



Plant Growth Promoting Fungi: Mechanisms and Applications for Crop Productivity

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Abstract

Trichoderma longibrachiatum is a soil fungus which is found all over the world but mainly in warmer climates. *Trichoderma longibrachiatum* T6 has been shown to promote wheat growth and induce plant resistance to parasitic nematodes, but whether the plant-growth-promoting fungi T6 can enhance plant tolerance to salt stress is unknown. Soil salinity is a serious problem worldwide that reduces agricultural productivity. *Trichoderma longibrachiatum* T6 (T6) has been shown to promote wheat growth and induce plant resistance to parasitic nematodes, but whether the plant-growth-promoting fungi T6 can enhance plant tolerance to salt stress is unknown. The effect of plant-growth-promoting fungi T6 on wheat seedlings' growth and development under salt stress, and investigated the role of T6 in inducing the resistance to NaCl stress at physiological, biochemical, and molecular levels.

Legumes, through symbiotic nitrogen fixation, meet a major part of their own N demand and partially benefit the following crops of the system by enriching soil. In realization of this sustainability advantage and to promote pulse production, United Nations had declared 2016 as the "International Year of pulses". Grain legumes are frequently subjected to both abiotic and biotic stresses resulting in severe yield losses. Global yields of legumes have been stagnant for the past five decades in spite of adopting various conventional and molecular breeding approaches. Furthermore, the increasing costs and negative effects of pesticides and fertilizers for crop production necessitate the use of biological options of crop production and protection. The use of plant growth-promoting (PGP) fungus T6 for improving soil and plant health has become one of the attractive strategies for developing sustainable agricultural systems due to their eco-friendliness, low production cost and minimizing consumption of non-renewable resources.

Keywords: *Trichoderma longibrachiatum* T6; Plant-growth-promoting; Mechanism; Application

Introduction

The idea of eliminating the use of fertilizers which are sometimes environmentally unsafe is slowly becoming a reality because of the emergence of microorganisms that can serve the same purpose or even do better. Depletion of soil nutrients through leaching into the waterways and causing contamination are some of the negative effects of these chemical fertilizers that prompted the need

for suitable alternatives. This brings us to the idea of using microbes that can be developed for use as biological fertilizers (bio fertilizers). They are environmentally friendly as they are natural living organisms.

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They increase crop yield and production and, in addition, in developing countries, they are less expensive compared to chemical fertilizers. In addition to PGPB, some fungi have also been demonstrated to promote plant growth. Apart from improving crop yields, some bio fertilizers also control various plant pathogens. The objective of worldwide sustainable agriculture is much more likely to be achieved through the widespread use of bio fertilizers rather than chemically synthesized fertilizers. However, to realize this objective it is essential that the many mechanisms employed by PGPF first be thoroughly understood thereby allowing workers to fully harness the potentials of these microbes. The present state of our knowledge regarding the fundamental mechanisms employed by PGPF is discussed herein.

The worldwide increases in both environmental damage and human population pressure have the unfortunate consequence that global food production may soon become insufficient to feed all of the world's people. It is therefore essential that agricultural productivity be significantly increased within the next few decades. To this end, agricultural practice is moving toward a more sustainable and environmentally friendly approach. This includes both the increasing use of transgenic plants and plant growth-promoting fungus as a part of mainstream agricultural practice. Here, a number of the mechanisms utilized by plant growth-promoting fungus are discussed and considered. It is envisioned that in the not too distant future, plant growth-promoting fungus (PGPF) will begin to replace the use of chemicals in agriculture, horticulture, silviculture, and environmental cleanup strategies. While there may not be one simple strategy that can effectively promote the growth of all plants under all conditions, some of the strategies that are discussed already show great promise.

Trichoderma longibrachiatum is a fungus in the genus *Trichoderma*. In addition to being a distinct species, *T. longibrachiatum* also typifies one of several clades within *Trichoderma* which comprises 21 different species ^[1]. *Trichoderma longibrachiatum* is a soil fungus which is found all over the world but mainly in warmer climates ^[1]. Many species from this clad have been adopted

in various industries because of their ability to secrete large amounts of protein and metabolites.

The cosmopolitan filamentous fungus *Trichoderma longibrachiatum* is the genetically distinct agamospecies belonging to the *Longibrachiatum* clad of *Trichoderma* (teleomorph *Hypocrea*, Ascomycota, Dikarya). *T. longibrachiatum* is usually a common component of *Trichoderma* communities isolated from soil and other environments such as mushrooms and food rotting fungi, marine and soil animals and dead wood. It appears to be abundant in indoor environments such as water-damaged buildings or mushroom farms infected by green mould disease. Consequently, *T. longibrachiatum* has also been detected in sputum and sinus of healthy humans. More importantly, it is (together with the closely related *Hypocrea orientalis*) the only *Trichoderma* spp. that is able to attack immunocompromised humans. It was shown that this species is able to control plant-pathogenic nematodes in soil.

T. longibrachiatum is phylogenetically very close to *Trichoderma reesei* (teleomorph *Hypocrea jecorina*), and has – like the latter – been used as a source for production of plant biomass degrading enzymes. Notably, it has been confused with *T. reesei* between 1984 and 1996, and several cellulase preparations from *T. reesei* are still sold under the name “*T. longibrachiatum*”. Its genome sequence and comparative analysis with other *Trichoderma* species is therefore expected to yield understanding what made an environmental opportunistic fungus an opportunistic human pathogen, and to complement the genetic resources for industrial enzyme production.

Soil salinity is a serious problem worldwide that reduces agricultural productivity. *Trichoderma longibrachiatum* T6 (T6) has been shown to promote wheat growth and induce plant resistance to parasitic nematodes, but whether the plant-growth-promoting fungi T6 can enhance plant tolerance to salt stress is unknown. Wheat seedlings were inoculated with the strain of T6 and then compared with non-inoculated controls. Shoot height, root length, and shoot and root weights were measured on 15 days old wheat seedlings grown either under 150 mM NaCl or in a controlled setting without any NaCl. A number

of colonies were re-isolated from the roots of wheat seedlings under salt stress. The relative water content in the leaves and roots, chlorophyll content, and root activity were significantly increased, and the accumulation of proline content in leaves was markedly accelerated with the plant growth parameters, but the content of leaf malondialdehyde under saline condition was significantly decreased. The antioxidant enzymes-superoxide dismutase (SOD), peroxidase (POD), and catalase (CAT) in wheat seedlings were increased by 29, 39, and 19%, respectively, with the application of the strain of T6 under salt stress; the relative expression of SOD, POD, and CAT genes in these wheat seedlings were significantly up-regulated. The possible mechanisms by which T6 suppresses the negative effect of NaCl stress on wheat seedling growth may be due to the improvement of the antioxidative defense system and gene expression in the stressed wheat plants.

Phosphorus is abundant in soils in both organic and inorganic forms; nevertheless, it is unavailable to plants. Accordingly, soil becomes phosphorus (P)-deficient, making P one of the most important nutrient elements limiting crop productivity. To circumvent the P deficiency, phosphate-solubilising microorganisms could play an important role in making P available for plants by dissolving insoluble P. The dissolution of inorganic P by microbial communities including fungi is though common under *in vitro* conditions; the performance of phosphate-solubilising microbes *in situ* has been contradictory. Fungi exhibit traits such as mineral solubilisation, biological control, and production of secondary metabolites. As such, their potential to enhance plant growth when present in association with the roots is clear. The challenge is how to make use of such biological resources to maintain soil health while increasing the crop productivity by providing P to plants through the application of phosphate-solubilising fungi. The present review focuses on the mechanisms of phosphate solubilisation, development and mode of fungal inoculants application and mechanisms of growth promotion by phosphate-solubilising fungi for crop productivity under a wide range of agro-ecosystems, and the understanding and management of P nutrition of plants through the

application of phosphate-solubilising fungi will be addressed and discussed.

Salt stress is one of the major abiotic stresses that affect plant growth, development, and crop yield [2, 3]. Wheat (*Triticum aestivum*), the most important cereal crop in the world, is considered to be salt sensitive [4]. Grown under salt conditions, wheat plants often produce a significantly low grain yield with poor quality. Studies have shown that salt stress can induce several morphological, physiological, and metabolic responses of plants, which causes ROS stress and osmotic stress in plants, leading to increased peroxidation of lipid and antioxidant enzyme inactivation [5]. Also, plants grown under salt stress conditions usually synthesize several kinds of soluble compounds including soluble sugars and proteins, which may help adjust osmoticum, retain cell turgor, and stabilize cell structures [6].

At the present time, about 6% of the arable land on the earth is salt affected, especially in arid and semiarid regions [7]. This seriously threatens global agricultural sustainability and food security. Thus, it is critically important to develop effective and practical techniques to alleviate the negative effects of salt stress on plant growth and development. Conventional breeding and transgenic technology have been used to develop new cultivars with improved salt tolerant traits, but breeding salt tolerance has not been successful [8]. The long breeding cycle and low breeding efficiency for the quantitative trait presents challenges. Transgenic technology has the ability to incorporate salt tolerant genes in new plant materials [9, 10, 11], but the effectiveness has been low and also enveloped in controversy [12]. Furthermore, gene loss, high cost, and other regulatory issues are the main bottlenecks for commercial transgenic plants use [13]. A newer attempt is to apply exogenous compounds to decrease the negative effect of abiotic stress; this technique has been shown to increase plant tolerance to salt stress, such as using oligochitosan [2], nitric oxide and calcium nitrate [4], chit oligosaccharides [12], and jasmonic acid [14] in wheat, as well as gibberlic acid and calcium chloride in linseed [15], and ascorbic acid in broad bean. These exogenous compounds have been shown to improve the salt tolerance of plants, but

the exact physiological mechanisms are unknown. A new, innovative technique that has attracted a great deal of attention in recent years is to use plant-growth-promoting bacteria and fungi to induce plant resistance to abiotic stress. It is an effective approach for enhancing plant tolerance to salt stress and this approach may play a role in the development of sustainable agricultural systems. *Trichoderma spp.* is one of the important groups of rhizosphere microorganisms, which can impart some beneficial effects on promoting plant growth and development [16, 17]. The *Trichoderma* species have also been known to be used by plants as biological control agents for controlling different species of plant fungus diseases for decades [16, 18] have reported that *Trichoderma afroharzianum* T22 can enhance tomato (*Solanum lycopersicum*) seed germination under biotic and abiotic stresses, alleviating oxidative damage in osmotic stressed seedlings. However, the underlying mechanisms responsible for the alleviation of oxidative damage remain to be explored. Little information is available regarding the potential and possible mechanisms of plant-growth-promoting fungi T6 in enhancing the tolerance of wheat to salt stress. *Trichoderma sp.* is useful in industry because of their high capacity to secrete large amounts of protein and metabolites. It has been suggested that *Trichoderma longibrachiatum* could be used as a biocontrol agent for its parasitic and lethal effects on the cysts of the nematode *Heterodera avenae*. [19] Because *T. longibrachiatum* is a mycoparasite, it has also been investigated for use in combating fungal diseases on agricultural crops. [20] Its enzymatic capacity could potentially be useful in bioremediation, for use in remediation of polycyclic aromatic hydrocarbons (PAHs) and heavy metals. [21] Other industrial uses include using the various cellulases for staining fabrics in the textile industry, increasing digestibility of poultry feed, and potentially in the generation of biofuels. [22] *Trichoderma longibrachiatum* has also been reported in promoting plant growth by increasing nutrient uptake, inhibiting the growth of plant parasites, increasing carbohydrate metabolism, and phytohormone synthesis. The high level of salinity is one of the major environmental stress factors that cause biochemical alterations in plants, limits plant

growth, and decreases plant productivity [23, 24]. *Trichoderma* species are one of the most versatile opportunistic plant symbionts which can colonize plant roots [25]. These symbionts are well-known for their remarkable interactions with host plants and their ability to induce broad-spectrum resistance to plant pathogens [16, 26, and 27]. Although, the plant-growth-promoting capability of *Trichoderma spp.* has been previously reported, there is little information concerning plants' systemic responses induced by T6 under salt stress conditions.

[28] Reported that host roots colonized by *Trichoderma* strains enhanced whole-plant tolerance to biotic and abiotic stresses. The enhancement was indicated by increased plants root growth and nutritional status [29], and induced systemic resistance to diseases [16]. In the present study, we found that T6 has a great ability to colonize the roots of wheat seedlings under salt stress, which significantly improved wheat seedlings growth and development under salt stress. The cacao (*Theobroma cacao*) seedlings which were colonized by *Trichoderma hamatum* isolate DIS 219b enhanced seedling growth and development. In a similar study, [30] found that the plant saplings grown with *T. afroharzianum* T22 produced more biomass than non-inoculated controls in metal contaminated soil. Our findings are supported by a number of previous observations where *Trichoderma spp.* has the ability to colonize plant roots, establish symbiotic relationships with a wide range of host plants, and promote plant growth and development [28,31]. Moreover, similar results were reported that *Trichoderma parareesei* increased the tomato lateral root development and growth promotion under salt stress conditions [32]. Plant roots are critical for plant growth and development which is attributed to their function and importance in absorption of nutrients and water from soil [33]. The content of proline was increased in wheat seedling grown with NaCl alone, compared to the control. The previous research indicated that the increased level of proline in plants under salt stress condition may have been due to the activation of proline biosynthesis which enhances protein turnover [15]. Proline is an important nitrogen source that is available for plant recovery

from environmental stress and restoration of growth^[34], and it can act as an osmolyte that reduces the osmotic potential of the cell and the uptake of toxic ions^[35]. Thus, proline plays a predominant role in protecting plants from osmotic stress^[15]. Alleviating effects of oligochitosan on salt stress-induced oxidative damage in wheat leaves might be related to its regulation roles in proline levels. The content of MDA significantly increased in NaCl-stressed wheat seedlings in comparison to the control plants, which is consistent with the findings of^[36] in wheat. Thereafter, the content of MDA significantly decreased after wheat seeds were soaked in the suspension of T6 before NaCl stress. Taken together, our results are consistent with data from^[37], who demonstrated that wheat seed bioprimering with salinity-tolerant isolates of *T. harzianum* Th-14, Th-19, and Th-13 reduced the accumulation of MDA content, whereas, it increased the proline content in wheat seedlings under both salt and non-saline conditions.

It is widely accepted that osmosis molecules, including soluble sugars and proteins, are important indicators in response to abiotic stress^[38]. The increased accumulation of glucose and sucrose in plants usually indicates a highly protective mechanism against oxidative damage caused by high salinity in the plant environment^[6, 39]. However, most previous studies determined the physiologic role of soluble sugars and utilization by plants.

In plants, the overproduction of ROS is considered a biochemical change under salt stress^[40], which is the most important factor responsible for NaCl-induced damage to macromolecules and plants cellular structures^[41]. To alleviate the damage associated with the overproduction of ROS, plants have naturally developed a wide range of enzymatic defense mechanisms to detoxify free radicals and thereby help protect themselves from destructive oxidative damage^[42, 43]. One of the important protective mechanisms in plants is the enzymatic antioxidant system, which involves the simultaneous action of a number of enzymes including SOD, POD, and CAT^[2]. The findings from the present study demonstrate that NaCl stress induced plants produce a higher level of SOD, POD, and CAT activity in wheat seedlings than the control samples. However, the

use of T6 increased SOD, POD, and CAT activity in wheat seedlings regardless of salt concentration, which was in accordance with the findings of^[44], who demonstrated that the role of *T. harzianum* in Indian mustard (*Brassica juncea*) was to mitigate NaCl stress by an antioxidative defense system.

Some plant-beneficial fungi *Trichoderma* species can induce profound impacts or changes in different species of plant gene expression under biotic and abiotic stresses^[18]. Increased SOD activity in stressed plants may be attributed to the significantly increased level of ROS, which causes an increase of gene expression responsible for encoding the activity of SOD^[45, 46]. A number of previous studies have also demonstrated that there is a higher level of gene family expression for genes involved in plant protection against abiotic stresses^[47, 48] in *Trichoderma* spp. pretreated plants. However, there are no in-depth studies on specific gene expression of wheat seedlings treated with plant-growth-promoting fungi T6. The activity of ROS-scavenging enzymes in T6-challenged wheat plants, which indicated that the important role of ROS was detoxifying cellular survival and regulating plant acclimation^[49]. In addition, ROS also served as a critical signalling molecule in cell proliferation and survival. Similar results have been reported that salinity is one of the environment factors that can change the normal homeostasis of plant cells, and causes an increased production of ROS within plants. The ROS molecule functions as a toxic by-product of stress metabolism and is important in signalling transduction molecules in response to salt stress^[49].

Grain legumes also called ‘Poor man’s meat’ are an essential entity in food and feed due to its protein, minerals, and other bioactive molecules. Increasing nutritional awareness increased the per-capita consumption of grain legumes across the world^[50]. Their better adaptation as an inter-crop with cereals or tuber crops helps in increased income generation and livelihood resilience of small holder farmers. However, production level of such leguminous crops has constraints in various forms such as pest and pathogen attacks, infertile soils, and climate changes. Development of improved cultivars through breeding and molecular techniques had

been practiced; still, the productivity remains stagnant for the last two decades. All these together attracted the attention at global level, and thus, the general assembly of United Nations has announced this year as 'International Year of Pulses' to emphasize the need for focusing on pulses for food and nutritional security and to create awareness and understanding of the challenges faced in pulse farming and trading. Hence, this review emphasizes to document mainly on PGP traits of T6 and how far it was studied in the context of growth-promotion, biocontrol against pests, and pathogens, as mitigators of abiotic stress, as a tool for enhanced phytoremediation and bio-fortification.

Conclusion

In summary, the strain of plant-growth-promoting fungi T6 has a remarkable effect on alleviating the adverse effects of salt stress on wheat seedling growth and development. Multiple tests employed in the study allowed us to explore the possible mechanisms at a physiological and molecular level in which T6 provides the ability of alleviating the suppression effect of salt stress. The mechanisms may include (i) T6 increasing the activity of antioxidative defense system in wheat seedlings to resist salt stress, and (ii) enhancing the relative levels of antioxidant gene expression in the stressed plants. However, there are some issues that need to be addressed in future studies, such as the efficacy of the strain of plant-growth-promoting fungi T6 interactions with other plant species and other abiotic stresses. More detailed studies may be necessary to determine which compound plays the signaling role in T6 that induces systemic changes in the expression of encoding antioxidant enzymes and genes. The available information suggests that *Trichoderma longibrachiatum* represent a hidden repertoire and sustainable source for bioactive and chemically novel natural products, which can be explored to a great extent in various fields of agricultural sector. However, such an extent of success especially on legumes under field conditions is limited. This indicates the existence of large gaps between research and development of potential fungus T6 inoculums for field application. Therefore, generation of comprehensive knowledge on screening, characterization, and formulation strategies and

understanding of molecular mechanisms behind their action and evaluation at field levels are necessary.

The world that can support only a limited number of people. Unless new sustainable agricultural approaches and technologies are soon developed, food availability in the next 50 years approximately might be a great challenge for the growing population. To address this problem, one of the approaches that might be undertaken is the more widespread use of PGPB, initially in addition to, and possibly eventually instead of, the current use of agricultural chemicals.

The last 30–40 years have seen researchers develop an exhaustive, precise understanding of how PGPF facilitate plants growth so that the more widespread application of these organisms has now become feasible. The latter using bacteriophages in biocontrol while the former shows the activities of PGPF in reduction of stress. However, in order to make this approach a worldwide reality, a number of steps must be undertaken. (1) New and improved techniques for the large-scale growth, storage, shipping, formulation and application of plant growth-promoting bacteria need to be developed. (2) Reasonable, safe, efficacious and consistent regulations for the use PGPF need to be developed in all countries of the world so that the technology may readily be transferred from one country to another. Also, unnecessary regulatory hurdles need to be kept to a minimum. (3) Broadly-based campaigns of public education regarding the nature of PGPF need to be initiated so that the public comes to understand that these bacteria are not sources of disease but are natural products playing a positive role. (4) Following additional fundamental work to better understand PGPF and their biochemistry, genetics and physiology, scientists, laymen and regulators need to accept that "optimal" PGPF strains may require some genetic manipulation and that the use of such genetically manipulated strains will not present any new hazards or risks to humans or the environment. (5) It is likely that different crops and varying situations will necessitate the use of PGPF that are either rhizospheric or endophytic. It will be necessary to delineate those situations where either rhizospheric or endophytic PGPF strains are most appropriate so that the most

effective combination of plant and PGPF can always be applied. (6) Given that the growth of more than 90% of crop plants is enhanced by the plants' interaction with mycorrhizae, it is necessary to develop a much better understanding of how PGPF interact in a way that optimally promotes plant growth. (7) As much as possible, this technology should be kept in the public domain so that a few large companies do not end up owning all of the key technology.

While there is still a lot more basic and applied work to be done, application of PGPF is already a success, on a relatively small scale, in several countries. If scientists, and the agencies that fund their work, direct their efforts toward addressing the above-mentioned and related issues, there is every reason to expect that agricultural practice worldwide can become both sustainable and highly efficacious.

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