



The Role of *Trichoderma* Species in Plants Response to Salt Stress

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Authors' contributions

This work was carried out in collaboration among all authors. Authors SZ, ACU and BX revised the write up and contributed to the inputs. Authors SB, RI and LT did the write up. All authors contributed vividly to this work. All authors read and approved the final manuscript.

Article Information

DOI: 10.9734/AJRCS/2021/v6i230114

Editor(s):

(1) Dr. Al-kazafy Hassan Sabry, National Research Centre, Egypt.

Reviewers:

(1) Maria Eunice Lima Rocha, Universidade Estadual do Oeste do Paraná, Brazil.

(2) Dr. Kartar Singh, ICAR-NBPGR, India.

Complete Peer review History: <http://www.sdiarticle4.com/review-history/58262>

Review Article

Received 17 April 2020

Accepted 22 June 2020

Published 05 April 2021

ABSTRACT

Soil salinity is a pending threat to global agricultural sustainability and food security. The natural means of alleviating this stress have become the major concern as to which methods, mechanisms, and organisms to be used. Soil-borne fungi *Trichoderma* has proven to alleviate salinity stress in plants. This review aimed to shed light on the roles and mechanisms of some species of *Trichoderma* in response to salt stress and other merits to plant growth and development. Detailed of this research reviewed the level of growth promotion induced by *Trichoderma* species with an estimated increase of 200% of total plant biomass compared with control plants from literature. The defined mechanisms of *Trichoderma* in combating salinity stress in plants are; formation of ion channels in host plants, activation of ion exchange (K^+/N^+), increase Reactive Oxygen Species (ROS) scavenging enzymes, antioxidants, and genes, production of phytohormones and their signal pathways, stimulates root formation and developments, regulate stomata conductance through the increment of carotenoids in host plants which corresponds to the functions of the photosystems.

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Keywords: Salinity mechanisms; antioxidants enzymes; reactive oxygen species and genes.

ABBREVIATIONS

Sodium chloride (NaCl)
Reactive Oxygen Species (ROS)
Malondialdehyde (MDA)
Hydrogen peroxide (H₂O₂)
Peroxidase (POD)
Catalase (CAT)
Superoxide dismutase (SOD)
1-aminocyclopropane-1-carboxylate (ACC)
Plant growth-promoting rhizobacteria (PGPR)
Indole-3-acetic acid (IAA)
Ribonucleic acid (RNA)
Deoxyribonucleic acid (DNA)
Ascorbic acid (AsA)
Glutathione (GSH)
Ascorbate peroxidase (APX)
Glutathione peroxidase (GPX)
Glutathione transferase (GST)
Dehydroascorbate (DHA)
Volatile organic compounds (VOCs)
Adenosine triphosphate (ATP)

1. INTRODUCTION

Soil salinity is the pending threat in agricultural productions and its management in the entire universe especially the arid and semi-arid areas is a major concern. Among the several abiotic stresses that affect plant growth, developments, and yields failure is salinity stress [1].

Salinity has taken almost 7% of the entire arable land surface and left not approximately one-third of the world's irrigated land at potential risk [2]. This poses a serious threat to global agricultural sustainability and food security.

Several studies have indicated that increased salt concentration especially sodium chloride (NaCl) in soils affects the morphological, physiological, and biochemical processes which directly or indirectly leads to osmotic stress, plant-ionic imbalances and Reactive Oxygen Species (ROS), peroxidation of lipids and antioxidants inactivation in plants [3]. Under salt stress, plants that accumulate more than 3% of toxic sodium ion (Na⁺) experience dehydration, nutrient deficiencies, membrane dysfunction, and oxidative stress, which lead to tissue damage or early senescence [4,5]. The intensity of salinity stress multiples osmotic stress and ionic stress in susceptible plants [6].

Plants naturally have mechanisms of mitigating salinity stress by reducing the transpiration rate

while maximizing water uptake to maintain osmotic equilibrium. Again minimize the toxic effects of ionic Na⁺ by the exclusion of Na⁺ from leaf tissues and by compartmentalization, mainly into vacuoles [6,7]. Exogenous chemical control such as foliar application of a chlorophyll precursor, 5-aminolevulinic acid (ALA) mitigated salinity stress damages in perennial grass species by regulating photosynthetic activities, ion content, antioxidant metabolism, or metabolite [8] but left to questions whether it will not accumulate another stress type.

Crop breeding and transgenic technologies have been used to develop new cultivars with improved salt-tolerant traits, but breeding salt tolerance cultivars have not been successful [9]. Notwithstanding these practices, salt stress still holds the highest percentage among the abiotic stresses that deteriorates plants growth and development. Therefore it is of importance to generate effective and practical techniques to lessen the damaging effects of salt stress on plant growth and development. The commercial use of transgenic plants to combat salinity resulted in the loss of genes, high cost, and other regulatory issues [10]. Thus, improving salt resistance in agriculturally important plants is immediately needed to overcome the problem of soil salinization and to guarantee global food security and saves more lands.

Many studies suggested the use of plant growth-promoting fungi (*Trichoderma*) which is environmentally friendly and induce plant resistance to abiotic stresses and support agricultural development. *Trichoderma* plays an important role in the alleviation of salinity [11] due to its anti-microbial potential to colonize diverse substrates under different environmental conditions. However, the roles, mechanisms, and other growth-promoting benefits to their symbiotic plant hosts to tolerate salt stress are still unclear. This review shed more light on the roles of some *Trichoderma* species to salinity stress in plants, mechanism of tolerance, and their growth-promoting benefits.

2. SOIL SALINITY IMPACT ON PLANTS LIFE

Soil salinization is known as the concentration of dissolved mineral salts in the soil solution to its unit volume or weight basis [12]. It is estimated by measuring the electrical conductivity (EC) of

an extracted soil solution. Soil salinization is caused by several factors such as rock weathering, low precipitations, bad irrigational practices using seawaters, or other waters that contains trace amounts of sodium chloride [13] and continuous application of chemical fertilizers on arable lands.

Salinity in natural phenomenon improves soil structure and eliminates to some degree the deleterious effect of sodium ions, but its excess accumulation in plants affects their life processes. Abnormal salt concentration in the soil solution produces hyperosmotic stress on plant roots. Directly, salinity in the soil causes ion-specific toxins to plants through the uptake of water containing sodium, chloride, boron, and other salt solutes leading to the elevation of water stress and root rehydration of plants.

Apart from the physiological effects on plants, indirectly soil salinity damages plant through the uptake of non-essential nutrients. Imbalance salts uptake cause antagonism, for instance; excess chloride reduces the uptake of nitrate, phosphorus reduces the uptake of manganese, and potassium limits the uptake of calcium.

Recent studies reinforce the perception that NaCl causes growth inhibition by changes in net photosynthetic rate, PN [14], and likewise, Sharma et al. [15] also added that net photosynthetic rate (PN), stomatal conductance (gs), and transpiration rate (E) reduced with the addition of NaCl to wheat (*Triticum aestivum* L.) genotypes K-65 (salt-tolerant) and HD 2329 (salt-sensitive). Salinity stress caused stomata closure, which decreases the CO₂/O₂ ratio in leaves and inhibits CO₂ fixation. These disorders or disproportion of CO₂/O₂ increased the rate of reactive oxygen species (ROS) like superoxide radical (O⁻²), hydrogen peroxide (H₂O₂), and hydroxyl radical (OH) enhanced leakage of electrons to oxygen zone.

Additionally plants experience dehydration, nutrient deficiency, membrane dysfunction, and metabolic and death [16,5]. Common physiological symptoms that signals salinity injury on plants include; bud damage or death, twig and stem dieback, tufted and stunted appearance, wilting, reduced plant vigor, flower and fruit development delay, etc.

Salt stress detrimentally affects protein synthesis and genes transcriptions, energy production, and lipid metabolism in plants. The primary plant response is a reduced leaf surface expansion,

followed by a diverse closure of stomata as the stress intensifies and finally leads to photosynthesis inhibition [17]. Directly or indirectly the reduction of photosynthesis affects the pigments and chlorophyll contents of plants [18,19].

3. SOIL SALINITY AND GLOBAL FOOD SECURITY

Soil salinity is a major drawback in agricultural productivity, and estimates predict that 50% of all arable land will become saline by 2050 [20]. Soil salinization plays a crucial role in both social and economic development in the entire universe. Given the tendency of soil salinity to hinder agricultural productivity, its impacts threaten both the global food supply and agricultural profits.

Worldwide, approximately 831 million hectares of arable land is affected by soil salinity [21]. This is over 6% of the world's total land area. Soil salinity exists naturally, but human activities cause its increment. The advanced climatic change, including rising average temperatures, more severe droughts develops salinity stress extremely.

A significant proportion of recently cultivated agricultural land has become saline due to irrigation and other human activities such as chemical fertilizer application. Out of the 1500 million ha of land farmed by dry land agriculture, 32 million (2%) are affected by secondary salinity to varying degrees. Of the current 230 million ha of irrigated land, 45 million ha are salt-affected (20%) [22]. Irrigated land is only 15% of total cultivated land, but as irrigated land has at least twice the productivity of arable land, it produces one-third of the world's food.

Currently, the problem of food security is higher than in the past decades, with more than 800 million people persistently hungry and millions more at risk [23]. Deductively, it is assumed that plants such as cereals of which much are sensitive to salinity stress productions will be less, which indirectly will starve the world.

Globally, US\$12 to 27.3 billion are lost annually due to reductions in crop productivity [24]. The human race is projected to increase by more than the current populations of China and India combined in the next 35 years [25]. Moreover, little or no efforts to minimize hunger will be made at ease by rapid population growth. Cheeseman [26] reported that bad irrigation

practices have degraded arable soil and salinized underground water, thereby major crops are proving insufficient to supply the calories, proteins, fats, and nutrients people need. Rice and wheat are major crops grown almost in the entire universe, molecular-based approaches to improve the salt tolerance of these crops have made only painfully slow progress; even their successes are not all that remarkable [27,28,29,30] this is to notify the attention of how salinity can affect food security and increase the world starvation in this generation and next to come generation.

4. TRICHODERMA IMPACTS ON PLANTS UNDER SALINITY STRESS

The amelioration of salinity stress has always been in the line of chemical control which in many ways causes more harm than good. Biological Control Agents (BCAs) are plant growth-promoting rhizobacteria (PGPR) that stimulate plant growth directly by altering plant hormone levels, facilitating iron acquisition through siderophore production, fixing atmospheric nitrogen, and solubilizing minerals [31].

Trichoderma species have been known over 70 years to supports plant growth and antagonized plant pathogens [32]. *Trichoderma* species increase nutrient uptake from the soil, enabling plants to tolerate salt stress and decreasing the activity of the soil-borne pathogens that ultimately affect the growth of plants [33]. *Trichoderma* genes induce resistance to salinity and other abiotic stresses such as heat and drought in plants [34]. These genes have their specific functions and mechanism such as cell wall degradation, hypha growth, stress tolerance, and parasitic activity. Peculiar genes from this genus include; protease, chitinase, glucanase, tubulins, proteinase, xylanase, monooxygenase, galacturonase, cell adhesion proteins, and stress-tolerant genes [35].

Among the various species of the *Trichoderma*, *Trichoderma harzianum* is considered to be the most effective biocontrol agent [36]. According to Zhang et al. [37], *Trichoderma longibrachiatum* T6 (TL-6) enhanced wheat (*Triticum aestivum* L.) to tolerate salt stress by promoting wheat seed germination and seedling growth under different levels of salt treatments. The mode of action of T6 increased proline content by an average of 11%, ascorbate 15%, and glutathione 28% and decreased the contents

of malondialdehyde (MDA) by an average of 19% and hydrogen peroxide (H₂O₂) 13%.

Additionally, Mastouri et al. [38] reported the effects of seed treatment with *T. harzianum* strain T22 on germination of Jubilee tomato seed exposed to vary the degree of salinity. The mode of action of T22 increased the speed of germination, seedling vigor, and ameliorates water and osmotic stress in unaged and the aged seed of Jubilee tomato as compared to the untreated jubilee tomato seeds.

Likewise, *T. asperellum* is shown to enhance the availability of phosphorus and iron to plants, with a significant increase in dry weight, shoot length, and leaf area [39]. Maize rhizosphere colonization by *T. virens* also induced higher photosynthetic rates and systemic increases in the uptake of CO₂ in the leaves [40]. Rawat et al. [41] reported the seed biopriming treatment with isolates of *Trichoderma harzianum* in response to rice (*Oryza sativa* L.) subjected to salt stress significantly increased both the length and fresh weight of shoot and root, number of leaves, leaf area, photosynthetic rate, chlorophyll fluorescence, chlorophyll content comparison to control at all stress levels. Equally, Zhang et al., [42] recounted the effect of wheat seeds with *Trichoderma longibrachiatum* (T6) increased relative water content in the leaves and roots, chlorophyll content, and root activity.

From various works of literature, root hairs are increased in *Trichoderma* treated plants which directly or indirectly supports plants in physiological activities. Montesinos et al. [43] revealed the salinity tolerant *Trichoderma* strains support plant growth, antagonist to *Pythiummultimum*, and as a means of reducing chemical fertilization application. This work disclosed three *Trichoderma* named *T. longibrachiatum*, *T. aggressivum* sp., and *T. saturnisporum* regardless of their origin, alleviated the stress produced by salinity, resulted in larger plants with an air-dry weight percentage above 80% in saline stress conditions on melon seedlings. Yasmeen and Siddiqui [44] detected that the presence of *Trichoderma* in a saline environment increased the activity of antioxidant enzymes in plants.

Viterbo et al. [45] revealed the role of 1-aminocyclopropane-1-carboxylate (ACC) deaminase activity in *Trichoderma asperellum* T203 as the sole nitrogen source showed high enzymatic activity. The ACC

deaminase (ACCD) activity promoted canola (*Brassica napus*) root elongation in pouch assays. But lately, Tucci et al. [46], published the effects of interaction between different tomato cultivars and two biocontrol strains of *T. atroviride* and *T. harzianum*. *Trichoderma* treatment did not exert any plant growth promotion effect and was even seen to be detrimental to one tomato cultivar. The detrimental effect on the tomato cultivar raised an alarm that not all *Trichoderma* species can support plant life; hence more work needs to be done to know species that can support plant life.

5. TRICHODERMAMECHANISMS OF SALT TOLERANCE

Several strains of *Trichoderma* have been known as biocontrol agents against the stresses of plants. The various mechanisms include antibiosis, parasitism, host-plant resistance, and competition but the salinity tolerance mechanisms are still unclear. The common house mold, *Trichoderma longibrachiatum* contains amino acids called trilongins [47]. The trilongins formed voltage-dependent, Na^+/K^+ permeable channels in biomembranes. Normal ion channels perform dynamic cellular functions such as electrical and chemical signaling, regulation of cytoplasmic or vesicular ion concentration and pH, and cell volume regulation during stress. Thus in simple justification, in salinity stress, the formed ion channels enhances much absorption of either Na^+ or K^+ or both in a balanced ratio [48]. Hence the absorption of the cations (Na^+ or K^+) leaves the anion (Cl^-) weak to affect the normal functioning of the cells.

China et al. [49] revealed that locally emitted fungal spores of coarse super-micrometer size contribute considerably to sodium salt particles. Thus active discharge, uptake, and efflux processes are likely responsible for the sodium content in the spores. When fungi contain excess Na^+ , they activate Na^+ efflux ATPase (adenosine triphosphatase) which acts as a key enzyme for the biological evolution of fungi [50].

Rodríguez [51] stated fungi require K^+ for electrical and osmotic equilibria of their cells. Previous studies suggested that K^+ can be partially replaced by Na^+ and it can enhance the growth of fungi [52] under K^+ deficient conditions. The growth of fungi and uptake of Na^+ varies with their physiological conditions and uptake rates depend on the species and their genes [53].

Additionally, the enzyme 1- aminocyclopropane-1-carboxylate (ACC) deaminase is central to the functional interactions of various plant-associated bacteria and fungi. Thus bacteria and fungi that produce ACC deaminase can lower the impact range of different stresses that affect some microbial growth and development [54]. Thus if ACC deaminase can use multiple substrates, equally the production of ACC deaminase can be important for cleavage of substances, thus, giving an organism the strength to use other nutrient sources or to grow under otherwise toxic conditions. This can have key implications in fungi fitness, especially when living under limiting conditions [55]. However, the Lrp-like regulatory protein AcdR is a common mechanism regulating ACC deaminase expression in some fungi and bacteria. Thus manipulation or alternation of *acdS* genes (i.e. the structural gene encoding ACC deaminase) from a wide range of different organisms, mostly bacteria and fungi may affect the production of ACC deaminase [56]. This suggests that organisms that produce ACC deaminase more readily survive in stressed environments by the mutualistic interaction with or without a plant host.

Again, catalase enzyme leads a foremost task in organism protection against toxic free radicals that are produced predominantly beneath environmental, mechanical, and chemical stresses and could promote plant growth via an indirect way [57]. Under salinity stress, *Trichoderma* increased catalase enzyme activity [58]. Thus higher production of catalase enzymes by the fungi enhanced its survival and functioning on saline stressed medium or environment.

Biosynthesis and secretion of Indole-3-acetic acid (IAA) in fungi account for a mechanism for their growth and tolerance to stress. From previous studies, IAA biosynthesis evolved independently in bacteria, microalgae, fungi, and plants. IAA controls the physiological response and gene expression in these microorganisms [59]. IAA is produced from tryptophan via indole-3-pyruvate, with the last step of this biosynthetic pathway being catalyzed by aldehyde dehydrogenase in fungi. A fungus specific to spruce called *Tricholomavaccinum* was shown to produce IAA from tryptophan and excrete it from its hyphae. This induced branching in cultures, and enhanced Hartig net formation [60]. Thus the production of IAA and its precursors induced elongated cells and hypha ramification of IAA producing *Trichoderma*. Zhang et al. [61] suggested that the possible mechanisms

responsible for *Trichoderma longibrachiatum* T6 (TL-6) in promoting wheat (*Triticum aestivum* L.) growth and enhancing plant tolerance to NaCl stress were through the production of indole acetic acid (IAA) and 1-aminocyclopropane-1-carboxylate-deaminase (ACC-deaminase). IAA aids the loosening of plant cell walls, allowing the fungus to enter the host root and to manipulate the host physiological functions as a mutual benefit. Thus the mutual interactions of the fungi and the host act as a surface for the exchange of nutrients and signals between the two symbiotic partners [60].

To emphasize on the *Trichoderma* –plant salinity tolerance mechanisms, the fungi again improved the antioxidant enzymes such as peroxidase (POD), polyphenol oxidase (PPO), phenylalanine ammonia-lyase (PAL), catalase (CAT), superoxide dismutase (SOD), ascorbate peroxidase (APX), and glutathione reductase (GR), increased the levels of proline, soluble sugars, soluble protein, ascorbic acid (AsA) and chlorophyll as well as improving root activity of host plants [61].

6. ROLE OF TRICHODERMA IN ALLEVIATING REACTIVE OXYGEN SPECIES IN PLANTS

Reactive oxygen species (ROS) are chemical species naturally produced by living organisms that in one way or the other effectively uses or produces oxygen. The commonly known ROS are superoxides, peroxides, hydroxyl radicals, singlet, and alpha oxygen. The general effects of overproduction of ROS in cells include; RNA/DNA damage or changes of the nuclear transcriptomes, oxidation of amino acids in proteins, oxidative deactivation of specific enzymes by oxidation co-factors and finally causes lipid peroxidation [62]. The changes in the function of ROS between biotic and abiotic stresses might arise from the action of hormones and cross-talk between different signaling pathways or from differences in the locations where ROS are produced and accumulated during different stresses. These thoughts raise the inquiry of how plants can regulate ROS production and scavenging mechanisms when they are exposed simultaneously to salinity stress.

ROS production enacts signal response of plant cells that intervenes in the perception of microbe-associated molecular patterns [63,64]. From various studies, salinity stress elevates levels of

H₂O₂ and lipid peroxidation in plants [65]. Notably, low levels of ROS participate in cell signaling and improved stress tolerance, while its overproduction beyond the elimination capacity of antioxidants causes damage and induces oxidative stress [66]. Thus to sustain homeostasis in salinity stressed plants depends on the ratio of ROS production and ROS scavenging.

ROS scavenging depends on some plants or microbes support machinery such as antioxidants; Ascorbic acid (AsA) and Glutathione (GSH) and ROS scavenging enzymes such as superoxide dismutase (SOD), Ascorbate peroxidase (APX), catalase (CAT), Glutathione peroxidase (GPX). Consistently *Trichoderma* enhanced antioxidant potential to equalize the overproduced ROS and decreased the transcript. Mastouri et al. [67] found the higher activity of ROS scavenging enzymes such as superoxide dismutase (SOD), catalase (CAT) and ascorbate peroxidase (APX), as well as AsA and GSH contents in *Trichoderma*-colonized tomato plants. Similarly, *Trichoderma virens* deploy another role to quench oxidative stress produced by ROS overproduction thereby multiplied the expression of glutathione transferase (GST) gene in tobacco (*Nicotianatabacum*) thus increased the activities of antioxidant enzymes such as GST, SOD, APX, POD, and CAT [68].

Lopez et al. [69] figured out that, *Trichoderma virens* secreted a group of proteins that are involved in cell wall hydrolysis, ROS scavenging, and secondary metabolism during colonization in maize (*Zea mays*). Evidence from previous reports shed light on *Trichoderma* non-enzymatic ROS scavenging antioxidants mechanisms including the major cellular redox buffers ascorbate, glutathione (GSH), tocopherol, flavonoids, alkaloids, and carotenoids and enzymatic ROS scavenging mechanisms in plants including superoxide dismutase (SOD), ascorbate peroxidase (APX), glutathione peroxidase (GPX), and catalase (CAT). Thus through these mechanisms, *Trichoderma* helps the plant to alleviate ROS effects (Fig.1).

7. TRICHODERMA GENES FUNCTIONS RELATED TO SALINITY TOLERANCE

Trichoderma spp. are cosmopolitan fungi resistant to many adverse environmental conditions. They accumulate a series of potential genes for survival and growth in many habitats.

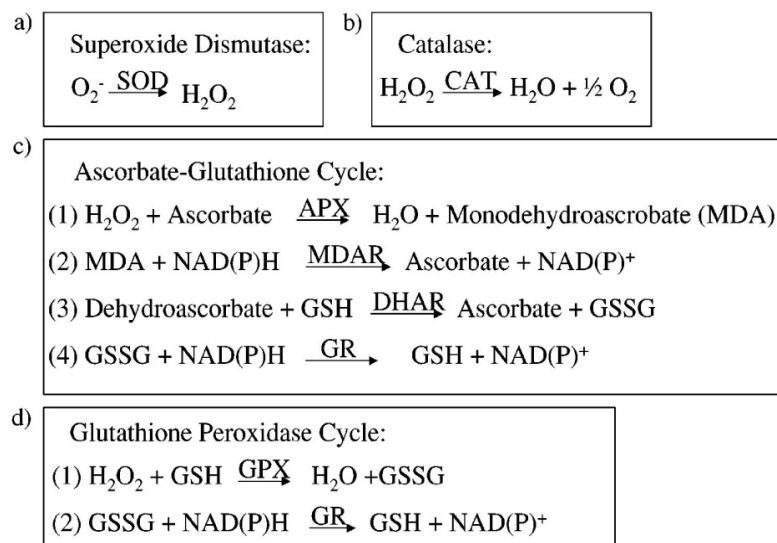


Fig. 1. The principal modes of enzymatic ROS scavenging by superoxide dismutase (SOD), catalase (CAT), the ascorbate-glutathione cycle, and the glutathione peroxidase (GPX) cycle

SOD converts hydrogen superoxide into hydrogen peroxide. CAT converts hydrogen peroxide into water. Hydrogen peroxide is also converted into water by the ascorbate-glutathione cycle. The reducing agent in the first reaction catalyzed by ascorbate peroxidase (APX) is ascorbate, which oxidizes into monodehydroascorbate (MDA). MDA reductase (MDAR) reduces MDA into ascorbate with the help of NAD(P)H. Dehydroascorbate (DHA) is produced spontaneously by MDA and can be reduced to ascorbate by DHA reductase (DHAR) with the help of GSH that is oxidized to GSSG. The cycle closes with glutathione reductase (GR) converting GSSG back into GSH with the reducing agent NAD(P)H. The GPX cycle converts hydrogen peroxide into water using reducing equivalents from GSH. Oxidized GSSG is again converted into GSH by GR and the reducing agent NAD(P)H. Sited from [70]

Several genes from these symbiotic fungi have been transferred to plants, successfully enhancing tolerance to heat, salinity, heavy metals, and toxic xenobiotics bioremediation [71]. They communicate to plants through hormonal signals and pathways.

Relatively most phytohormones' response to salinity tolerance is equally produced by these fungi, thus their interaction to host plants increased plants' survival during salinity stress. Abscisic acid a vital phytohormone (ABA) produced under salinity stress manipulates the stomata closure and triggers the activation of stress-related genes, thus controlling abnormal water loss and photosynthetic activities [72].

Heat shock proteins (hsp70), Thkel1, nag70, glu78, glucanase, Glutathione-s-transferase (GST) are known to be produced by *Trichoderma* to combat salinity. But some of the controversies which frequently draw the attention of the public are; (i) how many *Trichoderma* species can produce these genes (ii) can a species produce several of these

genes? Therefore, Usman et al. [73] revealed that the Hsp70 is essential regulators of protein have the tendency to maintain internal cell stability like proper folding protein and breakdown of unfolded proteins. Thus Hsp70 holds together protein substrates to help in movement, regulation, and prevent aggregation under physical and or chemical pressure. Hsp70 genes and transcription factors are up-regulated to combat salinity in different plant species [74].

Ion transport or homeostasis genes (e.g., SOS genes, AtNHX1, and H^+ ATPase), senescence-associated genes (e.g., SAG), molecular chaperones (e.g., HSP genes), and dehydration-related transcription factors (e.g., DREB) are sequenced from several *Trichoderma* strains and their host species. Within the stress-responsive genes, the SOS transcription gene family is considered to play a very vital role in ion homeostasis thereby confers salt tolerance in many plant species [75,76]. Thus it is clear that most salt-tolerant *Trichoderma* can produce several genes capable to resist salinity effects in their host plants.

Table 1. *Trichoderma* strains and their functions on plant under salinity stress

| <i>T. spp</i> | Plant | Stress | Function | Reference |
|--|----------------------|-------------------|--|-----------|
| <i>T. aspererellum</i> | Rice | None | Involved in non-photochemical quenching, protecting the plant against photo-oxidative damage | [104] |
| <i>T. longibrachiatum</i> (T6) | Wheat | salt | Improved antioxidants (SOD,POD,CAT) expression and gene defense and increased growth | [42] |
| <i>T. afroharzianum</i> | Tomato | Salt, drought | Enhanced Glutathione reductase which catalyses the reduction of glutathione disulphide (GSSG) and curb oxidative stress by maintaining the reducing environment of the cells | [67] |
| <i>T. asperellum</i> | Cucumber | Salt or drought | Protects against oxidative damage by reactive oxygen species (ROS) and increased shoot and root length. | [103] |
| <i>T. harzianum</i> , <i>T. koningii</i> , <i>T. longibrachiatum</i> , <i>T. tomentosum</i> , <i>T. virens</i> | Tomato | salt | Increased the photosynthesis intensity in the leaves, increased chlorophyll a content and controlled <i>B. cinerea</i> pathogen | [101] |
| <i>Trichoderma isolate</i> 1.3.3 | Chilli pepper | None | maximized seed germination, increased root length from 2.7 to 4.7 cm, and shoot length from 3.2 to 4.75 cm | [90] |
| <i>T. viride</i> | Cotton | salt | Shoot and root length elongation increased four- and threefold respectively | [91] |
| <i>T. harzianum</i> T22 | Crack willow | salt | Increased germination rate, shoot and root length 40% compared to control samples. | [93] |
| <i>T. isolate</i> | Arabidopsis cucumber | salt | Improved seed germination | [94] |
| <i>T. viride</i> | Arabidopsis | None | Produces VOCs which increased plant size, fresh weight, chlorophyll, root and shoot elongation and number of flowers | [87] |
| <i>T. asperellum</i> | Tomato | Pathogen | Produced cellulases, chitinases, IAA, protease and siderophores significantly reduced <i>Fusarium wilt</i> disease severity | [88] |
| <i>T. harzianum</i> (PDBCTH 10) <i>T. viride</i> (PDBCTV 32) <i>Trichoderma virens</i> (PDBCTV 12) | Chickpea | None | Increased plant height and branches, increased uptake of nitrogen and maximized shoot and root phosphorus uptake | [89] |
| <i>T. longibrachiatum</i> | None | pathogen | Produced strong lethal and parasitic effect on the second juvenile of <i>M. incognita</i> | [58] |
| <i>T. longibrachiatum</i> T6 | Wheat | salt | Increased proline content, ascorbate and glutathione and decreased the content of malondialdehyde(MDA) and hydrogen peroxide (H ₂ O ₂). Controlled the transcriptional levels of ROS. | [61] |
| <i>T. asperellum</i> | maize | Saline - alkaline | Upgraded the content of photosynthetic pigments, enhanced the photochemical activity of the photosystem II reaction center, increased the activities of ATP enzymes in the chloroplasts | [102] |

8. AMELIORATION OF SALINITY STRESS BY TRICHODERMA SPECIES

The use of *Trichoderma* to improve plants' strength to withstand salinity stress has gain attention in Agricultural works. Hashem et al., [77] reported the role of *Trichoderma hamatum* in mitigating the deleterious effects of NaCl stress in *Ochradenusbaccatus* thereby increased antioxidant enzymes activities together with pigment contents as compared with the non-treated plants. Equally, Hassan et al., [78] reported that salinity tolerant *T. harzianum* mutants showed higher growth abilities with convinced sporulation in growth media containing NaCl in comparison with their parent strain. Notably, *T. harzianum* was projected to produce certain active metabolites, such as chitinases, cellulases, β -galactosidases, as well as antibiotics such as trichodermin, gliotoxin, and gliovirin. The mutants significantly reduced wilt disease incidence and improved yield and mineral contents of tomato plants under both saline and non-saline soil conditions, as well as, under infested and natural conditions.

9. TRICHODERMA ROLES IN PLANT NUTRIENT UPTAKE UNDER SALINITY STRESS

Trichoderma and other plant growth-promoting rhizobacteria (PGPR) are among the microorganisms contained in bio-fertilizers that contain mineral solubilizing enzymes [79], and thus able to transform nutrients from nonabsorbent to absorbable in biological processes [80]. From previous studies the effect of *Trichoderma spp.* on plant growth and development via the increase of root elongation, abiotic stress tolerance; use and uptake of nutrients, and crop productivity [81] have been reported. From such a perspective, deeper plant roots enhance mineral such as potassium and water uptake from soil.

Trichoderma-treated plants in saline environments develop adventitious roots which enhance water and nutrient absorption. Growth promoting bacteria in association with *Trichoderma spp.* improved the quantitative and qualitative yield of crops through nitrogen (N) fixation, increased solubility of phosphorus (P), and potassium (K), increased the biological availability of soil nutrients [82], and further exhibited resistance by inhibiting pathogenicity and also producing plant growth-regulating hormones.

Pretreatment, biopriming, and inoculation of seeds with *Trichoderma* extracts or suspensions increased root development and increased the tendency of nutrient absorption from deep rhizosphere [83]. Recent studies showed that plant growth-promoting *Trichoderma* increased plant growth by producing ACC deaminase to reduce the amount of ethylene in the roots of developing plants [84] and produced plant growth regulators such as indole acetic acid [85]. A similar report has shown that *Trichoderma* is prolific producers of volatile organic compounds (VOCs) which are significant in the agriculture yard [86].

Relatively little is known about the metabolic origin of these compounds in fungi. Likewise, Lee et al., [87] reported the ability of mixtures of VOCs from *Trichoderma viride* stimulated plant growth in the absence of pathogen attack in *Arabidopsis thaliana* and *T. viride*-derived VOCs increased plant size, fresh weight, chlorophyll content, root growth, and the number of flowers under saline environment. In the same context, Li et al., [88] also reported the biocontrol efficiency of *T. asperellum* CHF 78 which showed several plant growth-promoting traits including the ability produce cellulases, chitinases, indole acetic acid (IAA), proteases, and siderophores under salinity stress. Rudresh et al., [89] reported the mixture of three *Trichoderma* strains (*T. harzianum* PDBCTH 10, *T. viride* PDBCTV 32 and *Trichoderma virens* PDBCTV 12) as a talc-based formulation to chickpea in a glasshouse trial increased plant height and the number of branches, increased uptake of nitrogen and maximum shoot and root phosphorus uptake.

10. THE ROLE OF TRICHODERMA IN SEED GERMINATION AND ROOT DEVELOPMENT

For many decades it has been well established that microbes closely associated with plant roots can directly influence plant growth and development, and this has been reported about *Trichoderma* species. Joshi et al., [90] demonstrated the effect of *Trichoderma* isolate which gave maximum seed germination (63%), increased root length from 2.7 to 4.7 cm, and shoot length from 3.2 to 4.75 cm of chili plant under salinity stress.

Similarly, Shanmugaiah et al., [91] also reported that shoot and root elongation increased four and threefold respectively after cotton seeds pretreated with *T. viride* compared with the

control. Moreover, *Trichoderma* species tested for growth promotion of silver oak (*Grevillea robusta*) seedlings gave a significant increase in seedling height and girth compared with the control over 120 days [92]. Likewise, Adams et al., [93] demonstrated the significance of *Trichoderma harzianum* T22 in the stimulation of crack willow (*Salix fragilis*) growth, the mode of treatment increased the germination rate of the treated plants in clean soil.

Arabidopsis and cucumber (*Cucumis sativus* L.) plant treated with *Trichoderma* before salt stress significantly improved seed germination [94]. It is known that several factors affect root elongation and roots physiological functions. For example, biosynthesis of ethylene in plants under salinity stress inhibits root growth and finally affects the overall plant growth. Several studies have publicized that ethylene level in plants is controlled by a major enzyme 1-aminocyclopropane-1-carboxylic acid (ACC)-deaminase. This enzyme present in plant growth-promoting bacteria (PGPR) and *Trichoderma* [95] lowers the ethylene level by metabolizing its precursor ACC into α -ketobutyrate and ammonia. Therefore treatment of seeds or plants under salinity stress with *Trichoderma* having ACC-deaminase activity mitigates the inhibitory effects of salinity on root growth by lowering the ethylene concentration in the plant [96].

11. EFFECT OF TRICHODERMA ON PLANTS PIGMENTATION UNDER SALT STRESS

Salinity stress imposes damage to photosystems and other cellular functions which lead to a high accumulation of reactive oxygen species in plants [97]. Improving photosynthetic efficiency of crop plants is important. However, efforts to increase plants' photosynthetic efficiency by plant selection and breeding techniques generated more frustration and failure than success [98]. Recent works to increase photosynthetic efficiency through genetic engineering have focused on the chloroplast, frequently using genes from photosynthetic bacteria [98,99]. Some early efforts to make such improvements have proven successful [100]. But root colonization with *Trichoderma spp.* increased photosynthesis and chlorophyll content in multiple folds. Work done by Alexandru et al., [101] discovered six species of *Trichoderma*; *harzianum*, *koningii*, *longibrachiatum*, *tomentosum*, *virens*, and *viride* increased the photosynthesis and chlorophyll in the leaves of

tomato plantlets. Similarly, Fu et al., [102] reported the tremendous effects of *T. asperellum* possible upgraded the content of photosynthetic pigments, heightened the photochemical activity of the photosystem II reaction center, accelerated the activities of ATP enzymes in the chloroplasts, reduced the non-stomata limitation of photosynthesis due to saline-alkaline stress, and promoted photosynthesis to provide more raw materials and energy for nitrogen metabolism, thereby improving the activity of nitrogen metabolism and the capacity for material production in maize seedlings.

12. CONCLUSION

Soil salinity is a serious threat to global agricultural sustainability and food security. The idea of using soil-borne fungi capable of stimulating plant growth and induce tolerance to salt stress is highly recommended. The primitive fungi type, *Trichoderma* proved to be useful in such functions. Several species of *Trichoderma* can heighten the growth of different plant species especially cereals. The level of growth promotion induced by *Trichoderma* species can be estimated with increases up to 200% of total biomass compared with control plants regularly reported. This must be considering as a means or an apparatus to reduce salinity effects on crop productions and increase food productions on salinized agricultural lands.

Under salinity stress, *Trichoderma* species activate biochemical pathways that reduce ROS via scavenging enzyme activities, gene expression, increased proline content, ascorbate and glutathione and decrease the content of malondialdehyde (MDA) and hydrogen peroxide (H_2O_2).

The defined mechanisms of *Trichoderma* in combating salinity stress in plants are; increase the formation of ion channels in host plants, activation of ion exchange (K^+/Na^+), increase ROS scavenging enzymes and genes, increase the production of phytohormones and their signal pathways, enhance root developments to enable water absorptions, regulate the stomata conductance through the increment of carotenoids in host plants which corresponds to the functions of the photosystems.

13. RECOMMENDATION

The excessive usage of chemical fertilizers, bad irrigational practices, and other human activities

that exposes farming lands to salinization is generating more abiotic stresses to crop plants and as a matter of fact, will affect global food security.

Trichoderma plays a vital role in combating salinity effects in the plants' life. However primitive species of this genus are getting to extinct and advocating the usage and its benefits are low beyond measure.

Therefore, researchers must pay attention to the primitive and the newly identified species which have multiple mechanisms as a biological control agent and growth promoter. Again the combination of effective genes from different strains or species of the fungi could produce effective tolerance genes to several plants therefore cloning of such genes to improve plant growth and stress tolerance should be the lookout.

ACKNOWLEDGEMENTS

This research was supported Gansu Agricultural University, College crop protection and under the care and supervisions of Plant Pathology Research Team.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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