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Plant protection properties of the Plant Growth-Promoting Fungi (PGPF): Mechanisms and potentiality

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Abstract

For the past few decades, arbuscular mycorrhizal fungi have been applied as effective inoculants to enhance plant growth and productivity. The rhizosphere-inhabiting microorganisms which result in improvement of growth and protection of plant can be collectively defined as plant growth promoting microorganisms (PGPM). Plant growth-promoting rhizobacteria **(**PGPR**)** improve plant growth and supports the plant to endure abiotic and biotic stresses. Plant growth-promoting fungi (PGPF) are known to colonize the region of the root of plants, and they enhance the plant nutrient uptake. The utilization of proper preparations of beneficial microorganisms is an inevitable demand to diminish the inputs of inorganic fertilizers, herbicides, and pesticides; moreover, it's one of the most promising trends for sustainable agriculture and maintaining agricultural productivity. The production of strong inhibitory compounds by PGPF affects many plant pathogens. Fungi are omnipresent on organic compounds. The majority is saprobes and decomposes dead organic matter. Many excellent reviews about endophytic fungi in woody plants have already been published. However, only limited studies focused on the rhizosphere free-living fungi efficacy for plant growth promotion. This review will consider the mode of actions of these fungi to better understand the promising contributions of PGPF in enhancing plant growth and protection.

Keywords – Biocontrol – Environmental impacts – Fungi – Rhizosphere

Introduction

The broad use of chemical application *viz.* pesticides and chemical fertilizers adversely affect the environment as well as the soil microflora (Cekic et al. 2012, Raghukumar 2008). Current soil management approaches are mainly dependent on inorganic chemical fertilizers, which caused a severe threat to human health and the environment. Due to potential hazards regarding human safety and environmental impacts, there are public worries regarding the use of agrochemicals (Raghukumar 2008). Furthermore, the application of chemical substances over a long period may cause in plant pathogenic fungi emerging resistance. The innovative view of farming production cheers the growing demand for biological based organic fertilizers exclusive of an alternative to agrochemicals. The collective genomes of rhizomicrobial community enveloping plant roots are larger compared to those of plants and are referred as the microbiome, whose interactions determine crop quality in the natural agriculture ecosystem by providing several services to plant viz., organic matter decomposition, nutrient acquisition, water absorption, nutrient recycling, weed control, and

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biocontrol (Rocha et al. 2019). Therefore, beneficial microorganisms' application could be a new strategy to improve plant health and productivity. In recent years, the biological method is most wildly used to alleviate the soil stresses including salinity and it has received greater attention (Khan et al. 2012). Over the past 30 years, microbiome has been identified, characterized, and tested for their utilization as biocontrol agents against plant diseases caused by soil-borne phytopathogens. Because of their rich diversity, the complexity of interactions and numerous metabolic pathways, microbes are an amazing resource for biological activity (Raghukumar 2008). The use of microbes as biocontrol agents to suppress plant diseases is a potentially functional alternative method (Köhl et al. 2019). Moreover, many microbial including fungal genera inoculants are commonly known as biofertilizers, which can enhance the nutrients uptake of minerals, such as, phosphorus, iron, and potassium (Begum et al. 2019). Biofertilizers keep the soil content rich in all categories of macro- and micro-nutrients via phosphate and potassium solubilization or mineralization, the release of plant growth regulating substances, biosynthesis of antibiotics and biological degradation of organic substances in the soil (Cycon et al. 2019, Alori et al. 2017). The following review illustrates and summarizes the activities of rhizosphere free-living fungi and aims to provide insights into the potential application of PGPF inoculants in terms of improving crops.

Plant Growth-Promoting Fungi (PGPF)

Plant roots facilitate the growth and activity of a group of microbiomes that exhibit clear effects on plant growth and protection. These microbiomes contain a variety of bacteria, fungi, actinomycetes, and other eukaryotic microorganisms that can be cultured under controlled conditions. Plant growth-promoting rhizobacteria referred collectively to those bacteria residing in the rhizosphere and associating in the enhancement of plant growth and yield of crops. The rhizosphere-inhabiting microorganisms can mediate plant growth by different direct and indirect mechanisms (Glick 2012). Similar to plant growth-promoting PGPRs, some rhizosphere fungi improve plant growth following root colonization and are functionally named 'plant-growth-promoting-fungi' (PGPF) (Khan et al. 2011). *Penicillium*, *Trichoderma*, *Fusarium*, and *Phoma* are the most important PGPF. Many PGPF species have induced systemic resistance against numerous pathogens in the cucumber (Romera et al. 2019). PGPF are soil-dwelling, non-pathogenic saprophytes, and are reportedly beneficial to many crop plants, not only by promoting plant growth but also by serving in disease protection (Begum et al. 2019, Liu & Zhang 2015). For example, Ismail et al. (2018) mentioned that the plant growth-promoting fungus *Penicillium* sp., and its cell-free filtrate enhanced the defense system of *Arabidopsis thalina* against the bacterial bit pathogen. The growth *T. harzianum* has for quite some time been introduced as a biological control agent to retrain an extensive variety of pathogens furthermore, it has been effective in improving plant growth and yield. These increases were typically associated with a reduction in plant disease. In addition to biocontrol advantages, *T. harzianum* exhibits plant growth promotion traits that enhance plant growth. *T. harzianum* applications in plant production have led to reductions in chemical fungicide application, growth regulators, and human labor, with overall decreased production costs, and minimal environmental impacts (Mohammadi et al. 2011). In efforts to make solubilized phosphate and micronutrients accessible to plants, *T. harzianum* was investigated (Hussein & Joo 2015). Also, the non-pathogenic *Fusarium* species are detected to possess effective plant growth-promotion activity (El-Maraghy et al. 2020a). Modes of action include competition and host defenses induction. Many strains of the non-pathogenic *Fusarium oxysporum* were reported to control Fusarium wilt in different crops (El-Maraghy et al. 2020a). *Phoma* sp. and *P. simplicissimum* are plant growth-promoting fungi, which effectively induced cucumber systemic resistance against *Colletotrichum orbiculare*, which causes anthracnose (Muslim et al. 2019). *Piriformospora indica* (Hymenomycetes: Basidiomycota) was cultivated under controlled conditions, and results showed the species was an endophyte, and plant growth-promoting fungus (Begum et al. 2019). Chandanie et al. (2006) estimated the performance of cucumbers' systemic resistance against anthracnose symptoms by the plant growth-promoting fungi *Phoma* sp., *P. simplicissimum*, and *Glomus mosseae*. Frac et al. (2018) exhibited that sugars or sugar alcohols may constitute main signals to soil fungi and determines fungal diversity in natural rhizosphere environments. The sugar alcohol mannitol initiated the growth of rhizosphere fungi. Consequently, PGPF can exhibit more benefits in terms of modes of actions against numerous pathogens, and other factors e.g. nutrients unavailability and stress conditions over spatial agriculture landscape.

PGPF Mode of actions

Biological control may due to direct or indirect interactions among the beneficial rhizosphere microorganisms and the pathogens (Berg et al. 2013). Direct interaction may include physical contact and synthesis of toxic compounds, hydrolytic enzymes or antibiotics as well as antagonism. An indirect interaction may cause induced resistance in the plant, also antagonists use the organic amendments in the soil to improve their activity against the pathogens (Mendes et al. 2013). The different mode of actions that PGPF conduct widely in the rhizosphere and improve plant growth can be summarized as 1) Siderophores biosynthesis. 2) Providing plant by phytohormones such as 3-indole acetic acid, gibberellic acids, and cytokinins. 3) Increasing the bioavailability of insoluble nutrients due to mobilization. 4) Mitigation of the stress effect on plant and elevate the plant tolerance against stress conditions e.g. drought, salinity, and temperature, and secretion of 1-aminocyclopropane-1-caroxylate deaminase (ACCD) that depress the ethylene level in the plant body. 5) Production of antagonistic compounds like hydrogen cyanide, and antibiotics that protect the plant against pathogens and diseases (Fig. 1). The most common mechanisms used by the microbial biocontrol agent are competition and production of metabolites. These metabolites may include antibiotics, siderophores, HCN, and cell wall-degrading enzymes (Bhardwaj et al. 2014). Siderophores biosynthesis by microorganisms is an important feature in the suppression of plant pathogens. Furthermore, siderophores act as indicators of ISR under iron scarcity conditions. Moreover, it has been reported that auxins strongly inhibit mycelium growth, sporulation and spore germination of *F. culmorum in vitro* (Pusztahelyi et al. 2015). Parasitism is another category, which may involve the production of hydrolytic enzymes such as chitinase, protease, and cellulases, that degrade pathogen cell wall, inhibit the pathogen by discharging antimicrobial compounds and trigger induced systemic resistance (ISR) in host plants (Balakireva & Zamyatnin 2018). There is an early report indicating that a volatile acetaldehyde compound emitted by *Trichoderma* sp. had an inhibitory effect on phytopathogenic fungi (Dennis & Webster 1971). One of the detected mechanisms of *T. harzianum* to control the growth of *Rhizoctonia solani* was to produce a volatile pentenyl pyrano and pentane-pyran antibiotics (Cordovez et al. 2017). Hence, PGPF co-inoculation with an understanding of the microorganisms’ functions is of great interest to increase uniformity in the field.

Siderophore production

Siderophores are low molecular weight protein (400-10,000 Da) produced by microorganisms under iron starved conditions (Silva et al. 2020). Some rhizomicrobes developed systems for iron uptake; these systems involved an iron-binding legend (siderophore). Siderophores (*sid* = iron, *phores* = bearer) virtually ferric specific proteins produced by microbes as scavenging agents in case of iron scarcity. This protein uptake and transport iron into the cell (Sherman et al. 2018). Both siderophores and antibiotics have been involved in the biocontrol of various soil-borne plant pathogens by PGPR (Köhl et al. 2019). Research in the field of siderophores began about five decades ago, which was mostly related to virulence factors in microorganisms pathogenic to plants as well as animals (Hussein & Joo 2012). Siderophores are produced from a wide range of micro-organisms including bacteria and fungi. Siderophore is considered one of the major approaches of PGPF that is implicated in the biological control of plant diseases (Li et al. 2016). Since iron is essential for a variety of functions including reduction of oxygen for the synthesis of ATP reduction of ribotide precursors of DNA, for the formation of heme, and other essential purposes. A level of at least one micromolar iron is needed for optimum growth (Robinson 2019). The host could decrease the access of the other organism to iron if host cells could efficiently acquire and sequester iron chelated to its siderophores. Once internalized by these cells. Such iron would no longer be accessible to other organisms. Therefore, such inaccessibility of iron would lead to inhibition of growth. The main siderophores of fluorescent Pseudomonas species are pyoverdines (Meyer et al. 1987). These fluorescent pyoverdines demonstrated an adverse effect in vivo against plants root-associated pathogens (Ghysels et al. 2004). Consequently, it is a vital constribution in the biocontrol approaches by applying the pseudomonads (Hussein & Joo 2014). The pyoverdines are fluorescent due to the presence chromophore moiety in chemical structure (Ahmed & Holmstrom 2014). It has been detected that linking of antibiotics with siderophores enhances the penetration and hence improves the antimicrobial efficacy of the antibiotics. One siderophore type can deliver several drugs to the target microbial pathogens (Hussein & Joo 2019). Almost all fungi produce siderophores (Pereg & McMillan 2015), except some species (e.g., *Saccharomyces*); nevertheless, *Saccharomyces cerevisiae* can use the exotic siderophores (Aznar & Dellagi 2015). Fungi produce mainly the hydroxamate category of siderophores. However, several reports indicated that the siderophores release can be served as a chemo-taxonomic marker in the identification of different species of microorganisms. For example, *Mycobacterium* spp. and *Burkholderia* spp. are characterized to excrete mycobactin and ornibactins siderophores, respectively (Hussein & Joo 2019). Ferrichrome was isolated for first time in 1952, and was detected to be operated by the fungi genera *Aspergillus*, *Penicillium*, and *Ustilago* (Tedstone et al. 2016). The improvement and commercialization of siderophore-producing fungi as biocontrol agents depend on understanding the mechanisms involved in these antagonistic processes among PGPF, pathogens and their plant host.

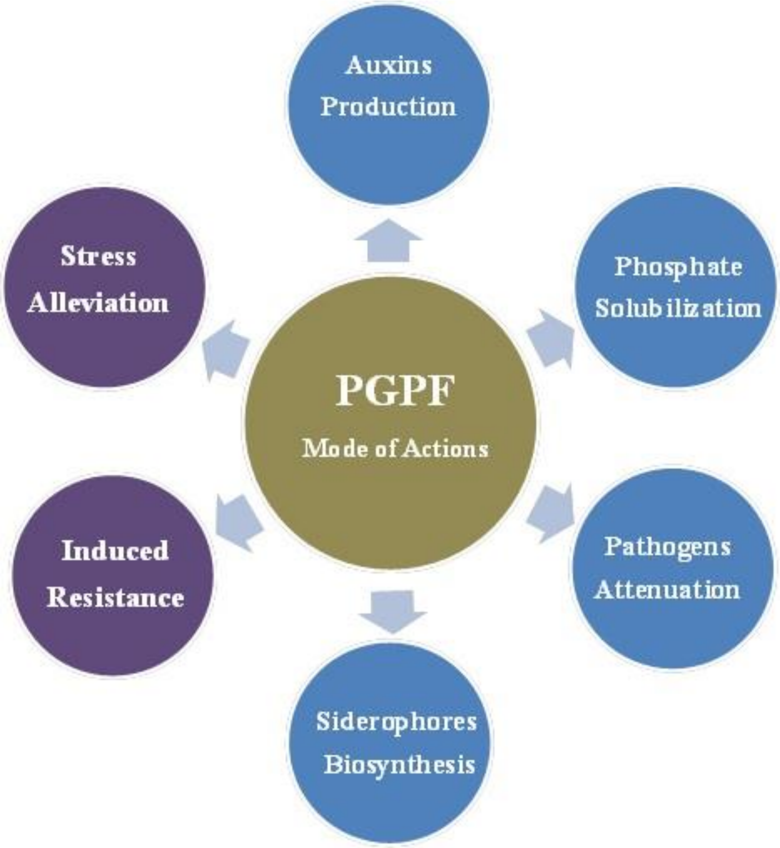

Fig. 1 – Plant growth promoting microorganisms (PGPF) can enhance plant growth directly via synthesis of phytohormones, siderophores biosynthesis, antagonistic compounds production as well as the solubilization of inorganic phosphate and mineralization of organic phosphate, which makes phosphorous available to the plants or indirectly via repression of phytopathogens, stimulation defence response, and attenuation of abiotic stresses on plant. The figure was modified from Deka et al. (2015).

HCN production by PGPF

Another effective mechanism in suppressing the growth of phytopathogen is hydrocyanic acid production. The volatile compound of HCN can extremely degrade the cell wall of the fungal pathogen and render its pathogenicity (Hussain et al. 2016). Volatile-mediated interactions between microbes and plants have been gaining more attention in agriculture (Piechulla & Degenhardt 2014). For example, Lee et al. (2015) suggested the volatiles produced by interacting microorganisms as biological control agents for the control of plant pathogens. Furthermore, it is known that fungal volatiles promote the growth of the plant and activate induced resistance against phytopathogens (Lee et al. 2015). However, the impacts of volatile organic compounds released by *Trichoderma* species on plant growth have been recognized only recently. HCN was characterized as a biocontrol agent, due to its attributed toxicity against plant pathogens (Rijavec & Lapanje 2016). Bulgarelli et al. (2015) demonstrated that HCN is beneficial for biological control of diseases suggesting that HCN plays a role in the suppression of peanut disease caused by *M. phaseolina*, charcoal rot disease of sunflower, and all disease of wheat. The presence of trace concentrations of hydrogen cyanide is toxic to mostly all aerobic microorganisms and blocks the cytochrome oxidase pathway. Only, the fungal producer was demonstrated to be resistant (Bashan et al. 2014). Prasad et al. (2017) screened several fungal isolates for growth-promotion and protection of Tomato (*Lycopersicon esculentum* Mill.), they noticed that the highly HCN producers e.g. *Trichoderma viride* and *T. harzianum* were effective as biocontrol agents against *Pythium debaryanum*, *Sclerotium rolfsii*, and *Rhizoctonia solani*. HCN production by PGPF may convey great benefits in the prospective development of biopesticides for the eco-friendly control of plant pathogens and proposes the potential use of the antimicrobial compound from fungi.

Phosphate-solubilization by PGPF

Phosphorus plays a critical role in many biochemical processes (e.g. cell division, photosynthesis, and nutrient transfer). Phosphorus is one of most nutrients commonly limiting the growth and health of the plant. Plants absorb phosphorus with soil solution as in anion form. However, phosphate anions are strongly able to be immobilized through precipitation with different cations such as Al^{3+}, Ca^{2+}, Fe^{3+}, and Mg^{2+}, depending on the physicochemical properties of the soil. The soluble phosphate concentration in soil is usually very limited approximately 1 mg kg^{-1} or less (Goldstein 1994). In these insoluble forms, phosphorus can't be available to plants. Subsequently, the amount of available phosphorus to plants is usually a small proportion. The availability of phosphorus depends largely on microbial activity (Kumar et al. 2012). The phosphorus cycle in nature is greatly influenced by the activity of various microorganisms that affect phosphorus mobilization in soil. The precipitated inorganic phosphate is solubilized by the action of minerals and organic acids produced by soil microorganisms (Alori et al. 2017). Several works of literature have reported the ability of different microbial species to solubilize the inorganic phosphate compounds e.g. tri-calcium phosphate, zinc phosphate, and rock phosphate. The bioavailability of phosphate is highly dependent on soil type and pH. The solubilization of soil inorganic phosphate has commonly be attributed to fungi, *Aspergillus* and *Penicillium*, among others, which solubilize insoluble phosphate through the excretion of acids (Teodosieva & Bojinova 2016). Phosphate is an essential element for early growth and a better yield of crops. The phosphate-solubilizing fungi are strongly suggested for the utilization of unavailable native phosphate by bringing about changes in soil producing chelating agents and organic acids (Kumar et al. 2012). In acidic soils, even when added in sufficient quantities as fertilizer, phosphorus precipitates with iron or aluminum cations, whereas in alkaline soil phosphorus precipitates as calcium phosphates (Penn & Camberato 2019). The microbial capacity to release metabolites particularly organic acids indicates phosphorus-solubilizing ability (Alori et al. 2017). *P. italicum* and *P. radicum* are also phosphate-solubilizing taxa (El-Azouni 2008). Some species of *Aspergillus* have been described to be effective in the mobilization of inorganic phosphates like *A. niger* and *A. terreus* (Pinto et al. 2018). Therefore, phosphate solubilizing fungi could play a great potential role in using a cheaper source of phosphate (e.g. rock phosphate instead of superphosphate).

Phytohormones production by PGPF

Fungi have been a substantial source of a wide range of bioactive secondary metabolites (Singh & Joshi 2011, Abd El-Fattah et al. 2013). The rhizosphere fungi releasing plant growth phytohormones "auxins", in the present case, 3-indol acetic-acid (IAA) and *gibberellic acid*s (GAs) can enhance plant growth (Khan et al. 2012). Several reports also confirm that fungal species produce phytohormones. For instance, Hassan (2002) reported that *Aspergillus flavus*, *A. niger*, *F. oxysporum*, *P. cyclopium*, and *Rhizopus stolonifer* can biosynthesis GAs, while *F. oxysporum* can produce both IAA and GAs. Similarly, Khan et al. (2012) reported that *P. funiculosum* can produce bioactive GAs and IAA. *Phaeosphaeria* sp. L487 was also found to possess the GAs biosynthesis apparatus and can produce GA1 (Huang et al. 2019). The fungal cell-free culture contained IAA, which is synthesized by plant species and different microbes (Egamberdieva et al. 2017), *P. formosus* LHL10 produced several physiologically inactive and active IAA and GAs, which helped the Dongjin-byeo and Waito-C rice plants to grow healthy and significantly mitigated the negative effects of salinity stress on cucumber seedlings (Khan et al. 2012). Moreover, Roy Choudhury et al. (2019) suggested that cytokinin, IAA and abscisic acid ABA could be involved in the autoregulation of nodulation; however, jasmonic acid (JA) has an unclear role in the nodulation and the rhizobial symbiosis. Plants treated with rhizosphere fungi are often healthier than those missing such interaction (Hu et al. 2013, Khan et al. 2012), which may be attributed to the PGPF secretion of phytohormones such as IAA (Khan et al. 2012). Predominately, PGPF synthesizes IAA and the impact on plants is closed to that of exogenous IAA.

PGPF and induced resistance

Induced resistance is defined as the trigger of defensive compounds as a result of pathogen or insect attack. Induced resistance may be sorted into two categories, induced systemic resistance (ISR) and the systemic acquired resistance (SAR), depending on which chemical pathways are involved and how the resistance was triggered. ISR has triggered also in response to particular pathogens, drought stress, herbivores, and mechanical injuries. ISR is mediated through the activation of the jasmonate pathway (Cong & Lingyun 2019). SAR (Systemic Acquired Resistance) is regulated by the salicylic acid-dependent signaling pathway, and its activation involves local and systemic increases in endogenously synthesized salicylic acid (SA) leading to the promotion of the pathogenesis-related (PR) proteins (Backer et al. 2019). Plant growth-promoting fungi can elevate a plant's defense mechanism against insects and pathogens by induced resistance or eliciting plant defensive responses (Adesemoye & Kloepper 2009). Induced resistance of plants can be launched, depending on the source, type, and amount of stimuli (Aranega-Bou et al. 2014). *Trichoderma* strains inoculated to the rhizosphere protect host plants against numerous pathogens including bacteria, and fungi, due to the induction of resistance responses similar to the hypersensitive mechanism, SAR, and ISR in plants (Singh et al. 2016, Jyoti et al. 2014). Singh et al. (2016) also reported that peroxidase reactive oxygen species (ROS) activity was triggered by *T. virens* in cotton plants more than in the control. Other fungal species can also induce resistant mechanisms in plants, e.g. *Chaetomium globosum* releases chaetoglobosin C and can stimulate restricted and systemic oxidative reactions in carrots, sweet potatoes, potatoes, tobacco, and tomatoes and this substance can lead to induce plant defense for disease resistance (Hu et al. 2013). Ultimately, it should be mentioned that a lot of studies is important to interpret the interrelations of hosts and microbiome in growth-promotion terms and to comprehend the consistent mechanisms of PGPF-plant resistance relationships.

General characteristics of induced resistance

Induced resistance is a physiological "stage of enhanced defensive capacity" stimulated by specific environmental impetuses, whereby the plant's native defenses are potentiated against successive biotic challenges. This superior state of resistance is very effective against a wide-ranging of pathogens and parasites (Köhl et al. 2019). Moreover, there is another well-known form of induced resistance named as systemic acquired resistance (SAR), which could be distinguished depending on the regulatory pathways and nature of the involved elicitor (El-Maraghy et al. 2020b). SAR can be initiated by exposing the plant to violent, avirulent, and non-pathogenic microbes (Fig. 2). According to the plant and elicitors, a specific duration of time is necessary for the launch of SAR in which accumulation of pathogenesis-associated proteins (glucanase and chitinase), and salicylic acid (SA) occurs. Unlike SAR, ISR does not require the accumulation of salicylic acid or PR proteins, but instead, depending on pathways regulated by ethylene and jasmonate (Yang et al. 2009). A network of consistent signaling pathways regulates induced defense mechanisms of plants against the pathogens. The primary motifs of the network are the plant signal molecules–SA, ethylene, jasmonic acid, and probably nitric oxide.

Salicylic acid (SA) signaling in plant defense

Many studies have demonstrated that SA plays a critical role in the plant defense against pathogens. SA level increases in both infected and intact leaves in response to pathogen penetration, the exogenous application of SA can activate the PR genes and launch SAR (Backer et al. 2019). Despite the presence of active defense systems, many bacterial pathogens can suppress and evade the host defense or temper the metabolism of the host cell to obtain nutrients for their establishment and colonization through virulence strategies. For instance, the Gram-negative bacteria *P. syringae* secrete pathogenesis proteins, called effectors, via a type III secretion system directly into the host cell to promote pathogenicity (Cong & Lingyun 2019). Previous studies have revealed that primary plant auxin IAA levels, increased in plants infected by *P. syringae* pv. DC3000. Moreover, the type III proteins AvrRpt2 modulate host IAA levels to promote pathogenicity and disease development in *Arabidopsis* (Chen et al. 2013). The latest microarray analysis has demonstrated that infection with *P. syringae* pv. activates genes involved in IAA biosynthesis and represses auxin transporter genes, suggesting that *P. syringae* pv. impacts auxin signaling probably by activating IAA production, changing the IAA movement, and depressing the auxin pathway (Eduardo et al. 2019). Nevertheless, little is known about genes involved in auxin signaling in response to the infection and changing of the auxin signaling responsible for enhanced pathogenicity. Auxin rapidly induces many genes called early response genes. Aux/ IAAs, SAURs, and GH3s are the three major classes characterized as early auxin response genes (Leyser 2018). Numerous studies have been published investigating the fungi-plant defense interactions, most of these studies focused on the potential of some rhizofungi to enhance plant-defense by increasing SA and suppress plant diseases.

Stress mitigation activity of PGPF

Plants are sessile and cannot escape stressful conditions originating from the physical environment (abiotic stress) and interactions with insects and microorganisms such as fungi and bacteria (biotic stress). Salinity is widespread abiotic stress that restricts yield on almost one-third of the irrigated land on earth (Hussein & Joo 2018). Shrivastava & Kumar (2015) estimated that approximately 50% of the arable land will be affected by salinity stress by the year 2050. Being a crucial environmental factor, salinity is known to affect plant metabolism and result in the rising of organic solutes that come to the aid of turgor maintenance. The plant's defense mechanism against such stressful conditions is comprised of a cascade of signals either primary such as changes in ionic/osmotic levels, stomatal closer or secondary e.g. phytohormones and secondary metabolites responses. Salinity can significantly restrict the growth of legumes especially soybean plants. Sharifi et al. (2007) demonstrated that soybean grown in saline conditions exposed symptoms of leaf chlorosis and biomass reduction due to chloride-induced toxicity.

Under salinity stress, auxins like ABA can protect host plants by closing the stomata to minimize loss of water and then mitigates stress damage (Dahal et al. 2019). Begum et al. (2019) observed the same findings after an association of *G. intraradices* with lettuce seedlings. Some physiological evidence advocates those plants with the fungal disease often have a special advantage against abiotic stress and biotic over their non-infected counterparts (Rodriguez et al. 2006). Many previous reports are showing the ameliorative properties of exogenous application of

IAA and GAs on cucumber plant-growth under abiotic stress (Dahal et al. 2019, Khan et al. 2011), however, few data are available on the harmony of phytohormones producing fungi in association with plant endogenous hormones under abiotic stress conditions. Hamayun et al. (2017) noticed that GA-deficient plants are more vulnerable to stress than those with sufficient levels of this hormone. Vesicular arbuscular mycorrhizae treatment to the *Sapindus emarginatus* could be able to increase the tolerance of the seedlings to pH 8.9 and high slat concentration. As biotic and abiotic stresses commonly result in the production of ROS (reactive oxygen species), rapid and strong activation and scavenging of ROS is potentially a prime mechanism in maintaining this balance (Nguyen et al. 2017). Khan et al. (2012) showed that *P. formosus* treatment significantly alleviated salinity induced stress and improved plant growth. Ismail et al. (2018) reported that IAA producing fungi can improve rice plant growth under drought, salinity, and temperature stress. Hamayun et al. (2017) also reported that GAs secreting fungi promote soybean plant growth. Several other studies also detected similar findings narrating that fungi application can enhance plant growth under stress conditions (Khan et al. 2012, 2011, Stumpe et al. 2015). Khan et al. (2012) suggested that the fungal treated plants not only overcome stress but also can fetch higher water contents from a source usually inaccessible to control plants. Khan et al. (2012) showed that plants inoculated with *P. formosus* had lesser electrolytic leakage than control ones under salinity stress. However, it's well-recognized that the ACC deaminase- producing microbes may improve plant growth by declining the detrimental effects of stress ethylene and the ACCD-expressing fungi could mitigate the different stresses that affect plant crops and development.

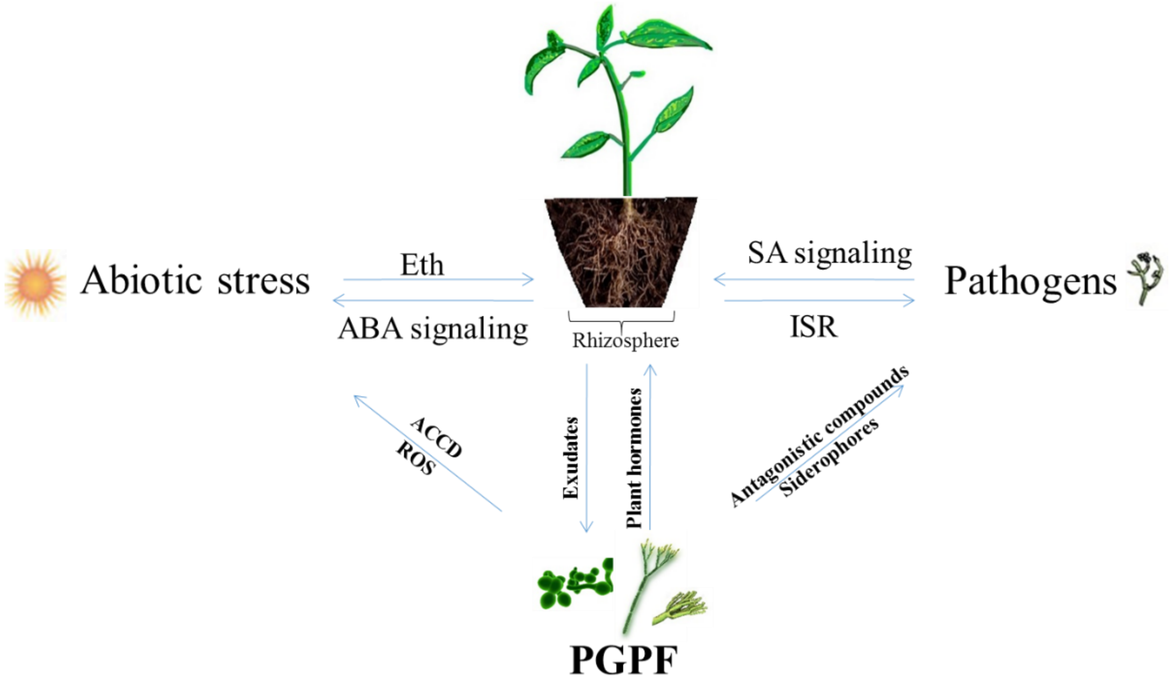

Fig. 2 – Schematic representation of the complex interactions mediated by plant root-exudates that take place between plant roots and other microbiomes in the rhizosphere. The diagram illustrates also, the signaling pathway in plants responsible for the disease/stress resistance in plants. SAR may be triggered by plant pathogens and some insects, such as aphids attack, and is mediated through the activation of the salicylic acid pathway. Rhizosphere microbes can minimize the different types of abiotic and biotic stresses for enhancement of plant-growth and development. Image produced based on concepts adopted from (Alori & Babalola 2018, Glick 2012, Adesemoye & Kloepper 2009).

Antagonism effect by PGPF

Competition is another means that the microorganisms use to survive, and scientists exploit for plant growth promotion. The rhizosphere is a main concern where competition for nutrients and space occurs (Mendes et al. 2013). Competition can be categorized into saprobic competition for nutrients in the rhizosphere and soil, and competition for infection sites in and on the root (Fravel 2005). For example, *T. harzianum* T-35 suppression of *Fusarium* species on different crops occurs via antagonism and competition for rhizosphere colonization and nutrients (Mendes et al. 2013). The diverse mechanisms of fungal biofertilizers are impacted by temperature, pH, soil type, the moisture of the soil environment, and the company of other microorganisms (Ahmad et al. 2018). Many biological control agents produce different types of antibiotics or non-specific metabolites that inhibit or destroy the pathogenic microbe in a process named as antibiosis. These antibiotics are synergistic when pooled with different cell wall-degrading enzymes thus forming a strong inhibitory effect against many plant pathogens (Vinale et al. 2008). *Penicillium, Gliocladium,* and *Trichoderma* species are well known to produce a vast range of anti-biotics and suppress disease by dissimilar modes of action (Singh et al. 2016). Trichotoxin A50 produced by *T. harzianum* can inhibit the mycelial development and sporangia formation of *Phytophthora palmivora* (Wang et al. 2019). *Ampelomyces quisqualis* is the anamorph of the ascomycetous mycoparasite that reduces the development and kills powdery mildews (Liyanage et al. 2018). Biswas et al. (2012) found that *C. cochliodes* and *C. globosum* occurring on oat seeds provided some protection against *Helminthosporium victoriae.*

Many species of *Chaetomium* e.g. *C. globosum*, *C. cochlioides*, and *C. cupreum* can also be aggressive against numerous soil microorganisms (Zhai et al. 2018). Several fungal taxa have been detected to be antagonist against phytopathogens and have been successfully packaged as biological control products or mycofungicides e.g. *Aspergillus niger*, *Ampelomyces quisqualis*, *Candida oleophila*, *Ch. globosum*, *Ch. cupreum Cryptococcus albidus*, *Coniohyrium minitans*, *G. catenulatum*, *G. virens*, *F. oxysporum*, *Pythium oligandrum*, *Rhodotorula glutinis*, *Phlebiosis gigantean*, *T. harzianum*, *T. polysporum*, *T. viride*, (Mendes et al. 2013, Ezziyyani et al. 2007). Many species of *Chaetomium* possess the potentiality to be biocontrol agents suppress the growth of fungi and bacteria through competition for nutrients and substrate (Dahal et al. 2019). *Chaetomium* spore suspension has been assessed for its antagonistic effect on the plant pathogenic fungi *F. oxysporum*, *Botrytis cinerea*, *Didymella applanata*, and *Rhizoctonia solani*. Additionally, a new strain of *C. cupreum* RY202 has initially proved to be antagonistic against the pathogenic *Rigidoporus microporus* responsible for white root disease in rubber trees (Ahmad et al. 2018). Chaetoviridins A inhibit the fungal growth of different plant mycopathogens such as *Pyricularia oryzae*, *Pythium ultimum*, and *Magnaporthe grisea* (Park et al. 2017). *Ch. cupream* produces rotiorino which can prevent the growth of pathogens (Zhai et al. 2018). Mycoparasitism is another strategy to reduce plant disease by biological control agents (Köhl et al. 2019). Moreover, the strong rhizosphere iron competition and the high iron affinity of PGPF-produced siderophore should affect the iron nutrition of other soil organisms, such as plant pathogens (Ferraz et al. 2019). Indeed, many studies have been published examining the heavy metals-siderophore interactions, most of these studies focused on the potential of some rhizomicrobes to suppress soil-borne diseases and consequently enhance plant growth.

Applicability of PGPF inoculants

The communities of miscellaneous rhizosphere-dwelling fungi incorporate a vast diversity and contain species that may prove beneficial in biofertilizer applications. The communities of other various fungi living in the rhizosphere may establish a relationship with plants similar to those reported for mycorrhizal symbioses. These root-associated fungi are diverse and present a broad spectrum of species that show beneficial in biofertilizer applications. These fungi can elevate plant nutrient uptake (Begum et al. 2019) or allow the plant to reach otherwise unavailable nutrient sources (Courty et al. 2015). Various strains originating from plant rhizosphere can enhance plant growth and crop performance, not only in a controlled laboratory or greenhouse studies but also under field conditions, (Hussein & Joo 2018). Several species of bacteria and fungi can provide a wide range of extracellular enzymes, which help improve crop yields and minimize of inorganic fertilizers. The multi-inoculations regime in the field trials is highly needed. These inocula integration of different species possessing variable benefits to the crop plants may be of greatest value. These treatments may reduce the chemical application of pesticides to crop plants. Multifunctional biofertilizers is another strategy to reduce the chemical fertilizers, diseases and to increase soil fertility in tea (Nepolean et al. 2012). Several applications have been successfully done using microbial species as biocontrol agents along with chemical pesticides for disease control and yield improvement (Table 1).

The association of different microbial properties into combined biofertilizers with several potential yield-promoting activities is desirable. Also, the application of microbial fertilizers at field scale convenient to agricultural practices is likely to be achieved. Coming on approaches and costs for reconciliation research facilities and the biotechnology industry seems like the rational first step. These properly coordinated approaches will allow a wheel start for commercial and economically viable production of biofertilizers for direct marketing. Rhizosphere microbes have been isolated from the rhizosphere soils and roots of different plant species, and some of them are available as a commercial product for agricultural uses (Saharan & Nehra 2011). Rhizobial inoculation is an old practice in agriculture that has been carried out since one century ago in the United Kingdom and the United States (Bashan et al. 2014, Rocha et al. 2019). In several countries, *B. subtilis* has already formulated in commercial products due to its great potential for use in agriculture (Dey et al. 2014). *P. bilaiae* has been prepared as a commercial formulation named Jumpstart® and was produced to the market as a wettable powder (Burton & Knight 2005). Such inoculation is important particularly when the natural occurrence of rhizobial populations is either poor or known to be very low (Heijden et al. 2016). In this case, inoculation with proper rhizobial fungi is likely to prove highly advantageous. Various forms of fungal inoculum can be used for inoculating tree seedlings, but the most recommended form is vegetative mycelium (Tikhonovich & Provorov 2011). Vegetative mycelium can be produced by using either solid substrate cultivation or submerged cultivation. Sorghum grain and sphagnum-vermiculite carriers have been used to produce inoculum through solid substrate cultivation (Sermons & Balint-Kurti 2018). Inocula produced through these processes are not physiologically consistent and are difficult to maintain (Sermons & Balint-Kurti 2018). Furthermore, the substrate that remains at the end of the process is difficult to remove and invites contamination during application and finally leads to the loss of inoculum (Sermons & Balint-Kurti 2018). Most of these issues can be overcome by producing physiologically consistent mycelium through submerged cultivation (Bonito et al. 2014, Toghueo & Boyom 2019).

Sturdy inoculum then can be produced by physical entrapment of this mycelium in alginate gel (Malusa et al. 2012, Costa et al. 2019). *Gliocladium* species are soil dwellers saprobes and some species have been described to be parasites of several plant pathogens (Mendes et al. 2013). *G. virens* produce anti-biotic compounds such as gliotoxin which have antifungal, antibacterial, antiviral and antitumor activities. *Coniothyrium minitans* is the anamorphic coelomycete (Gong et al. 2007) that has been detected to be mycoparasite of *Sclerotinia* species. The main biological control activity of *C. minitans* is parasitism which uses *S. sclerotiorum* sclerotia as a food source for survival (Whipps et al. 2008). The effectiveness of *C. minitans* can be enhanced by combinations with *Trichoderma* spp. (Park et al. 2017). *Trichoderma* species are ubiquitous saprobes in root and soil ecosystems (Vinale et al. 2008). *T. harzianum* is described to be most broadly used as an active biological control agent (Abd El-Fattah et al. 2013). *Trichoderma* species have been used as biocontrol agents against a wide spectrum of plant pathogenic fungi e.g. *Botrytis cinerea*, *Rhizoctonia* spp., *Pythium* spp., and *Fusarium* spp. (Kottb et al. 2015). The main biocontrol mechanism in *Trichoderma* is mycoparasitism, *Trichoderma* species have been effectively used as biofungicides because they are rapid-growing, have the high propagative capacity, inhibit a broad range of fungal diseases, have an array of control mechanisms, are distinctive competitors in the rhizosphere, can modify the rhizosphere, are resistant or tolerant to soil fungicides, can survive under stress conditions, are efficient in consuming soil nutrients, have strong antagonism against phytopathogenic fungi, and promote plant growth (Vinale et al. 2008).

The non-pathogenic species of *Fusarium* are known to have effective biocontrol activity (Kottb et al. 2015). Mechanisms of action include competition and induction of host defenses (Toghueo et al. 2018). The use of non-pathogenic strains of *F. oxysporum* to control wilt disease has been detected for many crops (Ahmad et al. 2018). *Pythium oligandrum* has shown the ability to control soil-borne phytopathogens either in the laboratory or in the field. *P. oligandrum* oospores have been used as seed treatments that reduce damping-off disease in sugarbeet caused by *P. ultimum* (Rocha et al. 2019). This fungus has indirect influences by controlling mycopathogens in the rhizosphere or/and direct effects (mode of action) by inducing plant resistance. It also supports plants to respond more speedily and efficiently to microbial infections and increase phosphorus absorption (Campos et al. 2018). Also, *P. nunn* is an antagonistic fungus or mycoparasite of pathogens such as *Pythium ultimum*, *P. aphanidermatum P. vexans*, *Rhizoctonia solani*, *Phytophthora parasitica*, and *P. cinnamomi*. Moreover, *Aspergillus* and *Penicillium* species were effective against the white-rot disease caused by basidiomycetes (Kowalczyk et al. 2019). The fungal antagonists *Ulocladium atrum* and *Aureobasidium pullulans* have also been reported to control the onion neck rot caused by *Botrytis aclada* (Panebianco 2012). The new PGPR candidates are expected to assist in diminishing the use of biocides and chemical fertilizers. However, the risk assessment should be conducted before the release of any transgenics into the environment.

Table 1 Example of PGPF strains suggested being able to promote growth, mitigate the abiotic stress, and suppress phytopathogens in plant

PGPF	Activity/Mode of action	Plant/Crop	Effect	Reference
Absidia spp.	Catechol and hydroxymate type of siderophores, IAA production	In *Vitro*	Phosphate solubilization and plant growth promotion activity	Nenwani et al. (2010)
AMFs *Glomus manihotis* and *Entrophospora colombiana*	Phosphate solubilization activity	*Sorghum bicolor*	Synergistic effect with rhizobacteria and have a potential to be developed as biofertilizers in acid soil.	Masood & Bano (2016)
Arbuscular mycorrhizal (AM) fungi	Increased phosphate nutrition in AM roots	*Bouteloua gracilis*	Increases the cytokinins (CK) levels in the plant and promote shoot growth	Hause et al. (2007)
Arbuscular mycorrhizal fungus *Glomus mosseae*	strong increase Abscisic acid (ABA) and Jasmonic acid (JA) levels	Soybean (*Glycine max* L.) cv. Bragg	Suppress subsequent root colonization in other parts of the root system	Meixner et al. (2005).
Arthrobotrys oligospora	Production of organic acids		Has the ability to solubilize the phosphate rocks	Duponnois et al. (2006)
Aspergillus fumigatus and *Aspergillus niger*	Increases in phosphatase activity	*Cajanus cajan* (L.) Mill sp.	Improved the growth of pigeon pea	Ogbo (2010).
Aspergillus niger	Enhance phosphate solubilization		Increases in the levels of soluble phosphate and titratable acidity, as well as increased acid phosphatase activity	Braz & Nahas (2012)

Table 1 Continued.

PGPF	Activity/Mode of action	Plant/Crop	Effect	Reference
Aspergillus niger and *Penicillium notatum*	Mechanisms such as production of phytohormones, vitamins or amino acid can be involved in the P-solubilizing fungi effect	Ground nut (*Arachis hypogaea*)	Increased the bioavailability of soil phosphorus for plants.significantly increased dry matter and yield of groundnut	Malviya et al. (2011)
Azospirillum sp.	Siderophores production	Rice	Change the root morphology	Gupta & Sahu (2017)
Azospirillum sp.	Producing plant growth regulating substances	Rice	Increases the number of lateral roots and enhances root hairs formation to provide more root surface area to absorb sufficient nutrients	Moghaddam et al. (2012)
Botrytis aclada, Penicillium chrysogenum, Aspergillus niger, and *Cladosporium* sp.	Siderophores production	*Pinus koraiensis* shrubs	Rhizospheric fungi are stronger siderophores producers rather than fungi isolated from heavy metal contaminated area	Hussein & Joo (2012)
Cladosporium sphaerospermum	Gibberellin production	Cucumber (*Cucumis sativus* L.)	Plant growth promotion	Hamayun et al. (2010)
Cladosporium sphaerospermum DK-1-1	Gibberellin production was higher than the wild type *Gibberella fujikuroi*	*Glycine max* (L.) waito-c rice and soybean	Gibberellin production and plant growth-promoting ability	Hamayun et al. (2009)
Curvularia sp.	The fungal endophyte produces cell wall melanin that may dissipate heat along the hyphae and/or complex with oxygen radicals generated during heat stress	*Dichanthelium lanuginosum*	Act as a “biological trigger” allowing symbiotic plants to activate stress response systems	Redman et al. (2002)
Fusarium oxysporum strain 162 (Fo162)	Metabolic organic compounds	Tomato (*Solanum lycopersicum*)	Enhanced plant growth	Menjivar et al. (2012)
Gibberella fujikuroi	Produced active gibberellins (GAs) as secondary metabolite	*Atriplex gemelinii*	Culture filtrate treatment increased shoot lengths of plant seedlings after 15 days	Khan et al. (2008)
Glomus fasciculatus	Gibberellins (GA) production	*Hordeum vulgare* seeds	Significantly increased GA activity in leaves	Hause et al. (2007)
Glomus intraradices	An early increase in synthesis of indole-3-butyric acid (IBA)	*Soybean (Glycine max* L.) cv. Bragg	Increase of free IBA levels	Meixner et al. (2005)

Table 1 Continued.

PGPF	Activity/Mode of action	Plant/Crop	Effect	Reference
Glomus intraradices	Improve nutrient uptake by plant root	Tomato (*S. lycopersicum*)	Inoculation with the mixture (Bacillus amyloliquefaciens and Bacillus pumilus) at 70% fertility consistently produced the same yield as the full	Adesemoye & Kloepper (2009)
Glomus intraradices	Increased jasmonic acid (JA)	*Medicago truncatula* L.	Improve plant antimicrobial activity	Stumpe et al. (2015)
Glomus mosseae	Increased phenolics	*S. tuberosum roots*	Ethylene biosynthesis is repressed	Barker & Tagu (2000)
Glomus intraradices and *Glomus mosseae*	Decrease Salicylic acid (SA) production	*Nicotiana tabacum* plants	May be enhance plant defence against pathogens	Hao et al. (2019)
Mucor sp.	Solubilize the phosphate		Shown to increase plant growth by 5–20% after inoculation	Gunes et al. (2009).
Paecilomyces formosus	Analysis of the CF showed presence of GAs gibrellenes and indole acetic acid IAA	Deficient mutant rice waito-C *Oryza sativa* L. cv.	Significantly increased the growth of Waito-C and Dongjin-byeo seedlings as compared to control	Khan et al. (2012)
Paecilomyces formosus		Cucumber (*Cucumis sativus* L.)	Under salinity stress enhanced cucumber shoot length and allied growth characteristics	Khan et al. (2012)
Penicillium and *Aspergillus*	Production of organic acids		The most powerful P solubilizers	Mohammadi & Yousef (2012)
Penicillium citrinum	Gibberellins (GAs) producers	Waito-c rice seedlings and *Atriplex gemelinii* seedling	Considerably promoted shoot lengths	Khan et al. (2008)
Penicillium MH7	Produced all physiologically active gibberellins	Crown Daisy (*Chrysanthemum coronarium*)	Significantly promoted the growth attributes of Crown daisy	Hamayun et al. (2010)
Penicillium sp. Sj-2-2.	Gibberellin production	Waito-c rice (WR) seedling	Provided plant growth promotion (PGP) to WR seedling	You et al. (2012)
*Penicillium*sp and *Trichoderma* sp.	Supplying the nutrients	*Brassica rapa*	Significantly increased shoot dry and fresh weight and leaf length	Hussein & Joo (2011)
Piriformospora indica	Produce antioxidative species and activate the glutathione -ascorbate cycle therefore increase in grain yield	Broad spectrum of plants	Provide strong growth-promoting activity	Waller et al. (2005)

Table 1 Continued.

PGPF	Activity/Mode of action	Plant/Crop	Effect	Reference
Piriformospora indica	Enhance resistance to the phytopathogen *Blumeria graminis*	Barley plants	induce resistance to fungal diseases and tolerance to salt stress in the plant barley	Waller et al. (2005)
Penicillium funiculosum LHL06	Isoflavone biosynthesis.	Soybean plants (*Glycine max* L.)	Significantly ameliorated the adverse effects of salinity induced abiotic stress	Khan et al. (2011)
Penicillium funiculosum LHL06	Secretes gibberellin	*Glycine max* L.	Reprograms *Glycine max* L. growth during copper stress	Khan & Lee (2013)
Penicillium minioluteum LHL09	Increased the daidzein and genistein contents, influencing biosynthesis of the plant's hormones and flavonoids	*Glycine max* L.	Offered Salinity Stress Resistance by Endophytic Fungal strain Promoted growth characteristics (shoot length, shoot fresh and dry biomasses, and chlorophyll content)	Khan & Lee (2013)
Piriformospora indica	Activation of the glutathione–ascorbate cycle and elevation of the antioxidative capacity of the plant	Barley (*Hordeum vulgare* L.)	Induce resistance to fungal diseases and tolerance to salt stress in the plant barley	Waller et al. (2005)
Trichoderma atroviride strain MT-20 and *T. atroviride* strain S-2	Defence to plants against pathogens and herbivores	Tomato	Induce resistance in tomato against the phloem-feeding insect *Trialeurodes vaporariorum*	Menjivar et al. (2012)
Trichoderma harzianum	Produce organic acid such as gluconic, citric and fumaric acids under P-limiting conditions	Chickpea	increase the solubility of poorly soluble phosphorus	Mohammadi et al. (2011)
Yarrowia lipolytica, *Schizosaccharomyces pombe*, and *Pichiafermentans* sp.	Production of organic acids		Has the ability to solubilize the phosphate	Vassilev et al. (2001)

Challenges and perspectives

Although the mutualistic relationship between plant and root-associated fungi has been known for decades, studies on the impacts of free-living fungi on plant performance are still insufficient. Rhizosphere fungi carry out vital biogeochemical cycles which are important to provide plants with nutrition sources and therefore improve crop production. Mycorrhizal fungi may also upgrade soil quality by having a direct influence on soil aggregation (Camenzind et al. 2016). Bernaola et al. (2018) reported that mycorrhizal inoculation practices are often not feasible with industrial-scale agriculture. Besides, the unculturability and obligate biotrophic nature of mycorrhizal fungi have impeded the development of large-scale inoculation programs (Asmelash et al. 2016). To solve the ecological issues resulting from the depletion of plant nutrients and to improve crop yields in the lack of resources for finding costly fertilizers, rhizosphere microscopic organisms that allow more efficient use of nutrients and increase nutrient availability can provide sustainable agriculture practices for present and future. The beneficial effects, growth-promoting or otherwise, are highly variable depending on host plant genotype and selected fungal species or strain and can change with environmental conditions or plant development. The association of different microbial activities into combined biofertilizers comprising numerous potential yield-promoting capabilities is desirable. Moreover, the application of microbial fertilizers at field scale convenient to agricultural practices is likely to be achieved. Coming on approaches and cost for reconciliation research facilities and the biotechnology industry seems like the rational first step. The multi-inoculations regime in the field trials is highly needed. These inocula integration of different species possessing variable benefits to the crop plants may be of greatest value.

The sequencing and amplification of simple genetic markers such as the 16S rDNA of bacteria and the 18S rDNA of fungi have been extensively used (Prates Júnior et al. 2019, Martins et al. 2020). Some housekeeping genes such as 26S/28S rDNA (De Almeida et al. 2019) and the ITS (Mulaw et al. 2013) were sequenced for fungal identifications. Sometimes, a combination of the multilocus sequences is also used to improve the reliability of the identification (Peterson et al. 2005). Recently, the complete genome sequencing using the technology of next generation sequencing (NGS) was also applied to sequence the genome of rhizosphere microbes (Muynarsk et al. 2019). This technology does not require cultivation of rhizomicrobes. This procedure was used to detect the endophytes (Oliveira et al. 2013) and AMF (symbiotic fungi) colonizing roots (Mahdhi et al. 2017), in which some DNA marker regions were extracted from DNA pool, amplified, and sequenced after some separation techniques e.g. the cloning of single sequences or denaturing gradient gel electrophoresis (DGGE).

Currently, the culturable-independent approach is increasingly used. The progress of the NGS technology allows performing metabarcoding detection involving the specific marker genes amplification and sequencing to identify a whole community without separation or cloning steps in an environmental DNA sample (Santos et al. 2020). De Beenhouwer et al. (2015) highlighted the differences of root-associated fungi communities using the NGS strategy during a study of plant crop management. Lamelas et al. (2020) detected the bacterial communities existing in the rhizosphere of *Coffea arabica* plant in order to survey the specific microbial groupings. In another study, the NGS investigation illustrated the influence of the topographical factor on the fungal and bacterial communities associated with the rhizosphere of *C. arabica* cherries (Veloso et al. 2020). James et al. (2016) identified the potential fungi responsible for coffee leaf rust disease using the NGS technique. Ultimately, the NGS methodology involving the random fragmented DNA extract sequencing (shoot -gun sequencing) now allows to detect the microbial diversity and to forecast associated genes function. This strategy was used to carry out a metagenomic investigation and to interpret the functional activities of the microbial communities present in the rhizosphere or a target environment (Zhang et al. 2019). However, it is also important to point out that each approach has its own defects. The culture-independent technique is high cost-effective in detecting the diversity of microorganisms because it allows identifying the uncultivable microbes. This approach can also expect the relative abundance of the species and the potential role of associated genes when the NGS strategy is used. Even though a fault can be introduced during the DNA extraction, the improvement of the DNA extraction protocols and introduction of an artificial community can help to standardize the result (Berg et al. 2020).

Nowadays, Volatile-mediated interactions between plants and microbes have been gaining more interest in agriculture (Piechulla & Degenhardt 2014). For example, Campos et al. (2010) recommended the volatiles produced by roots interacting microorganisms as biocontrol agents for the management of plant pathogens. Furthermore, the bacterial volatiles can promote the growth of crops and activate their induced resistance against phytopathogens (Cortes-Barco et al. 2010). Lee et al. (2015) detected the effects of volatile compounds discharged by *Trichoderma* species on plant growth. Hussein et al. (2020) investigated the fungicidal effects of the volatile organic compounds (VOCs) of *T. koningiopsis* T-403, rosemary essential oil, and two commonly used fungicides (fenhexamid and mancozeb) on mycelial growth of soil-borne ginseng pathogenic fungi. They demonstrated that the *T. koningiopsis* T-403 VOCs inhibited the growth of the soil-borne ginseng pathogenic fungi more effectively than rosemary essential oil and the chemical fungicides (fenhexamid 20 µgml^{-1} and mancozeb 20 µgml^{-1}). Several *Trichoderma* species have the possibility to prevent plant diseases and improve plant growth and productivity by different mechanisms including myco-parasitism (Hwang et al. 2001), antibiosis (Buck 2004) inducing of systemic resistance (Walker et al. 2011), and increasing nutrient uptake (Szabo et al. 2012). However, only a few studies concerned the volatile compounds emitted from *Trichoderma* and their importance in terms of plant protection. Hussein et al. (2020) reported the potentiality of *Trichoderma*-VOCs as a biocontrol resource against pathogenic rhizosphere microorganisms and emphasize the importance of VOCs emissions in regulating plants growth and development. The study may consolidate the application of antifungal natural products from *Trichoderma* in the management and control of the phytopathogenic species causing ginseng root-rot.

Several species of fungi can provide a wide range of extracellular enzymes, which help improve crop yields and minimize of inorganic fertilizers. These properly coordinated approaches will allow a wheel start for economic commercial viable product of biofertilizer inocula for selling directly to primary target farmers. Unfortunately, mycofungicides and fungal biofertilizers are still used on a small scale as compared to chemical compounds because of limited financial support in the research and investigation for developing fungal products. Greater communication is necessary between researchers and industry for PGPF application development.

Conclusions

Currently, effective microorganisms are increasingly used as inoculants for biocontrol, and biofertilization because the reduction of fungicides and fertilizers use in the agricultural field is unremitting demand to improve sustainable agriculture and to maintain the ecosystem. Seed or seedling processing with both bio-fertilizers and biocontrol approaches has been used to maximize the growth of various crops and minimize the negative effects on the environment (El-Maraghy et al. 2020a, Frac et al. 2018). *Trichoderma* spp. are environmentally important because of their plant growth-promoting activities, such as enhancing nutrients supply, inhibition of plant pathogens and stimulation of plant defense. The biogenic volatile organic compounds are a diverse of biochemical substances emitted by fungi and other microorganisms. The favorable role of VOCs in bio-control and plant growth-promotion has just recently been recognized. Hussein et al. (2020) asserted the importance of volatile organic compounds (VOCs) released by common fungi in the protection of ginseng plant from mycopathogens. Their results may help in the prospective development of the biopesticides for eco-friendly solution of crops pathogens and propose the potential application of the antimicrobial compounds from *Trichoderma*. They suggested good examples of biodegradable natural antifungal compounds from *Trichoderma* which are safe for application soon. PGPF as biocontrol agents can be an important component of an integrated agriculture management system (El-Maraghy et al. 2020b, Hussein et al. 2020, Hussein & Joo 2019, Adesemoye & Kloepper 2009). However, one of the vital problems in inoculant technology is the survival of the microorganisms during storage and several parameters influence their survival *viz.*, the culture medium, the physiological state of the microorganisms when harvested (Alori & Babalola 2018), the process of dehydration, rate of drying (Berninger et al. 2018), the temperature of storage and water activity of the inoculum (Mukhongo et al. 2016). All these factors lead to the shorter shelf life of inoculants i.e., three to six months under normal storage conditions. Hence studies to increase the shelf life of inoculants or finding alternate formulations for carrier inoculants are gaining importance. Notably, biotic and abiotic factors may influence the various mechanisms and limit the activities between plant and beneficial fungi, resulting in less than adequate performance in plant growth-enhancement and disease management (Hussein et al. 2020, Jones et al. 2019). There is a necessity for more studies on the plant-microbe interactions and their impacts in different ecologies and regions to understand well the interactions among PGPF and plants, particularly in the case of applications in new environments. Indigenous microflora is more preferred to improve crop performance due to ready adaptation to the local environment comparative to introduced strains. To find rhizosphere microbial strains that possess wider adaptability to different crops and can promote plant-growth under different conditions is of most of scientists' interest.

Abbreviations

ABA: Abscisic acid; ACCD: 1-aminocyclopropane-1-caroxylate deaminase; Eth: Ethylene; GA: *Gibberellic acid*; IAA: 3-indol acetic-acid; ISR: Induced systemic resistance; Plant growth-promoting fungi PGPF; PGPR: Plant growth-promoting rhizobacteria; PR: Pathogenesis-related; ROS: Reactive oxygen species; SA: Salicylice acid; SAR: Systemic acquired resistance.

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Data and materials in this study can be used as a reference by other researchers.

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Consent for publication

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