



REVIEW

The Mechanisms of *Trichoderma* Species to Reduce Drought and Salinity Stress in Plants

Mohammad Reza Boorboori and Haiyang Zhang*

College of Environment and Surveying and Mapping Engineering, Suzhou University, Suzhou, 234000, China

*Corresponding Author: Haiyang Zhang. Email: seazhang188@ahszu.edu.cn

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ABSTRACT

Environmental stresses caused by climate change have severely affected agriculture in the present century; Salinity and drought have challenged most forecasts for increased agricultural production in the past few decades, therefore, different methods that reduce the effect of these stresses on plants have attracted scientists' attention. The effect of beneficial soil microorganisms on soil health and increasing plants' resistance to stresses is one of the solutions that researchers have paid attention to. This study investigated how *Trichoderma* species can be affected by the molecular and morphophysiological mechanisms of plants and improve their salt and drought resistance. This study also studied the different *Trichoderma* species' functions to get a better understanding of how they reduce salt and drought stresses. Furthermore, the findings of this study provide a clear path for future research to focus on the unknown aspects of *Trichoderma* species and find effective ways to boost crop production under environmental stresses.

KEYWORDS

Dryness; microorganisms; molecular; morphophysiology; plant resistance; saline environment

1 Introduction

Trichoderma species are saprophytic or endophytic fungi that are found in almost all natural ecosystems, including forests, agricultural soils, and desert soils [1–3]. *Trichoderma* spp. which grow on plants' roots and the rhizosphere, are non-pathogenic fungi that colonize a variety of monocotyledonous and dicotyledonous plants [3–5]; Besides secreting secondary metabolites, they also produce hydrolytic enzymes that improve plant structure [6]. There are a number of commercial products based on *Trichoderma* spp., called plant protection products (PPPs), which are used in a wide range of crops (agricultural, horticultural, ornamental, as well as vegetables and fruits during post-harvest storage) [7]. The fungi, also known as opportunistic plant symbionts, colonize plant roots and improve soil fertility and texture, water-holding capacity, and plant growth, as well as plants' systemic resistance to pathogens [8,9]. Additionally, *Trichoderma* spp. interacts with a wide range of soil microorganisms and inhibits many diseases of plants without being pathogenic to plants or humans [3,10,11].



The hyphae of *Trichoderma* spp. penetrate the root cortex and form appressoria-like structures, colonizing the root intercellular space of the root vascular tissue; Eventually, force the surrounding plant cells to precipitate the cell wall material and establish a chemical relationship with plant compounds [3,4,11]. At the beginning of the third seed germination stage, *Trichoderma* spp. establish a symbiotic relationship with the host plant, and this relationship continues until the plant matures [5]. When *Trichoderma* spp. colonizes plant roots, they release viral-like genes products, enzymes, and low molecular weight compounds, reprogramming plant genes and proteomes and altering plant responses to the environment [5,12]; Besides colonizing plant roots, fungi also cause the expression of genes in leaves and stems [5].

As a plant growth promoter, *Trichoderma* spp. has become increasingly popular in recent years, and numerous studies have demonstrated that it increases plant growth throughout all growth stages [5,13]. Studies have shown that *Trichoderma* species improves root length, plant height, leaf surface, and dry weight of cucumber, millet, Luffa, bitter melon (*Momordica charantia* L.), and *Arabidopsis thaliana* [5]. With *Trichoderma* spp. as biofertilizers, chemicals can be reduced and sustainable farming can be improved [14,15]; In this way, they can maintain soil conditions, rehabilitate land, and protect rare seeds while enhancing the health of humans and preserve the environment [13,16] (Fig. 1).

In recent decades, it has been demonstrated that *Trichoderma* spp. improves plant growth and development by increasing its ability to absorb nutrients and water, and regulating phytohormones like ethylene, abscisic acid (ABA), cytokinin (CK), Indole-3-acetic acid (IAA, 3-IAA), Gibberellin (GA), and Zeatin [1,5,11,17–21]. As well, *Trichoderma* spp. activates nutrients in the soil by increasing the soil-rhizosphere contact zone and secreting extracellular enzymes including phosphatase, urease, sucrase, and organic acids [3,14,22]. Ramirez-Pimentel et al. found that *Trichoderma* spp. improved soil phosphorus bioavailability and plant availability of phosphorus [23], and additionally, Harman's study demonstrated that *Trichoderma* spp. reduced nitrogen (N) fertilizer use by about 40% to 50% [24]. In general, seed coating with *Trichoderma* spp. increases seed germination, plant growth, and seedling establishment significantly [13] (Fig. 2).

Trichoderma spp. is the most useful fungi for protecting plant products in organic systems due to its antagonistic properties [12,25]. It has recently been discovered that *Trichoderma* spp. is an effective biological control agent that helps plants resist both biotic (pests and pathogens) and abiotic stresses (salinity, high and low temperatures, droughts, heavy metals, etc.) [26–29]. Studies have also shown that *Trichoderma* species are effective at controlling plant pathogens, including *Pythium*, *Fusarium*, *Rhizoctonia*, *Phytophthora*, *Sclerotium*, *Botrytis*, *Colletotrichum*, and *Armillaria* [6,15,23,30,31]. In general, *Trichoderma* spp. play a crucial role in increasing the resistance of plants to various stresses by increasing photosynthetic efficiency, stimulating root growth, improving water and nutrient absorption, removing reactive oxygen species (ROSs), using chemical mutagens or T-DNA mutagenesis, producing alamethicins, producing metabolites, induce Hydrolytic enzymes genes expression including the endochitinase gene (*ech33*), and producing a trichodermin-trichothecene-type terpene toxin [7,12,13,23,27,32].

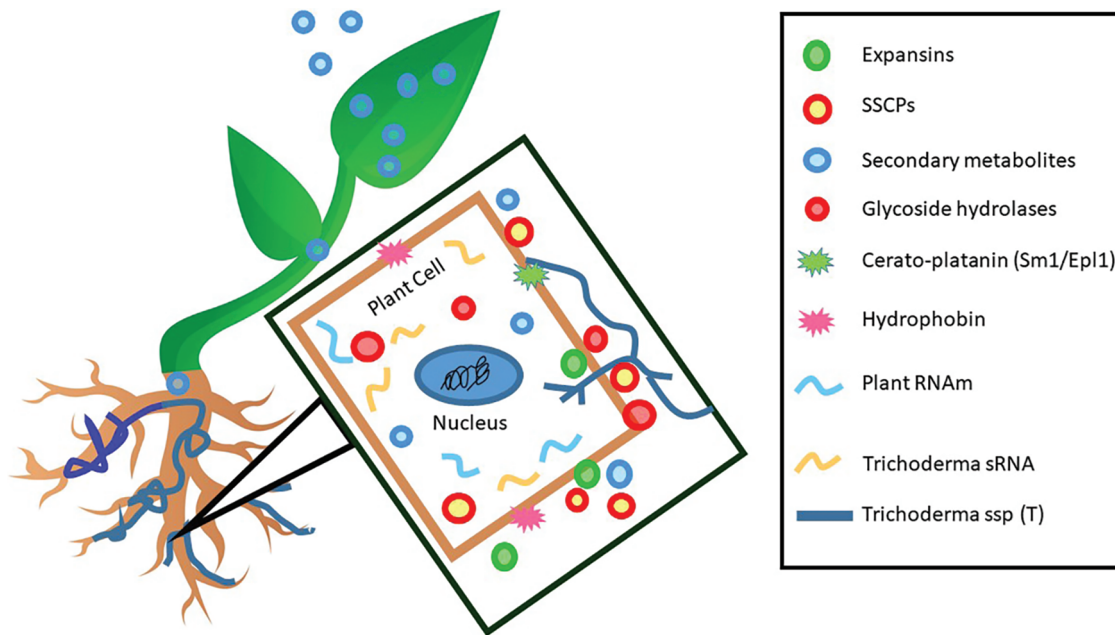


Figure 1: Involved effectors in the interaction between *Trichoderma* and plants. Nomenclature was proposed by Ramírez-Valdespino et al. [33]. SSCPs: Small Secreted Cysteine-Rich Proteins

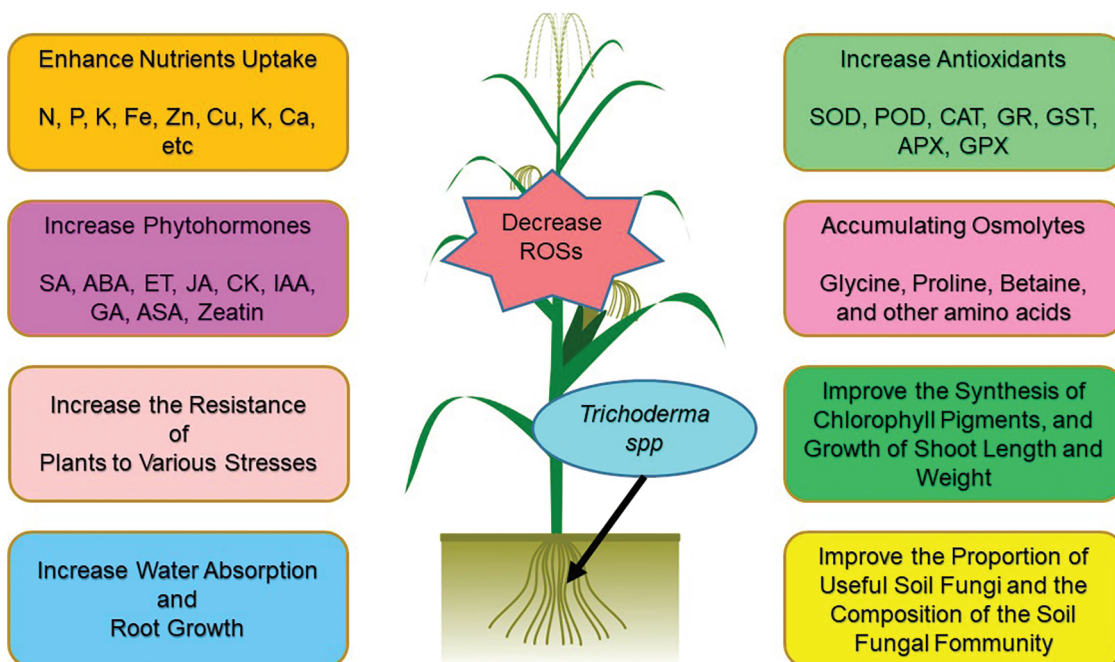


Figure 2: Positive effects of inoculation of plant roots with *Trichoderma* spp.

When plants are exposed to abiotic stresses, ROSs (including H_2O_2 , OH^- , and O_2^-) are increased in different organs, and plants attempt to reduce ROS by implementing different techniques, including increasing the non-enzymatic and enzymatic antioxidants in plant organs [5,34]. It was found that *Trichoderma* spp. inoculation increased levels of glutathione reductases (GR), glutathione S-transferases

(GST), superoxide dismutases (SOD), peroxidases (POD), and catalases (CAT) [5]. In response to diverse abiotic and biotic stresses, plants also regulate the opening and closing of their stomata with plant hormones such as Ethylene (ET), Jasmonic acid (JA), Salicylic acid (SA), and ABA [12]. Researchers have found that ABA preferentially signals abiotic stresses, while SA, JA, and ET signal pathogen and pest responses [12,35,36]. Studies have also shown that inoculating plant roots with *Trichoderma* spp. stimulates the expression of defense response genes, including Pathogenesis-related (PR) genes and proteinase inhibitor II gene [12,36,37] (Fig. 2; Table 1).

Table 1: Positive regulation of gene expression by *Trichoderma* species

Marker for	Gene	Protein function	Host plant	<i>Trichoderma</i> species
SA	<i>Cals</i>	Callose synthase, involved in callose biosynthesis	<i>Arabidopsis thaliana</i>	<i>T. harzanium</i>
	<i>ICS1</i>	Isochorismate synthase is involved in SA biosynthesis	<i>Arabidopsis thaliana</i>	<i>T. harzanium</i>
	<i>PAL2</i>	Phenylalanine and histidine ammonia-lyase. Enzyme involved	<i>Arabidopsis thaliana</i>	<i>T. asperelloides</i>
	<i>PAL1</i>	in the production of antimicrobial compounds	<i>Oryza sativa</i> <i>Arabidopsis thaliana</i> <i>Cucumis sativus</i>	<i>T. harzianum</i> , <i>T. erinaceum</i> , <i>T. atroviride</i> , <i>T. hebeiensis</i> , <i>T. parareesei</i> , <i>T. longibrachiatum</i> , <i>T. resei</i> <i>T. asperelloides</i> <i>T. asperellum</i>
ET	<i>CH5b</i>	Endochitinase precursor related to ethylene signaling	<i>Phaseolus vulgaris</i>	<i>T. velutinum</i>
	<i>ERF-A2</i>	Ethylene-responsive transcription factor	<i>Solanum lycopersicum</i>	<i>T. parareesei</i> , <i>T. asperellum</i> , <i>T. harzianum</i>
	<i>EIN4</i>	Key component in ethylene signaling	<i>Arabidopsis thaliana</i>	<i>T. asperelloides</i>
	<i>EIN2</i>		<i>Cucumis sativus</i>	
	<i>ETR1</i>	Ethylene signal-associated serine/threonine protein kinase	<i>Phaseolus vulgaris</i>	<i>T. asperellum</i>
	<i>CTR1</i>		<i>Cucumis sativus</i>	
JA/ET	<i>hGS</i>	Homogluthathione synthetase related with oxidative stress	<i>Phaseolus vulgaris</i>	<i>T. velutinum</i>
	<i>HPL</i>	Hydroperoxide lyase	<i>Cucumis sativus</i>	<i>T. asperellum</i>

(Continued)

Table 1 (continued)				
Marker for	Gene	Protein function	Host plant	<i>Trichoderma</i> species
	<i>Lox4</i>	Lipoxygenase enzyme involved in JA synthesis	<i>Solanum lycopersicum</i>	<i>T. atroviride</i> , <i>T. harzianum</i>
	<i>Lox4</i>		<i>Arabidopsis thaliana</i>	<i>T. asperelloides</i>
	<i>Lox3</i>		<i>Arabidopsis thaliana</i>	<i>T. asperelloides</i>
	<i>Lox2</i>		<i>Arabidopsis thaliana</i>	<i>T. virens</i> , <i>T. atroviride</i>
	<i>Lox1</i>		<i>Solanum lycopersicum</i>	<i>T. parareesei</i>
			<i>Arabidopsis thaliana</i>	<i>T. asperelloides</i>
			<i>Arabidopsis thaliana</i>	<i>T. harzianum</i>
			<i>Cucumis sativus</i>	<i>T. asperellum</i>

In recent years, specific genes from *Trichoderma* spp. have been identified and transferred to plants, increasing their resistance to biotic and abiotic stresses, among them, genes coding for aquaporins (AQPs), which play a crucial role in physiological processes and responses to a wide range of stresses [38–40]. AQPs belong to the major intrinsic protein (MIP) family and are essential for maintaining Cell Turgor, repairing xylem embolisms, regulating transpiration, regulating water balance, cell elongation, hydraulic conductance of root and leaf, and stomatal movements [6,41,42]. Research on transgenic *Arabidopsis*, tobacco, and rice with overexpressed aquaporin genes indicates that these plants are more resistant to various stresses [6,39].

Nomenclature was proposed by Pacheco-Trejo et al. [43].

Many studies have been conducted on *Trichoderma* species in recent years to understand how they increase plant resistance to biotic and abiotic stresses [44]; The most important types of *Trichoderma* are *T. atroviride*, *T. coningii*, *T. reesei*, *T. ghanense*, *T. viride*, and *T. harzianum* [45]. As an antagonistic mycobacterium, *T. harzianum* colonizes both monocotyledonous and dicotyledonous roots [46]; *T. Harzianu* is widely used as a biological fertilizer due to its beneficial effects on plants, including improving their structures as well as increasing their resistance to pathogens such as *Fusarium solani*, *Rhizoctonia solani* and *Botrytis cinerea* [47–50]. In addition to improving seed germination and reducing adverse effects of abiotic stresses on seeds, *T. harzianum* facilitates the absorption of nutritional compounds such as iron (Fe), manganese (Mn), phosphorus (P), copper (Cu), nitrogen (N), and sodium (Na), by improving the ability to dissolve them [5,23,29] (Fig. 2; Table 2).

Table 2: Some biocontrol traits of the main *Trichoderma* species used in agriculture

<i>Trichoderma</i> species	Biocontrol effect
<i>Trichoderma harzianum</i>	SA signaling pathway and priming in tomato
	Induction of several plant defense compounds in tomato
	Induction of JA, ISR, and Et pathways, and isoprenoid biosynthesis in tomato
	Induction of antioxidant enzymes in tomato
	Strong VOC priming in tomato
	Production of secondary metabolites regulated by ThMBF-1 and conferring tomato resistance
	Reduction of cucumber mosaic virus infection on cowpea
	Induction of priming, defense-related enzyme activity, and reduction of ROS accumulation in chili pepper
	Induction of antioxidant activity and redox homeostasis in cucumber
	Reduction of cell death in soybean
	In planta expression of ThKEL1 induces the expression of genes involved in SA and JA pathways in rapeseed
	The enzyme ThLAAO induces the expression of defense-related genes in tobacco
	Induction of SA accumulation, defense-related enzymes, and phenolic compounds in wheat
In planta expression of ThKEL1 induces the expression of genes involved in SA and JA pathways in Arabidopsis	
<i>Trichoderma atroviride</i>	Swollen in TaSwo1 confers protection in <i>Capsicum annum</i>
	Resistance conferred by strong VOC priming in Arabidopsis
	Induction of priming JA and SA pathways in Arabidopsis
	Enhancing SA accumulation in grapevine Tempranillo cultivars for plant protection
	Increasing the defense-related enzymatic activity in tomato
	Modification of gene transcripts related to plant defense, and induction of plant-defense VOCs in tomato
<i>Trichoderma viride</i>	Induction of VOCs related to defense enzymatic activity in okra
	Induction of antioxidant enzymatic activity and reduction of ROS accumulation in <i>Phaseolus vulgaris</i>
<i>Trichoderma virens</i>	Excess production of secondary metabolites confers protection in <i>Cicer arietinum</i>
	Induce secondary metabolites and JA and SA accumulation in Arabidopsis
	Induce ferricrocin, a siderophore, is involved in ISR induction in maize
	Induces Endopolygalacturonase TvPG2 regulation in tomato
	Priming and induction of JA and ISR defense pathway in tomato
Induce Cell-free supernatant and confers resistance in <i>Physalis peruviana</i>	

(Continued)

Table 2 (continued)	
<i>Trichoderma</i> species	Biocontrol effect
	Induction of defense-related genes in <i>Vigna radiata</i> susceptible and resistant varieties
	Induced systemic resistance in maize plant, via the induction of oxylipins and ketol, as ISR signals
<i>Trichoderma longibrachiatum</i>	The hydrophobin HYTLO1 induces the expression of defense-related genes in <i>Lotus japonicus</i>
	Induction of JA/Et and SA pathways, conferring resistance in cucumber
	Induction of defense-related enzymatic activity and flavonoids and lignin content in wheat roots
<i>Trichoderma asperellum</i>	Induction of Mycoparasitism and confers resistance in <i>Eriobotrya japonica</i>
	Induction of Hydrophobin HFBII-4 induces enzymatic activity and gene expression associated with plant defense responses in <i>Prunus davidiana</i> and <i>Populus alba</i>
	Induction of Elicitor protein Epl1-Tas induces enzymatic activity related to plant defense response in <i>Prunus davidiana</i> and <i>Populus alba</i>
	Induction of Crude citric extract and induces enzymatic activity related to plant defense response in tomato
	Vell1-derived SM induces the expression of defense-related genes in maize
	Strong VOC priming in tomato
	Induction of hypersensitive response in <i>Pisum sativum</i>
	Induction of systemic resistance and reduction of ROS accumulation in tomato leaves
	Induction of priming, defense-related enzymatic activity, antioxidant enzymatic activity, and reduction of ROS accumulation in chili pepper
	Induction of defense-related enzymatic activity in lettuce

It has been found that the colonization of roots by *T. harzianum* regulates hormones, antioxidants, phytoalexins, enzymes, and phenolic compounds (such as IAA, ABA, POD, β -1,3-Glucanases, Chitinases, and Lipoxygenases) [5,21,23,51]. According to Afifi et al., colonization of wheat roots by *T. virnes*, *T. harziunm*, and *T. viridie* improves photosynthetic pigments and, consequently, total photosynthesis and proline production [13]; Moreover, Sekmen Cetinel et al. reported that *T. virens* and *T. harzianum* increased antioxidant enzymes such as CAT, SOD, and POX in various plant organs [52]. Research shows that *T. asperellum* colonization of tomato roots results in improved plant growth, organic fertilizer replacement, and biotic stress resistance [53] (Table 2).

Nomenclature was proposed by [54–72].

Meanwhile, several studies have been conducted on the effects of simultaneous inoculation of soil microorganisms on plants in recent years [22,32,73,74]; Li et al. reported in their study that simultaneous inoculation of *Glomus* spp., *Trichoderma* spp., and *Bacillus* spp. not only protected plants more effectively against pathogenic microbes but also stimulated plant defense mechanisms in adverse environments [22]. Study results showed that the simultaneous application of arbuscular mycorrhizal

fungi (AMF) and *Trichoderma* spp. increased the antioxidant capacity of *Pinus sylvestris* [75]. Researchers have also found that the simultaneous application of AMF and *Trichoderma* spp. improves plant biomass, biochemical parameters, nutrient levels, and soil-borne disease resistance [76–78]. This study aims to determine investigation the action mechanism of *Trichoderma* spp. in plants to obtain a general understanding of how *Trichoderma* species affects plant performance under salt and drought conditions.

2 Drought Stress

Drought is one of the major abiotic stresses that can reduce crop yield more than all plant diseases combined worldwide [79,80]. As the global population has grown rapidly in recent decades, and crops need to be produced at about 60% more by 2050 to maintain human nutrition standards, the production of crops must be increased by using new technologies; On the other hand, it is also important to investigate the role of environmental stresses, particularly drought stress, in reducing crops production [5,29,81,82]. In general, drought is considered a stressful condition when the soil lacks water, causing an increase in soil temperature (especially during the day), a decrease in the availability of nutrients, and, ultimately, an increase in soil salinity [8,22]; And the risk of drought stress increases in soils with low fertility, such as those with sandy textures [8].

The most significant factor in the spread of drought in recent years has been climate change, which has shown its adverse effects in the subtropical and tropical regions of the world, resulting in unpredictable rainfall patterns [3,29]; Consequently, some areas experience flooding, while others experience a lack of rainfall, and in general, climate change has contributed to higher summer temperatures and decreased rainfall, which negatively affect crops and soil fertility [29,83,84]. As a result of global warming, air temperatures are predicted to rise by 2 degrees Celsius by the end of this century, and drought will affect 50% of agricultural lands by 2050 [29,85], and with the current trend of climate change by 2100, it seems that rice yield will fall by 20%–30%, corn yield will fall by 20%–45%, soybean yield will fall by 30%–60%, and wheat yield will drop by 5%–50% [29].

During drought stress, plants undergo irreversible changes in their morphology, anatomy, and physiology, which ultimately reduce their growth and productivity [7,8,86]. Water stress causes plants to lose their water content, turgor, and leaf water potential, and stop cell enlargement, resulting in a decrease in growth [87]. Drought stress also causes the leaves' stomata to close, reducing photosynthesis, respiration, leaf surface, and length of the vegetative growth phase, ultimately leading to the plant's death [29,86,88]. Furthermore, drought destroys soil structure, causing redox, reducing productivity, limiting root penetration, and limiting nutrients and water uptake [22] (Fig. 3).

Crop yields under drought stress are affected by a variety of factors, such as genotype, growth and development stage of the plant, duration, and intensity of drought, and other environmental conditions [89]. In recent decades, scientists have been looking for drought-resistant cultivars using genetic modification, however, using management methods that reduce environmental stress also plays a major role in reducing drought stress [8,90]. In drought-stress conditions, it is essential to use beneficial soil microorganisms that are highly compatible with the environment is one of the best ways to improve soil fertility and stimulate plant growth [11,91,92]. Among the most critical soil microorganisms with a high degree of compatibility with the environment is *Trichoderma* spp., of the Hypocreaceae family [7,91]. The species of *Trichoderma* are found in many ecosystems around the world, and they can be used in a variety of ways, including seed priming and root colonization [29,90].

It is believed that *Trichoderma* spp. increases plant tolerance to drought stress by improving morphological, physiological, and biochemical structures [92], and these changes can be categorized in the following three ways: (1) maximizing plant water utilization efficiency, (2) reducing ROS damage, and (3) secreting phytohormones [5]. Studies have shown that the treatment of seeds by *Trichoderma* spp. increases the germination rate in water deficit conditions, and studies conducted on tomato and Arabidopsis have shown that germination percentages of seeds treated with *T. harzianum* were increased in osmotic potential up to 0.3 megapascals [5,93].

The researcher found that inoculating plants with *Trichoderma* spp. increases root growth, which increases the root's access to water and nutrients, improving the water condition in various plant organs [5,7,27,46,94]; and through improving stomatal conduction increases plants' efficiency of water consumption and tolerance to drought stress [8,95]. Research conducted on cocoa seedlings has shown that the colonization of roots by *T. hamatum* under drought stress increases root growth and improves water status in the plan [96]. Cornejo-Ríos et al. found that inoculating tomatoes with *T. asperellum* increased root growth and water efficiency [29], and similar results were also reported in corn, sugarcane, and rice inoculations by *Trichoderma* spp [5,7,8,92]. In general, priming seeds with *Trichoderma* spp. delays drought stress by 3–5 days [97].

As mentioned, inoculating plants with *Trichoderma* spp. improves stomatal conductance regulation, impacting transpiration, carbon dioxide absorption, and photosynthesis [8,95,98]. Several studies have shown that various species of *Trichoderma*, including *T. viridie*, *T. asperelloides*, *T. virnes*, and *T. hariziumm*, improve the quality of photosynthesis in plants [13,46,94], by improving the quality and content of photosynthetic pigments, this increases plant growth and immunity [7,29,92]. Additionally, *Trichoderma* spp. inoculation has been shown to enhance various plant organ growth and biomass production under drought-stress conditions [5,98,99]. In several studies conducted on tomatoes, it has been shown that *Trichoderma* spp. improves the synthesis of chlorophyll pigments, growth of length and weight of different organs, electrolyte leakage, nutrient absorption, biomass, and plant performance in drought conditions [27,29,94]. Estévez-Geffriaud et al. also showed in their study on corn that *T. asperellum* improved photosynthetic factors, relative water content, and seed weight and numbers under drought stress [7]. Mishra et al. found that *Trichoderma* spp. boosts chlorophyll accumulation, root and shoot growth, tiller number, and crop yield in rice under drought conditions [92]; Additionally, studies on mung bean and sugarcane have shown that *Trichoderma* spp. inoculation improves plant morphology and physiological factors under drought stress [8,86].

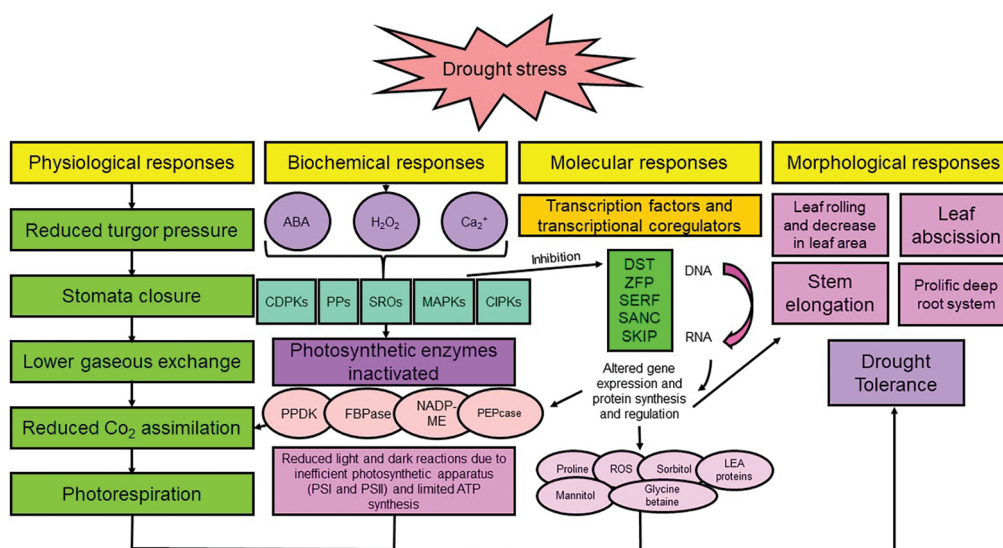


Figure 3: Responses of plants to drought stress at different levels. NADP-ME: NADP malic enzyme, FBPase: fructose 1,6-bisphosphatase, PEPcase: phosphoenol pyruvate carboxylase, PPKs: pyruvate phosphate dikinases, CIPKs: CBL interacting protein kinases, MAPKs: mitogen-activated protein kinases, SROs: similar to RCD-ONE, PPs: protein phosphatases, CDPKs: calcium-dependent protein kinases, ABA: abscisic acid, LEA: late embryogenesis abundant proteins, ROS: reactive oxygen species, SKIP: ski-interacting protein, SNAC: stress-responsive NAC transcription factor, SERF: serum response factor, ZFP: zinc finger transcription factor, DST: drought and salt tolerance. Nomenclature was proposed by Zargar et al. [100]

As a result of reducing oxidative stress, *Trichoderma* spp. increases plants' resistance to drought stress [5,101]. Studies have shown that inoculating plant roots with *Trichoderma* spp. increases the expression of enzymatic and non-enzymatic antioxidant genes, reduces ROSs, and reduces the amount of lipid peroxide in plant seedlings [44,46,102]. A study conducted on tomato has shown that root colonization by *Trichoderma atroviride* ID20G (Ta) not only increases the activity of antioxidant enzymes such as APX, GPX, CAT, and SOD, but also greatly reduces the level of MDA and Hydrogen peroxide, increasing tomato seedling resistance to drought stress [44]. Several studies on rice have also shown that *Trichoderma* spp. increases the expression of antioxidant enzyme genes, and inoculating rice seedlings with *T. harzianum* under drought stress increases the activity of antioxidant enzymes, such as POD, CAT, SOD, and APX [5,103,104]. A similar study on wheat has also shown that inoculation by *T. spirale*, *T. virens*, and *T. simmonsii* inhibits ROS formation in drought conditions and activates the mechanism of antioxidant enzymes [22]; Similar results have also been reported for cucumbers and maize [5,105].

The colonization of plant roots by *Trichoderma* spp. regulates the secretion of endogenous plant hormones, including auxin, ASA, SA, JA, ET, and ABA [12,22,99]. Some studies on the effects of *Trichoderma* spp. inoculation on different plant organs has indicated a decrease in the expression of ABA synthesis marker genes [ABA is under the control of genes encoding the enzyme 9-cis-epoxycarotenoid dioxygenase (NCED)], and ABA content, which may be an adaptive advantage since it inhibits plant growth when conditions are droughty [5,12,106]. *Trichoderma* spp., on the other hand, inhibits plant production of ACC deaminase (ACCD), which plays an essential role in ET biosynthesis and may decrease plant root growth under drought stress [107]. In a study on tomatoes inoculated with *T. brevicompactum*, the JA and SA marker genes were positively regulated in the roots and the leaves, respectively, although ABA content in the roots increased slightly [12]. Further, studies conducted on tomato seedlings under drought stress have found that root inoculation with *T. harzianum* improves the regulation of proline, phenol, flavonoid, indole butyric acid (IBA), IAA, ethylene, and GA contents [27,108]. As a result of the study on sugarcane, researchers confirmed that, in addition to increasing proline concentration, *T. asperellum* also increases sugar division and, thus, increases root and stem growth under drought stress [8].

According to a study conducted on rice under drought stress, root inoculation by *T. harzianum* caused the expression of 70% of genes, most of which are related to metabolic pathways, secondary metabolites, carbon cycling, phenylpropanoid biosynthesis, and glutathione biosynthesis [46]. It appears that *T. harzianum* plays a major role in delaying the effects of drought stress in rice. The simultaneous inoculation of *Trichoderma* spp. with other beneficial soil microorganisms may improve the performance of plants under stress [86]. For example, in studies conducted on *Astragalus mongholicus* under drought stress, it was shown that inoculating *Trichoderma* spp. simultaneously with *Dark septate endophytes* (DSE), *Paraboeremia putaminum*, or *Paraphoma radicina*, in addition to improving the plant's morphophysiology (such as improving root growth, antioxidant enzymes, and growth hormones), can also affect the soil environment (such as changes in the composition of the rhizosphere microbiome and improving the condition soil nutrients) [11,22]. In a study conducted on mung bean (*Vigna radiata*) under drought stress, it was also observed that the simultaneous use of *Mycorrhiza*, *Rhizobium*, and *Trichoderma*, in addition to improving the total soluble protein, increased the leaf area and internode length compared to the separate application of each of the microorganisms [86].

3 Salinity Stress

The degradation of soil quality is one of the main causes of land degradation, affecting hydraulic, erosion, geochemical, and biological cycles [14]. Salinity is one of the factors that directly affect the biological, chemical, and physical properties of soil and can directly destroy its texture and structure, as well as reduce its fertility [14,109]. Salinity is a major concern around the world, especially in arid and

semi-arid regions, as it causes agricultural lands to become barren [110,111]. Approximately 7% of the world's land has been affected by salinity, including 45 million hectares of cultivated land (20%), and 30% of all agricultural land is predicted to be affected under severe salinity stress by 2050 [25,112,113].

Recent decades have seen severe soil salinity in several areas, including India, Java Island, and Mediterranean countries, particularly the southeast of Spain [14,32,114,115]. Soil salinity has been elevated as a result of rising sea levels, irrigation by salty water, prolonged droughts, heavy rains, and improper land management [10,14,110,114,115]. Soil salinity, along with the proliferation of various diseases in the region, is a serious threat to agricultural production and environmental sustainability, which in severe cases leads to the abandonment of agricultural lands [14,25,116].

Salinity is one of the most common and harmful abiotic stresses, causing take in excessive sodium (Na^+) and chloride (Cl^-) ions by plants [52,117,118]. In addition to disrupting metabolism, it causes physiological, morphological, molecular, and biochemical changes in plants, and may even lead to death if it continues [1,2,32]. Salinity-sensitive plants cannot tolerate high concentrations of NaCl in the soil, and their behavior in a saline environment depends on their growth stage and the duration of their exposure to salt [32,119]. Plants are more sensitive to saline soil in the stage of seedling growth and early vegetative growth [32,120], and salinity generally reduces seed germination, seedling growth, number of leaves, fresh and dry weight of the plant, vegetative and reproductive growth, and lastly weakens the plant [21,25,118,121]. In a study conducted on *Suaeda salsa*, the branch number, the stem diameter, the length of the branch, and the plant height decreased as the NaCl content increased [122]. Similar results have been reported in the case of tomato, which has an average level of salt tolerance [32,123].

Increased salt concentrations affect various plant processes, such as photosynthetic pathways and pigments, protein content, respiration, metabolism of nitrogen and carbon, and absorption of water and nutrients, which lead to plant senescence and reduced yields [1,21,25,32,124]. In addition to blocking the phosphorylating and non-phosphorylating electron transfer pathways, the increase in salt concentration alters the osmotic pressure, and the processes of balance, uptake, and transport of ions, disrupting membrane function and causing cell dehydration [2,32,125]. In general, salinity stress affects water absorption, water use efficiency, leaf water potential, and transpiration rate, and disrupts plant metabolism [1,2] (Fig. 4).

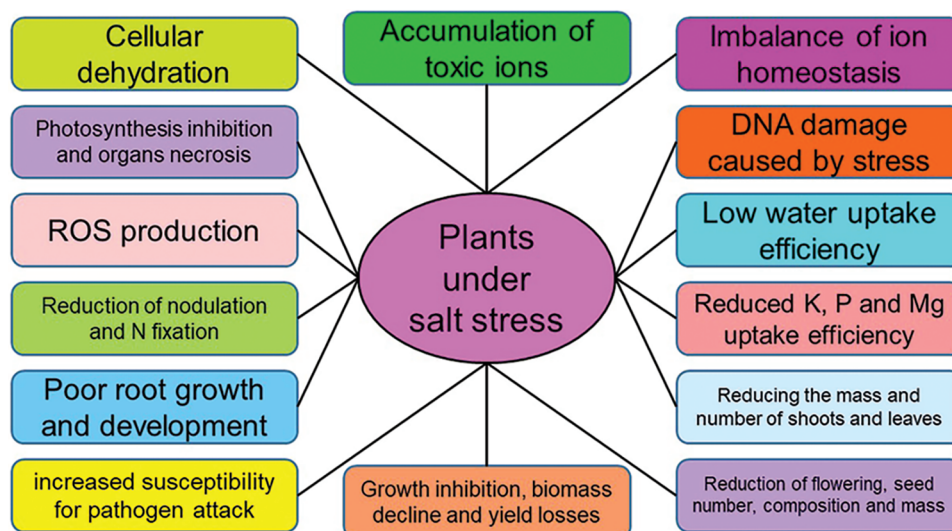


Figure 4: The effect of soil salinity on the morphophysiological factors of plants. Nomenclature was proposed by Otlewska et al. [113]

Plants exposed to saline stress produce ROS, which causes oxidative stress, resulting in damage to essential molecules, such as proteins, carbohydrates, lipids, and even nucleic acids [52,126–128]. In the studies conducted on maize, it has been determined that salinity, in addition to reducing plant yield by about 20% to 40%, causes the production of large amounts of reactive oxygen species, which, further to the mentioned cases, disrupts the activity of intracellular enzymes and increases the content of thiobarbituric acid reactive substances (TBARS) [129,130]. Also, the reduction of plant endurance due to salinity makes plants more susceptible to various diseases, such as *Fusarium oxysporum*, *Alternaria solani*, and *Phytophthora* [32] (Fig. 4).

Plants have some natural solutions to increase their resistance to salinity, including an increase in enzymes (POX, SOD, APX, GR, CAT, and POD) and non-enzymatic (Carotenoids, Flavonoids, Phenolic compounds, Ascorbate, and GSH) antioxidants in various organs to reduce ROS production [32,127,129,131,132]. On the other hand, plants reduce osmotic potential and water potential by accumulating ions and osmolytes (Glycine, Proline, Betaine, and other amino acids), which improves water absorption by cells while also removing accumulated ROSs [2,21,32,133]. Furthermore, plants increase their resistance to salinity by selectively absorbing Na^+ and Cl^- from the medium or by accumulating and separating these ions in vacuoles [2].

In the past decade, several strategies have been used to reduce the effects of salinity stress on plants and improve saline soils, including irrigation with fresh water, cultivating salinity-resistant cultivars, using organic fertilizers, using mineral fertilizers (nitrogen, gypsum, potassium, and sulfur) and mulching [14,76,114]. However, due to the high cost, time-consuming, and relatively low beneficial effects, scientists have been investigating new solutions that will have a permanent impact, be less expensive, and be harmonious with the environment [76]. One of the best solutions is manipulating the rhizosphere of plants using beneficial soil microorganisms, which in addition to improving plant growth, improve mineral and water absorption by plants [1,76,114,134]. *Trichoderma* spp. is known as a key symbiont for plants in saline conditions, and it has been studied in recent years for its benefits in reducing salt stress on plants [32,135,136].

Researchers have identified the positive effects of *Trichoderma* spp. on a variety of plants including wheat, corn, rice, soybean, cucumber, tomato, and French bean when exposed to salinity stress [1,114,129]. However, the growth and reproduction of *Trichoderma* spp. are affected by different environmental conditions, especially high salt concentration [1,14,109,137], thus, finding salt-resistant species of *Trichoderma* is crucial to the advancement of agricultural projects based on microorganisms. In a study conducted on *Trichoderma* spp., it was found that *T. asperellum* is more resistant to environmental salinity than *T. virens* [1]. And a study conducted in India found that *T. asperellum*, among all *Trichoderma* species isolated from the soils of eastern Uttar Pradesh, has the highest resistance to salinity and high temperatures [25].

As a result of studies done on cultivated plants under salt stress, it has been shown that inoculating plants with *Trichoderma* spp. improves seed germination and stimulates the growth of different plant organs, as well as improving plant productivity [2,129,135]. Studies conducted on corn grown under salt stress have shown that inoculating plants with *T. asperellum* and *T. harzianum*, in addition to increasing the production of IAA, improves germination percentage, seedling establishment, length of shoot and root, leaf area, fresh and dry weights, as well as total biomass [21,109,129]. The inoculation of peanuts cultivated in the saline medium by *T. harzianum*, *T. asperellum*, and *T. virens* also showed an increase in IAA production, germination, shoot growth, biomass, and minimizing plant death, which indicates that *Trichoderma* spp. reduces salinity stress in peanut vegetative and reproductive growth [1,114].

Inoculation of plants with *Trichoderma* spp. enhances their antioxidant defense system by modifying the expression of genes related to oxidative stress and thus, increases the resistance of plants against salinity

[2,129,135]. In their study on strawberries cultivated under salt stress, Sekmen Cetinel et al. found that *T. citrinoviride* treatment reduces hydrogen peroxide and lipid peroxidation as well as increases the activity of POX and SOD antioxidant enzymes [52]. Yasmeen et al. also found that *T. harzianum* treatment improved the morpho-physiological structure of rice seedlings and also reduced the destructive effects of ROSs in rice under salt stress through the activity of antioxidants (CAT and SOD) [118]. Studies conducted on maize showed that *T. asperellum* and *T. harzianum* reduced MDA accumulation in different organs of plants under salt stress, which demonstrated that these fungi reduce ROS levels [21,129].

Furthermore, *Trichoderma* spp. reduces the effects of salinity and improves the morpho-physiological and biochemical structures of plants, improving the absorption of water and nutrients, photosynthesis, and hormonal function [32,118,129]. The inoculation of corn with *T. harzianum* and *T. asperellum* improves photosynthetic processes and increases Ca^{2+} and K^{+} content in seedlings, thereby reducing Na^{+} content. These fungi also enhance the accumulation of osmolytes, which improves water absorption of cells, and they also enhance the activity of enzymes and non-enzymes antioxidants that reduce salt-induced oxidative damage [109,118,129]. A study conducted on *Cucurbita pepo* found that *T. harzianum* and *T. viride* treatments, in addition to increasing the synthesis of photosynthetic pigments, anthocyanins, carotenoids, GSH, proteins, and proline, enhanced water absorption and membrane stability, improving plant performance under salinity conditions [2].

The studies conducted on tomatoes and rice under salt stress found that *T. harzianum* increases the proline, flavonoids, and phenols content of the plant in addition to improving photosynthetic performance, water, and nutrition absorption [32,114,118]. According to studies done on strawberries (*T. citrinoviride*) and peanuts (*T. virens* and *T. asperellum*), *Trichoderma* spp. increases the photosynthetic efficiency and enzymatic and non-enzymatic antioxidants in saline environments [1,52]. It has been shown that using *Trichoderma* spp., including *T. harzianum* and *T. asperellum*, can significantly reduce soil pH and salt ions content, as well as improve the proportion of useful soil fungi (such as *Trichoderma* and *Ceratobasidium*), and the composition of the soil fungal community, thus improving maize yield and growth [14,109].

Additionally, *Trichoderma* spp. is capable of reducing the risk of other biotic and abiotic stresses at the same time as improving plant structures under salt stress [118,135]. Singh et al. stated that *T. asperellum* could be used for biological control of plant pathogens including *Sclerotinia sclerotiorum*, *Colletotrichum capsici*, *Scletotium rolfsii*, *Rhizoctonia bataticola*, and *Fusarium oxysporum*, as well as enhance plant resistance to salt stress [25]. Furthermore, the studies conducted on tomatoes have shown that *T. harzianum*, *T. asperelloides*, and *T. arenarium sp. nov.* can be used as a biocontrol method for *Fusarium oxysporum*, in addition to improving seedling resistance to salinity [10,32]. In their studies on strawberries, Sekmen Cetinel et al. discovered that inoculation of seedlings with *T. citrinoviride* by improving antioxidant enzyme activity, stimulating growth, reducing hydrogen peroxide accumulation, and improving photosynthesis can improve plant resistance to salinity as well as reducing the risk of *Rhizoctonia solani* infection [52]. Moreover, in a study on sorghum-sudangrass under the simultaneous stress of salinity and bauxite residues (red mud; a byproduct of alumina production), it was discovered that the inoculation of seedlings with *T. asperellum* improved the production of siderophore, IAA, phosphorus bioavailability, ACC deaminase, chlorophyll content, and biomass, which made the plants more resistant to both environmental stresses [135].

Although there have been not many studies on the combination of *Trichoderma* spp. with other factors that improve the soil environment, these few studies also indicate that when used in conjunction with other soil-improving factors, *Trichoderma* spp. can reduce salinity stress even more effectively [14,32]. In addition to increasing water penetration, stability of aggregates, salt leaching acceleration, and water storage capacity, organic matter can also reduce soil electrical conductivity and exchangeable sodium. Mbarki et al. reported in

their study that the simultaneous use of *T. harzianum* and compost in soil not only affected soil microbiology and saline soil modification but also caused a relative increase in this particular strain of *Trichoderma* [14]. In their study on tomato seedlings, Kasyap et al. found that when *T. harzianum* and *Hypocrea* are applied simultaneously, *T. harzianum* adapts more easily to saline environments, and also increases tomato resistance to root rot disease, as well as reducing the risk of salinity stress [32]. Additionally, Yang et al. found that simultaneous inoculation of roots with *Glomus* sp. and *T. longibrachiatum* not only enhanced biomass but also improved K^+/Na^+ ratio in seedlings and increased AMF growth in the rhizosphere of maize [76].

4 Conclusion

The present study found that *Trichoderma* spp. improves physiological, morphological, and biochemical characteristics of plants that are subjected to drought and salinity stress, Nevertheless, further studies are needed to determine how different strains of *Trichoderma* affect plants under different stresses. The study also revealed that some *Trichoderma* species have a higher sensitivity to stresses, therefore, more in-depth research should be conducted on the effects of these stresses on different *Trichoderma* species, so that more suitable species can be selected for use in fields. Additionally, the results of this study indicated that simultaneous inoculation of different species of *Trichoderma* with other microorganisms could increase plant resistance to salt stress and drought stress, however, more studies on simultaneous inoculation of *Trichoderma* species with other fungi and bacteria are needed because of the limitations of current knowledge. The increasing number of studies on the effects of *Trichoderma* spp. on plant molecular structures, as well as the expansion of field studies, allows us to examine in greater detail how *Trichoderma* spp. affects plants under salinity and drought stress, and the extent to which it improves plant performance in field conditions.

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