enhance Na^+ elimination through root exudates	Contreras-Cornejo et al., 2014
	AUX1	An auxin influx transporter		
	PIN2	An IAA efflux transporter.		
	TIR1, *ABF2* and *ABF3*	Auxin receptors		
ET	*ETO3*	Ethylene-over producing 3	A factor involved in ET production	Brotman et al., 2012;
	EIR1	EIR1 encodes the auxin transporter *AtPIN2*		Contreras-Cornejo et al., 2014
	*ACCD**	1-Aminocyclopropane-1-carboxylate deaminase	ACCD cleaves its substrate to produce α-ketobutyrate, ammonia and ET, which is a signaling phytohormone in response to abiotic stress *T. asperelloides* T203 ameliorates the negative effects caused by salinity in plants regulating the ACCD activity	Viterbo et al., 2010; Brotman et al., 2013; Zhang et al., 2019b
GA	*GAI, RGA, RGL1,* and *RGL2*	DELLA proteins	ET signaling can induce salt stress tolerance in a DELLA-dependent manner and this address needs further research during *Trichoderma*-plant interactions under abiotic stress	Achard et al., 2006; Zhao and Zhang, 2015
SA	-	-	*T. longibrachiatum* TG1 triggers the accumulation of SA, which increases the activity of antioxidants and expression of the genes *SOD*, *POD*, and *CAT* to cope with the oxidative stress provoked by salinity	Illescas et al., 2021; Boamah et al., 2022
	*CM**	Choristamate mutase	*CM* is a component of the shikimate pathway. In plants, over-expression of CM increases the levels of SA. Most likely, this enzyme in *Trichoderma* promotes tolerance to salinity and drought in plants by increasing the expression of genes related to the signaling mechanism mediated by ABA under drought, and ET under salinity	Poveda, 2020; Jan et al., 2021
Multiple	*MAPK3*	Mitogen activated protein kinase 3	This kinase participates in signal transduction cascades of defense responses and abiotic stress resistance, which need further research in *Trichoderma*-plant interactions	Bae et al., 2009

All these five phytohormones can be produced by *Trichoderma* spp. ABA: Abscisic acid; IAA: Indole-3-acetic acid; ET: Ethylene; GA: Gibberellic acid; SA: Salicylic acid. *, Component of the *Trichoderma* molecular machinery.

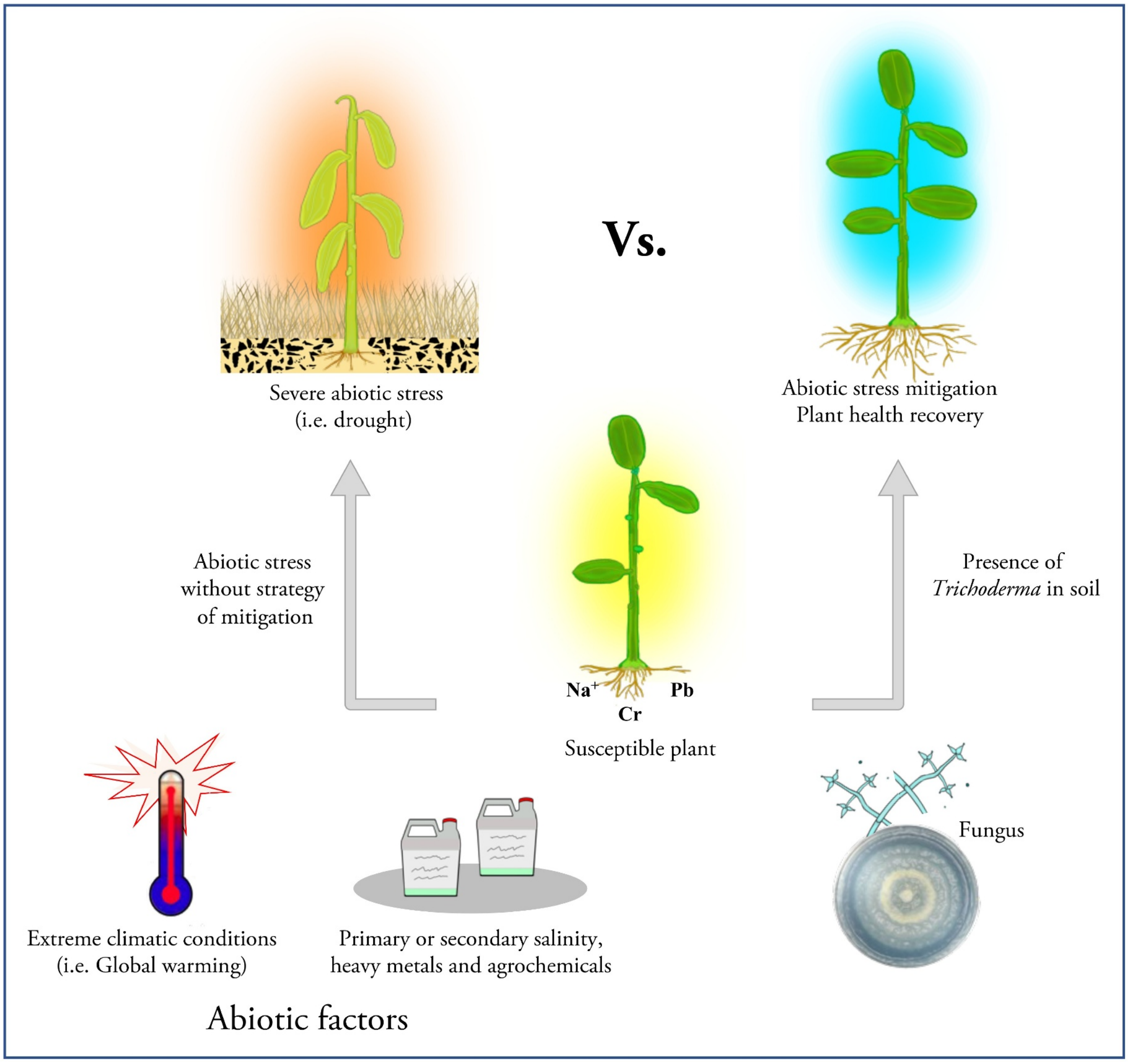

Fig. 1 Schematic representation on the negative effects of abiotic factors that damage plants and the role of *Trichoderma* on stress mitigation. Abiotic factors such as drought, primary and/or secondary salinity, heavy metals and toxic agrochemicals cause detrimental effects on plants. However, *Trichoderma* sp. can mitigate such effects and improve plant growth and productivity.

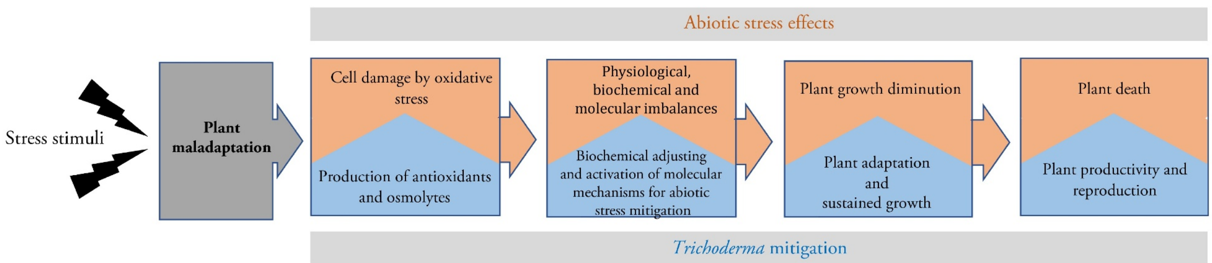

Fig. 2 Plant abiotic stress mitigation by *Trichoderma*. This image shows five boxes representing a continuous scenario of abiotic stress. The gray box is an initial and general condition of stress (i.e., salinity). Subsequent boxes show a progressive plant health degradation scenario that is represented by the orange section, but also show in blue the contribution of *Trichoderma* to mitigation of the stress.

compounds produced by *Trichoderma* play an important role in mitigating the burden caused by stressful conditions (Fig. 3). In the following sections, we describe how several species of *Trichoderma* impact on plants under adverse conditions.

4.1 Climate change

Climate change produces significant changes in environmental temperature, observed at regional and global scale. Changes in climate patterns induce biotic and abiotic

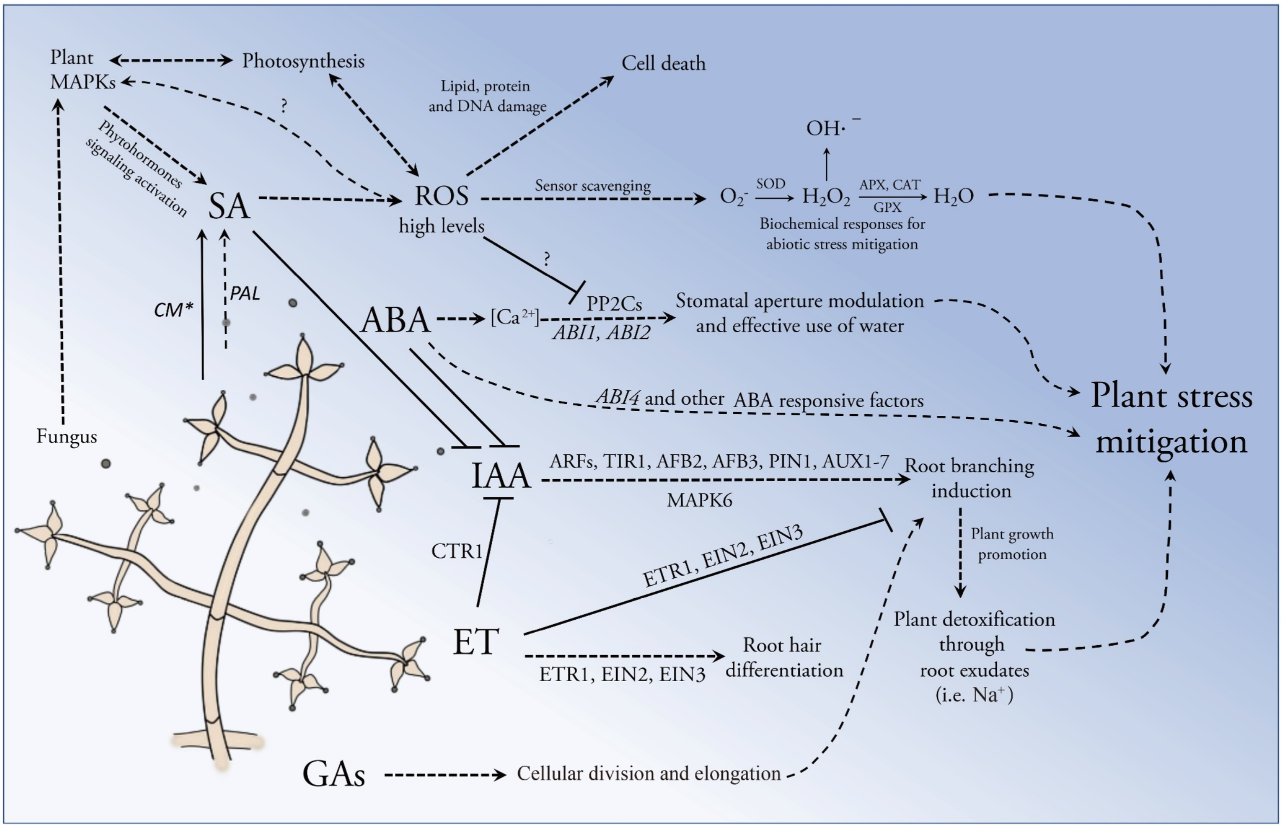

Fig. 3 Signaling mechanisms that *Trichoderma* activates in plants to promote abiotic stress tolerance. SA, ABA, IAA, ET and GAs are the canonical phytohormones produced by plants and *Trichoderma*. Initially, the abiotic factor that provokes stress causes signal translation involving the participation of secondary messengers and the activity of protein kinases; subsequently, the hormones are activated to trigger a response of tolerance or resistance to stress. The phytohormones in turn promote the gene expression, protein biosynthesis and their activity. Metabolic components as antioxidants (i.e., ascorbic acid) and osmolytes (i.e., proline) contribute with the correct cell functionality, protecting the cell from oxidative damage and cellular collapse during abiotic stress mitigation. CTR1: Constitutive Triple Response, which is a central modulator of the ET-signaling pathway. CTR1 allows EIN2 to relay ET signal to the correspondent transcription factors, including EIN3.

stresses that affect the growth, development, and productivity of plants in their natural habitats and in agroecosystems (Contreras-Cornejo et al., 2023). Alterations in environmental temperature, in the availability of water in the soil, in intensity of sunlight and the presence of contaminants in the air and soil, are critical abiotic factors for the survival of plants.

Changes in the environmental temperature leads to oxidative stress in plants, which alters multiple physiological processes involved with the growth of the vegetative phase. This in turn affects the subsequent performance of plants in their processes of adaptation, defense, and reproduction (Lesk et al., 2016). It has been observed that different *Trichoderma* species can help plants to cope with temperature changes (Cao et al., 2023). Interestingly, *Trichoderma* can resist adverse environmental conditions by activating efficient molecular mechanisms for environmental perception and oxidative stress mitigation (Karuppiah et al., 2022). For example, the *Trichoderma* isolate TaDOR673 seems to use the mitogen activated protein kinase (MAPK) signaling cascade in combination with heat shock proteins to resist heat shock (Poosapati et al., 2021). That is, the fungus induces significant changes in the metabolism of its host plant and activates key molecular mechanisms that are associated with stimulating tolerance to heat stress. Table 1 shows some cases in which *Trichoderma* had beneficial effects on plants under heat stress.

4.2 Salt stress conditions

High soil salinity is an environmental constraint that fundamentally affects plant growth (Zhang et al., 2019a, 2019b). For example, irrigated agriculture and the excessive use of chemical fertilizers that contain sodium ions (Na^+) frequently cause secondary salinity in arable soils (Moharana et al., 2019; Stavi et al., 2021). Soil salinity causes a reduction of growth in both roots and shoots, but also causes chlorosis, oxidative burst, and low rates of photosynthesis (Abogadallah, 2010). Several *Trichoderma* strains can alleviate the detrimental effects on plant physiology, acting alone or synergistically, and confer salt stress tolerance (Gupta et al., 2021; Zhang et al., 2022; Anshu et al., 2022; Irshad et al., 2023).

For example, *T. asperellum* diminished the negative effects of a naturally alkaline-saline soil (pH = 9.30) on two maize genotypes: Jiangyu 417, a saline-resistant line, and Xianyu 335, a saline-sensitive line. Indeed, *T. asperellum* promoted root and shoot growth with both maize genotypes, but with different degrees of protection against oxidative damage involving the antioxidant mechanisms. In non-inoculated soil, the Xianyu 335-line accumulated higher levels of superoxide anion (O^{-2}) than Jiangyu 417. Clearly, *T. asperellum* inoculation enhanced the activity of the antioxidant enzymes ascorbate peroxidase (APX), catalase (CAT), glutathione reductase (GR), guaiacol peroxidase (GPX), peroxidase (POD), and superoxide dismutase (SOD) in plants, which contributed to the decrease of Na^+ and reactive oxygen species (ROS) levels in the roots and shoots (Fu et al., 2017).

Further, it has been observed that *T. asperellum* Q1 alleviated the negative effects caused by salinity in cucumber plants by increasing plant concentrations of indole-3-acetic acid (IAA) and gibberellins (GAs) and modulating the levels of abscisic acid (ABA), which was related with increased root growth and phosphate solubilization by the fungus (Zhao and Zhang, 2015). More recently, it was reported that *T. hamatum* increases plant tolerance to salinity, modulating both antioxidant metabolism and photosystem II. The plant beneficial effects induced by *T. hamatum* included reduction of the oxidative stress by the activity of the enzymes SOD and CAT, reduction of the oxidative stress markers H_2O_2 and malondialdehyde, increases of the chlorophyll content from 81%−189% and growth promotion from 141%−209% (Irshad et al., 2023).

Zhang and coworkers (Zhang et al., 2019a) reported that “T-soybean”, a *T. harzianum* isolate from soybean rhizosphere, mitigated the negative effects caused by saline stress in cucumber plants by modulating multiple factors involved in the antioxidative mechanisms, such as APX, CAT, GR, POD, SOD, phenylalanine ammonia-lyase (PAL) and polyphenol oxidase, as well as by inducing the production of ascorbic acid (AsA), soluble proteins, sugars, proline, and chlorophyll. In addition, T-soybean regulated the proportions of glutathione (GSH) to oxidized glutathione (GSSG) and AsA to dehydroascorbate (DHA) in cucumber plants, and modulated the expression of some genes that form part of the AsA-GSH cycle and *CsAPX*. T-soybean provoked modulations in the ratios of K^+:Na^+ in soybean, since decreased concentrations of Na^+ were detected, while increased levels of K^+ occurred; moreover, the presence of T-soybean led to the maintenance of an adequate osmotic balance in its host, which resulted in better salt stress tolerance and sustained plant growth (Zhang et al., 2019a). Taken together these data show that *Trichoderma* confers salt stress tolerance by targeting multiple mechanisms in plants.

4.3 Drought and water fluctuations

Water availability modulates growth and adaptability in all terrestrial organisms. For example, drought substantially alters the overall community composition of fungi in the rhizosphere of grapevine (Carbone et al., 2021). However, several *Trichoderma* strains can increase tolerance and adaptation of plants to water fluctuations and/or drought stress (Illescas et al., 2021). Water potentials from −2.8Ψ to −8.5Ψ have a profound negative impact on the growth of several isolates of *Trichoderma*, including the commercial strain *T. afroharzianum* T-22 (Rawal et al., 2022). Under a water potential of −8.5Ψ the more sensitive isolates were *T. asperellum* NT4, *T. asperelloides* NT39, *T. hamatum* OT40, *T. ghanense* OT41 and *T. harzianum* NT5. However, some strains can confer beneficial effects on plants even under water stress. For example, *T. asperelloides* NT33 confers tolerance of tomato plants to water deficit (Rawal et al., 2022). During drought conditions at the early stages of the interaction of *Trichoderma* with seeds, germination is positively influenced. For example, tomato seed germination was dramatically affected by osmotic stress, particularly at –0.2 and –0.3 MPa, but seeds treated with *T. afroharzianum* T22 had a more homogenous and faster germination rate compared with non-inoculated seeds under osmotic stress (Mastouri et al., 2010). Beneficial effects of *Trichoderma* in rice (*Oryza sativa* L.) plants suffering water deficit include the modulation of genes involved in several processes such as photosynthesis, and mechanisms involving PSII subunit PSBY, PSI subunit Q, osmoproteins, aquaporins, chaperonins and antioxidative mechanisms, including that involving plastocyanin (Bashyal et al., 2021). In particular, an endophytic strain of *T. hamatum* conferred beneficial effects to cacao plants grown under water deficit and delayed the negative effects caused by drought. During such conditions, *T. hamatum* modulated the expression of key genes in cacao plants, including *MITOGEN ACTIVATED PROTEIN KINASE 3* (*MAPK3*)*, SORBITOL TRANSPORTER* (*SOT*), *PATHOGENESIS-RELATED 5* (*PR5*), and *LIPOXYGENASE* (*LOX*), suggesting that *T. hamatum* promotes the responses to environmental signals in its host, most likely by quickly triggering the molecular mechanisms for abiotic stress, including drought (Bae et al., 2009).

Like the protective mechanisms induced by *Trichoderma* in plants under salt stress, *T. afroharzianum* T22 has been found to regulate the expression of CAT, APX and SOD in tomato plants, genes that encode enzymes that serve as scavengers of ROS (Mastouri et al., 2012). Nevertheless, in response to water-deficit, such enzymes were induced in non-colonized plants but occurred to a lower level than in T22-colonized plants. Most likely because of the enzymatic function counteracting ROS-accumulation, the growth of tomato plants increased (Mastouri et al., 2012). In summary, these data reveal that *Trichoderma* confers tolerance to its host plants if available water is variable.

4.4 Heavy metals in soil

Trichoderma species also can induce plant tolerance to heavy metals and other elements present at toxic concentrations (do Rego Meneses et al., 2022). Particularly, *T. asperellum* can confer tolerance and support growth of *Suaeda salsa* plants when planted in soil contaminated with Na^+, Ca^{2+} and Pb. Sodium dodecyl sulfate polyacrylamide gel electrophoresis analyses showed that Pb and salt stress affected the total protein content in plants. Consequently, application of *Trichoderma* offers phytoremediation. Interestingly, the interaction with *T. asperellum* led to decreases of 13%−58%, 19%−30%, and 9%−42% of Na^+, Ca^{2+} and Pb concentrations, respectively (Li et al., 2019). The beneficial effects of *Trichoderma* on phytoremediation of soil contaminants are further important since high uptake of Na^+ by plants promotes the competence with K^+, which results in a cellular ion imbalance and subsequently induces cellular dysfunctionality (Li et al., 2019). Also *T. afroharzianum* T22 can promote the growth of crack willow in soil with elevated concentrations of metals, including Zn (1 109 ± 45 mg kg^{-1}), Sb (150 ± 64 mg kg^{-1}), Pb (351 ± 20 mg kg^{-1}), Ni (208 ± 74 mg kg^{-1}) and Cr (62 ± 26 mg kg^{-1}). After three months, saplings grown in the presence of *T. afroharzianum* T22 showed that the total dry biomass was 39% higher for saplings inoculated with the fungus compared with their respective control, and accumulated on average 60% more dry stem biomass than non-inoculated saplings (Adams et al., 2007).

Overall, the mechanisms involved in *Trichoderma* bioremediation of metal polluted soils remain to be further addressed. A possible mode of action is the remediation of single metal contaminants by calcite precipitation, where toxic metals are immobilized in the form of compounds by metal-resistant microorganisms (Su et al., 2015; Zhu and Dittrich, 2016; Govarthanan et al., 2019). However, this depends on the ability of the microorganisms to modify their microenvironment and create the physicochemical conditions favorable to metal precipitation (Gadd, 2010; Gadd et al., 2012). A particular case is the isolate of *Trichoderma* sp. MG, which can effectively immobilize As and Pb (Govarthanan et al., 2019). However, the molecular mechanisms activated by *Trichoderma* to confer tolerance in plants to heavy metals remain to be understood in more depth.

4.5 Accumulation of pesticides and other xenobiotics

Several *Trichoderma* species with plant growth-promoting activities can contribute to the biotransformation and detoxification of chemical contaminants, including chloroacetamide and other hydrocarbonated compounds (Dixit et al., 2011b; Jasińska et al., 2022). For example, *T. koningii* IM 0956, *T. harzianum* KKP 534, *T. viride* KKP792 and *T. virens* DSM 1963 promoted the growth of rapeseed (*Brassica napus*, cv. Monolit) seedlings treated with the herbicides alachlor and/or metolachlor. These four strains were found to produce key factors involved in plant growth promotion by rhizosphere microorganisms such as siderophores and ACCase, and were also efficient in solubilizing phosphate, even in the presence of herbicides. Among those strains, *T. harzianum* KKP 534 showed an outstanding impact on growth promotion of roots and shoots in the presence of both herbicides, when compared with uninoculated plants (Nykiel-Szymańska et al., 2020).

Phoxim is a broad-spectrum organophosphate insecticide, whose indiscriminate use can contaminate both the environment and plant-derived foods. Interestingly, *Trichoderma asperellum* TM can reduce the accumulation of phoxim in tomato roots by increasing the rate of elimination of this pesticide. Also, *T. asperellum* TM has been found to cause an increase of the transcript levels of *GST1*, *GST2*, *GST3* and accumulation of GSH in the plant. Furthermore, TM enhanced the conversion, conjugation, and sequestration of phoxim to stimulate the plant detoxification and leading to a reduced pesticide residue in tomato roots (Chen et al., 2020). Also, *T. harzianum* can degrade the herbicide metolachlor (MET), a chloroacetamide-derived compound. When present at a concentration of 20 mg L^{-1} of MET, after 24 and 72 h the fungal strain degrades 25% and 75% of the initial concentration of herbicide (Jasińska et al., 2022).

Considering bioremediation in a broader sense, *Trichoderma* spp. are also able to degrade polycyclic aromatic hydrocarbons (PAHs) (Zafra and Cortés-Espinosa, 2015), hexachlorohexane (HCH) (Russo et al., 2019), Dichlorodiphenyltrichloroethane (DDT) (Russo et al., 2019b), as well as kerosene, diesel, spent engine oil and crude oil (Ani et al., 2021). Consequently, *Trichoderma* spp. can become an important tool to support phytoremediation and bioremediation both by protecting the plants from pollutant-associated stress and by direct degradation of chemicals.

5 Molecular mechanisms activated by *Trichoderma* in plants under abiotic stress

Trichoderma might intervene in plant hormone signaling pathways by releasing certain substances such as auxins, ethylene, gibberellins and abscisic acid. In turn, these substances activate their respective signaling mechanisms leading to expression of genes related to abiotic stress tolerance or resistance that may be linked to both changes in the redox enzymatic machinery and osmolytes production. Fig. 3 illustrates the canonical mechanisms mediated by phytohormones and their molecular components that *Trichoderma* modulates in plants to mitigate abiotic stress.

6 Perspectives

In the last decade, agroecological and biotechnological interest in *Trichoderma* spp. has increased considerably due to its beneficial effects on plants and their limited effects on the environment. Thus, in the last 5 years, reports showing *Trichoderma* species as key mitigation microorganisms to resist abiotic stress caused by different physicochemical agents have gradually increased in rate of publication. However, there are still many questions to be answered in depth. For example: What are the physiological and biochemical responses of *Trichoderma* when it is growing in soils with water deficit or heat stress, which are two parameters that vary with climate change? What are the molecular mechanisms that the fungus activates in plants to resist adverse environmental conditions caused by water deficit? And in the context where *Trichoderma* is found in soils contaminated with heavy metals that can considerably affect the proliferation and activity of native microorganism communities, the question is: Can *Trichoderma* mitigate the negative effects and contribute to the adaptation of native microbial communities in the soil? It is also important to isolate and characterize new *Trichoderma* species with potential application as bioinoculants. The advance in knowledge in these fields will allow the continued use of these beneficial fungi in the soils of agroecosystems with environmental problems that affect the production of plants of food interest.

7 Conclusions

In this review we provide relevant and novel aspects on the role of *Trichoderma* when these fungi interact with plants and form part of a holobiont with ecological and agricultural importance. *Trichoderma* can promote plant growth under various scenarios of abiotic stress, such as those provoked by increases in environmental temperature, frequent periods of drought in agricultural lands and in protected ecosystems, and contamination of soil by chemical elements and agrochemicals.

A broad body of scientific literature strongly suggests that different species of *Trichoderma* activate considerable biochemical changes in plants that include the activation of molecular mechanisms modulated mainly by phytohormones such as auxins, ET, and ABA. Applying signaling networks, plants respond in this interplay and induce tolerance and/or adaptation to adverse conditions. Plants then alter the production and accumulation of osmolytes, antioxidant metabolites and key enzymes such as chaperones and others that participate in regulating the oxidation-reduction processes of cellular components. These effects together converge and contribute to mitigation of the negative effects caused by the different stress-inducing abiotic factors.

Multiple prediction efforts on the effects of climate change on terrestrial ecosystems suggest that the flora present in large portions of forest and agricultural lands will be severely affected. These concerns are calling for new strategies for plant biodiversity conservation and management of agricultural systems, as well as reduction of adverse anthropogenic practices that contribute to the deterioration of soils and the environment. Besides the naturally induced changes in the microbiomes caused by climate change, human induced changes by bio-inoculants and plant symbionts also have to be considered (Averill et al., 2022).

Since *Trichoderma* spp. are part of the soil and rhizosphere microbiomes worldwide, strains of this genus are optimal for regional enhancement of climate change resilience of plants without major disturbance of the local microbiome. However, although *Trichoderma* has great potential for agricultural applications, there are still several issues to address in terms of formulation and application methods and utilization. As spore formulations of *Trichoderma* are influenced by various natural factors such as humidity, temperature, soil pH, and soil microbial communities in the field, it is crucial to develop efficient formulations ensuring fungal performance in the soil. Finally, the use of *Trichoderma* as a bioinoculant represents a sustainable alternative for short term replacement of excessive use of agrochemicals, for increasing climate change resilience of crops and for discontinuing the use of substances that are used illegally in agricultural fields, especially in developing countries.

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Conflict of interest

The authors have no conflicts of interest to declare.

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