Chapter

Application and Mechanisms of Plant Growth Promoting Fungi (PGPF) for Phytostimulation

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Abstract

Plant growth-promoting fungi (PGPF) constitute diverse genera of nonpathogenic fungi that provide a variety of benefits to their host plants. PGPF show an effective role in sustainable agriculture. Meeting increasing demand for crop production without damage to the environment is the biggest challenge nowadays. The use of PGPF has been recognized as an environmentally friendly way of increasing crop production. These fungi have proven to increase crop yields by improving germination, seedling vigor, plant growth, root morphogenesis, photosynthesis, and flowering through either a direct or indirect mechanism. The mechanisms of PGPF involve solubilizing and mineralizing nutrients for easy uptake by plants, regulating hormonal balance, producing volatile organic compounds and microbial enzyme, suppressing plant pathogens and ameliorating abiotic stresses. Successful colonization is an intrinsic factor for most PGPF to exert their beneficial effects on plants. A certain level of specificity exists in the interactions between plant species and PGPF for root colonization and growth promoting effects. There is a gap between the number of reported efficacious PGPF and the number of PGPF as biofertilizer. Efforts should be strengthened to improve the efficacy and commercialization of PGPF. Hence, this chapter summarizes valuable information regarding the application and mechanisms of PGPF in sustainable agriculture.

Keywords: seed germination, seedling vigor, root morphogenesis, yield, root colonization, formulation

1. Introduction

The world's population exceeded ~7 billion just after 2010, and still continues to grow fast. Roughly, 83 million people are added to the world's population every year and with this pace of growth, the global population is projected to reach around 9.7 billion by 2050, ~24% higher than today [1]. In order to feed this large population, crop production must increase by approximately 25–70% above current production levels [2]. Intensification of agriculture is considered a potential solution. By relying on intensive use of fertilizers, pesticides and other inputs, agricultural intensification increases the productivity of existing farmland and delivers more food to the added population. However, the chemical-based crop

intensification produces more food in a way that the future production potential of farmland is being undermined and the environment is being affected. An increasingly degraded soil, overwhelming health hazards from soil and water pollution, disturbed natural microbial populations are a few of the direct implications in chemical-intensive agriculture. To avoid these potentially harmful effects of agrochemicals in agriculture, alternative approaches must be persuaded. An ecocentric approach that provides both environmental and economic benefits is increasingly needed. Organic farming is one of many such approaches that promote agroecosystem health, ensuring sustainable intensification in agriculture.

The uniqueness of microorganisms and the dynamic part played by them in sustaining agricultural ecosystems have made them likely candidates for playing a central role in organic-based modern agriculture. Fortunately, plant roots harbor an abundant association of beneficial microorganisms. Root exudates are the largest source of carbon that attracts the microbial populations and allow them to forge an intimate association with host plants [3]. In response, the rhizosphere microbial populations play versatile roles in transforming, mobilizing and solubilizing soil nutrients, which are crucial for plant growth and development. Among the diverse rhizosphere microbial population, fungi known as plant growth promoting fungi (PGPF) are receiving a growing attention in recent days. Over the decades, varieties of PGPF have been studied including those belong to genera *Trichoderma, Penicillium, Phoma* and *Fusarium* [4]. Studies have shown that PGPF modulate plant growth and enhance resilience to plant pathogens without environmental contamination [5]. The positive effects of PGPF on plant and environment make them well fitted to organic agriculture.

The course of plant growth promotion by PGPF is a complex process and often cannot be attributed to a single mechanism. A variety of direct and indirect mechanisms, including solubilization of minerals, synthesis of phytohormones, production of volatile organic compounds, exploitation of microbial enzymes, increases in nutrient uptake, amelioration of abiotic stresses and suppression of deleterious phytopathogens are involved. These wide arrays of interconnected mechanisms help PGPF maintaining rhizosphere competence and stability in host performance. Compared to the large number of PGPF identified in the laboratory, only a small fraction of them is in agricultural practice worldwide. Inconsistent performance of the inoculated PGPF under field conditions limits the commercial application of them. Development of appropriate formulation could improve the performance in the field and pave the way for commercialization of the PGPF. An ideal formulation of PGPF should fit with existing application technologies, protect biological actives from stress, ensure viability, remains unaffected after storage under ambient conditions, ensure microbial actives in the field and be cost effective [6].

Considering the aspects discussed above, the need for superior PGPF to supplement inorganic chemical fertilizers as one of the crucial steps of moving toward organic farming practices has been highlighted. Inclusion of new techniques in these processes has been vital to the development of novel PGPF applications. This review will therefore attempt to shed light on the recent findings related to the impact of PGPF on plant growth and yield, duration of their effects, host specificity of the cooperation, root colonization mechanisms, their modes of action and commercial formulation for enhancement of plant growth and yield. The knowledge produced from this review could be very useful to those who are apprehensive about environmental protection and agricultural sustainability.

2. Plant growth promoting fungi (PGPF)

Plants have intricate relationships with an array of microorganisms, particularly rhizosphere fungi and bacteria, which can lead to an increase in plant vigor, growth and development as well as changes in plant metabolism [7]. The group of rhizosphere fungi that colonize plant roots and enhance plant growth is referred to as PGPF [4]. PGPF are heterogeneous group of nonpathogenic saprotroph fungi. They can be separated into endophytic, whereby they live inside roots and exchange metabolites with plants directly, and epiphytic, whereby they live freely on the root

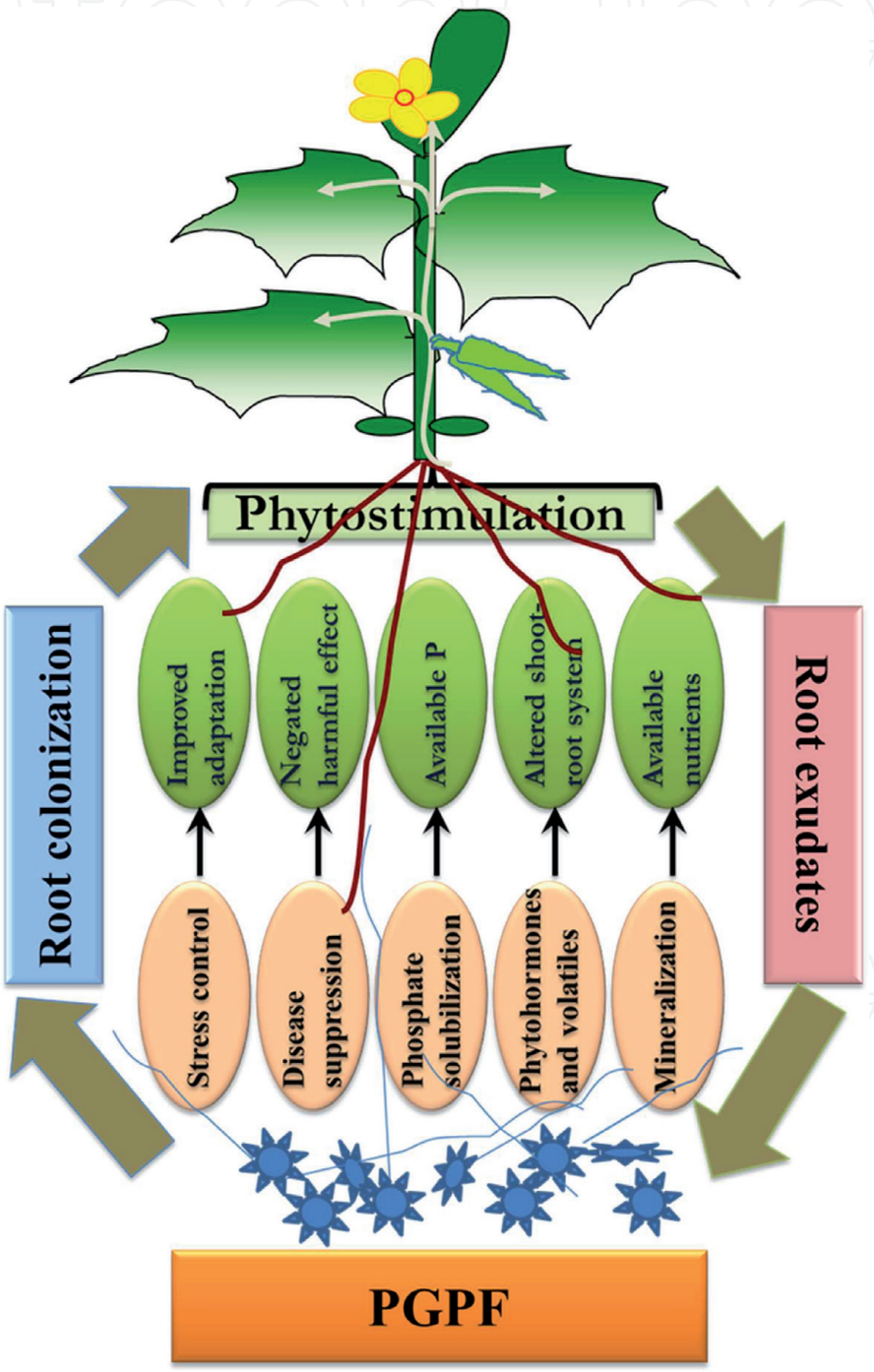

Figure 1.
Beneficial interaction between plant and plant growth promoting fungi (PGPF). PGPF can modulate plant growth and development through the production of phytohormones and volatile compounds. PGPF also influence plant nutrition via solubilization of phosphorus and mineralization of organic substrates. PGPF modify plant functioning against biotic and abiotic stresses by negating their harmful effects.

surface and free-living PGPF, which live outside plant cells, i.e., in the rhizosphere [5]. PGPF establish a non-obligate mutualism with a broader range of host plants. That is why symbiotic mycorrhizal fungi are not considered as PGPF, although they are known to improve growth of the plants [8]. Moreover, PGPF encompass a diverse taxonomic group in comparison to mycorrhiza. They are often involved in a range of complex interactions with plants and develop distinct strategies to mediate improvements in seed germination, seedling vigor, plant growth, flowering and productivity of host plants (**Figure 1**). PGPF are not only associated with the root to mediate positive effects on plant growth and development but also have beneficial effects on suppressing phytopathogenic microorganisms [9]. Not every organism identified as PGPF will improve plant growth under all conditions or in association with all plant hosts [10]. Some PGPF biocontrol inoculants usually contain necrotrophic mycoparasites such as *Trichoderma* spp. [11], while a limited number such as *Sphaerodes mycoparasitica* is biotrophic mycoparasitic agent [12]. Therefore, PGPF are considered one of the potential active ingredients in both biofertilizer and mycofungicide formulation.

3. The nature and composition of PGPF

PGPF are common root-associated and soil-borne fungi from diverse genera. Fungi reported as PGPF include Ascomycetes, Basidiomycetes and Oomycetes [5]. Some strains of hypovirulent binucleate *Rhizoctonia* (HBNR) are known to be PGPF [13]. PGPF also include isolates of mycelial fungi that do not produce any spores, generally known as sterile black fungus (SBF), sterile dark fungus (SDF) and sterile red fungus (SRF) [14]. The non-sporulating PGPF are often difficult to identify and mostly lack formal taxonomic status. Among the PGPF *Aspergillus*, *Fusarium*, *Penicillium, Phoma* and *Trichoderma* have a wide distribution and are, by far, the most extensively reported (**Table 1**). Each of the genera has a variety of species. *Aspergillus, Fusarium, Penicillium* and *Phoma* were frequently found in the rhizosphere or in the roots of plants. Instead, *Trichoderma* were mostly isolated from soil. Among the rhizosphere population, PGPF have a high relative abundance. A total of 619 (44%) out of 1399 fungal isolates collected from rhizosphere of six different plants were PGPF, while frequency of occurrence of PGPF in zoysiagrass, wheat, corn and eggplant rhizosphere were 46, 47, 38 and 10%, respectively [4]. This indicates that abundance of PGPF varies largely according to the host rhizosphere. Similarly, the dominating fungal genus is not necessarily the dominating PGPF in the rhizosphere population. The order of the frequency of the main genera among 1399 fungal isolates was *Fusarium* > *Trichoderma* > sterile fungi > *Penicillium* > *Pythium* > *Rhizoctonia* > *Mucor,* while that of PGPF from each plant genus was: *Trichodema* (~82%) > *Pythium* (~75%) > *Penicillium* (~69%) > *Alternaria* (~63%) > *Fusarium* (~44%) > sterile fungi (40%) > *Mucor* (~38%) [4]. The important characteristics of these fungi are their high rhizosphere competence and ability to promote plant growth.

Initial search for identification of PGPF was concentrated to rhizosphere fungi. Recent studies have demonstrated the potential of phyllosphere fungi as PGPF. The phyllosphere, which consists of the above ground surfaces of plants, is one of the most prevalent microbial habitats on earth. Phyllosphere fungi can act as mutualists promoting plant growth and tolerance of environmental stressors [53]. A few of other fungi isolated from tree bark, decorticated wood and water damaged building functioned as PGPF [43, 49]. More interestingly, the fungal entomopathogens also show potential to be PGPF and promote plant growth [54]. PGPF seem to have a cosmopolitan occurrence.

PGPF	Original source of isolation	References
Alternaria sp.	*Zoysia tenuifolia, Rosa rugosa*, *Camellia japonica*, *Delonix regia*, *Dianthus caryophyllus*, *Rosa hybrid*	[4, 15]
Aspergillus sp., *As. fumigatus, As. niger, As. terreus, As. ustus, As. clavatus*	*Capsicum annuum*, *Glycine max, Cicer arietinum, Elymus mollis, Solanum tuberosum, Nymphoides peltata*	[16–21]
Aureobasidium pullulans	Dark chestnut soil	[22]
Chaetomium globosum	*Capsicum annuum*	[23]
Cladosporium sp., *Cladosporium sphaerospermum*	*Cucumis sativus, Glycine max*	[24, 25]
Colletotrichum sp.	*Rosa rugosa*, *Camellia japonica*, *Delonix regia*, *Dianthus caryophyllus*, *Rosa hybrid*	[15]
Exophiala sp.	*Cucumis sativus*	[26]
Fusarium sp., *F. equiseti*, *F. oxysporum, F. verticillioides*	*Cynodon dactylon*, *Lygeum spartum, Zoysia tenuifolia, Musa* sp. and other environment	[27–32]
Non-sporulating sterile fungi	*Zoysia tenuifolia*	[14]
Penicillium sp., *Pe. chrysogenum, Pe. citrinum, Pe. kloeckeri, Pe. menonorum, Pe. resedanum, Pe. simplicissimum, Pe. janthinellum, Pe. viridicatum*	Halophyte, *Ixeris repenes, Cicer arietinum, Elymus mollis, Capsicum annuum, Zoysia tenuifolia*	[9, 16, 22, 33–40]
Phoma sp., *Phoma herbarum, Phoma multirostrata*	*G. max, Rosa rugosa*, *Camellia japonica*, *Delonix regia*, *Dianthus caryophyllus*, *Rosa hybrid, Zoysia tenuifolia*	[4, 14, 15, 34, 41, 42]
Phomopsis sp., *Phomopsis liquidambari*	*Rosa rugosa*, *Camellia japonica*, *Delonix regia*, *Dianthus caryophyllus*, *Rosa hybrid, Bischofia polycarpa* bark	[15, 43]
Purpureocillium lilacinum	Soil	[44]
Rhizoctonia spp.	Orchid, *Lycopersicon lycopersicum,* and soil	[13, 45, 46]
Rhodotorula mucilaginosa	Soil	[22]
Talaromyces wortmannii	Soil	[40]
Trichoderma asperellum, *T. atroviride, T. hamatum, T. harzianum, T. longibrachiatum, T. pseudokoningii, T. viride, T. virens*	Soil, wood and damaged building	[34, 47–52]

Table 1.
Different fungi reported as plant growth promoting fungi (PGPF) with their original source of isolation.

4. Impact of PGPF on plant growth promotion

PGPF exhibit traits beneficial to plant and as such, their capacity to enhance plant growth and development is well founded. PGPF mediate both short- and long-term effects on germination and subsequent plant performance. Improvement in germination, seedling vigor, shoot growth, root growth, photosynthetic efficiency, flowering, and yield are the most common effects decreed by PGPF. A particular PGPF may condition plant growth by exerting all or one or more of these effects.

4.1 Impact of PGPF on seed germination and seedling vigor

Seed germination and germinant growth are critical developmental periods of the young plantlet until it begins producing its own food by photosynthesis. Treatment with PGPF, particularly of the genus *Aspergillus*, *Alternaria*, *Trichoderma*, *Penicillium, Fusarium, Sphaerodes* and *Phoma* has been reported to improve seed germination and seedling vigor in different agronomic and horticultural crops (**Table 2**). Scarified seeds inoculated with spores from *Aspergillus* and *Alternaria* had significant increases in germination of Utah milkvetch (*Astragalus utahensis*) *in vitro*, and in greenhouse and fall-seeded plots near Fountain Green and Nephi [55]. The *Aspergillus*-treated seeds performed out seeds inoculated with *Alternaria*. An increase of 30% in seedling emergence was observed in cucumber plant raised upon the treatment of *T. harzianum* [47]. Application of *T. harzianum* also significantly increased seed germination, emergence index, seedling vigor and successful transplantation percentage in muskmelon compared to the untreated controls [59]. Early seedling emergence and enhanced vigor were observed in bacterial wilt susceptible tomato cultivar treated with *T. harzianum*, *Phoma multirostrata*, and *Penicillium chrysogenum* compared to untreated controls [34]. The culture filtrate of *Penicillium* was as effective as the living inocula in improving seed germination of tomato [70]. Significantly, higher germination and vigor index were observed in Indian spinach, when seeds were sown in sterilized field soil amended with wheat grain inoculum of *Fusarium* spp. PPF1 [27]. *Sphaerodes mycoparasitica*, a biotrophic mycoparasite of *Fusarium* species, improved wheat seed germination and seedling growth *in vitro* compared to *T. harzianum,* while under phytotron conditions, both *S. mycoparasitica* and *T. harzianum* had positive impact on wheat seedlings growth in the presence of *F. graminearum* [12]. These results show the positive impact of PGPF on seed germination and seedlings growth of a wide arrays of hosts.

4.2 Impact of PGPF on shoot growth

The most common form of growth promotion by PGPF is the augmented shoot in colonized plants. Shoot growth promotion has been shown by a great diversity of PGPF across a large number of plant species. Isolates of *Aspergillus, Trichoderma, Penicillium*, and *Fusarium* were capable of enhancing the shoot growth in model plant Arabidopsis [9, 20, 28, 33, 48]. Different species of *Aspergillus* are known to support shoot growth in chickpea [16], Chinese cabbage [56], cucumber [17], soybean [18, 65] and wheat [76]. Species of nonpathogenic *Fusarium* were reported to stimulate shoot growth in Indian spinach [27] and banana [29]. Application of barley grain inoculum of *Penicillium viridicatum* GP15-1 to the potting medium resulted in 26–42% increase in stem length, 37–46% increase in shoot fresh weight and 100–176% increase in shoot dry weight of cucumber plants [35]. Similarly, inoculation of cucumber plants with *Pe. menonorum* KNU3 increased cucumber shoot dry biomass by as much as 52% [36]. Stimulated shoot growth by *Penicillium* spp. was also reported in tomato [69], Waito-c rice [37, 38], chili [23, 39] and sesame [74]. Application of *T. longipile* and *T. tomentosum* increased shoot dry weight of cabbage seedlings by 91–102% in glasshouse trials [57]. Likewise, cottonseeds pretreated with *T. viride* showed four-fold increases in shoot length elongation and an almost 40-fold increase in plant dry weight compared to the control [66]. Augmented shoot growth by *Trichoderma* has also been reported in chickpea [16], wheat [79], maize [78], cucumber [60] and other plant species (**Table 2**). Isolates of *Phoma* were found to be an efficient stimulator of plant shoot [15, 41, 62]. A few hypovirulent *Rhizoctonia* isolates were able to induce significantly higher fresh leaves and stems weights in tomato plants grown in greenhouse [13]. Enhancement of shoot growth was also observed

Test crop	PGPF strain	Improvement	References
Arabidopsis thaliana	*Trichoderma virens* Gv. *29-8*	Biomass, lateral root development	[48]
	Penicillium janthinellum GP16-2	Shoot biomass, leaf number	[33]
	Pe. simplicissimum GP17-2	Shoot biomass, leaf number	[9]
	Fusarium oxysporum NRRL 38499, NRRL 26379 and NRRL 38335,	Shoot-root growth	[28]
	Aspergillus ustus	Shoot growth, lateral root, root hair numbers	[20]
Astragalus utahensis	*Aspergillus* spp., *Alternaria* spp.	Seed germination	[55]
Basella alba	*Fusarium* spp. PPF1	Germination, seedling vigor, shoot-root growth, leaf area, leaf chlorophyll content	[27]
Brassica campestris	*Talaromyces wortmannii* FS2	Shoot fresh weight	[40]
B. chinensis	*A. niger* 1B and 6A	Plant dry weight, N and P content	[56]
B. oleracea var. *capitata*	*T. longipile, T. tomentosum*	Shoot dry weight, leaf area	[57]
Capsicum annuum	*Pe. resedanum* LK6	Shoot length, biomass, chlorophyll content, photosynthesis	[39]
	Chaetomium globosum CAC-1G	Plant biomass, root-shoot growth	[23]
Cicer arietinum	*A. niger* BHUAS01, *Pe. citrinum* BHUPC01, *T. harzinum*	Plant growth	[16]
	T. harzianum T-75	Yield	[58]
Cucumis melo	*T. harzianum* Bi	Germination, seedling health, vigor	[59]
Cucumis sativus	*Pe. simplicissimum* GP17-2	Root-shoot growth	[4]
	Pe. viridicatum GP15-1	Root-shoot length, biomass	[35]
	T. harzianum GT3-2	Root-shoot growth	[60]
	F. equiseti GF19-1	Root-shoot growth	[61]
	Aspergillus spp. PPA1	Root-shoot length, biomass, leaf area, chlorophyll content	[17]
	Exophiala sp. *LHL08*	Plant growth under drought and salinity	[26]
	Phoma sp.	Root-shoot growth, yield in the field	[62]
	Phoma sp. GS8-2, GS8-3	Root-shoot growth	[63]
GiSeLa6® (*Prunus cerasus* × *P. canescens*)	*T. harzianum* T-22	Root growth, development	[64]
Glycine max	*A. fumigatus* HK-5-2	Shoot growth, biomass, leaf area, chlorophyll contents, photosynthetic rate	[65]
	A. fumigatus LH02	Shoot growth, biomass, leaf area, chlorophyll contents, photosynthetic rate	[18]
	*Phoma herbarum*TK-2-4	Plant length, biomass	[41]
Gossypium arboreum L	*T. viride*	Root-shoot length, plant dry weight	[66]

Test crop	PGPF strain	Improvement	References
Helianthus annuus	*Trichoderma* sp., *Aspergillus* sp., *Penicillium* sp., *Phoma* sp., *Fusarium* sp.	Seed germination, seedling vigor	[67]
Lactuca sativus	*F. oxysporum* MSA 35	Root-shoot growth, chlorophyll content	[68]
Lycopersicon lycopersicum	*T. harzianum* TriH_JSB27, *Phoma multirostrata* PhoM_JSB17, *T. harzianum* TriH_JSB36, *Pe. chrysogenum* PenC_JSB41	Seedling emergence, vigor	[34]
	T. harzianum T-22	Seed germination under stress	[69]
	Penicillium spp.	Seed germination, root-shoot growth	[70]
	F. equiseti GF19-1	Plant biomass, root-shoot growth	[71]
Musa sp.	*F. oxysporum* V5W2, Eny 7.11o, Emb 2.4o	Yield	[29]
Nicotiana tabacum	*Alternaria* sp., *Phomopsis* sp., *Cladosporium* sp., *Colletotrichum* sp., *Phoma* sp.	Root-shoot growth, chlorophylls, soluble sugars, plant biomass	[15]
Pinus sylvestris var. *mongolica*	*T. harzianum* E15, *T. virens* ZT05	Seedling biomass, root structure, soil nutrients, soil enzyme activity	[72]
Saccharum officinarum	*T. viride*	Yield	[73]
Sesamum indicum	*Penicillium* spp. NICS01, DFC01	Root-shoot growth, chlorophylls, proteins, amino acids, lignans	[74]
Solanum tuberosum	*A. ustus*	Root-shoot growth, lateral root, root hair numbers	[20]
Spinacia oleracea	*F. equiseti*	Plant biomass, root-shoot growth	[75]
Suaeda japonica	*Penicillium* sp. Sj-2-2	Plant length	[38]
	Cladosporium sp. MH-6	Shoot length	[24]
	Pe. citrinum IR-3-3	Root-shoot length	[37]
	Phoma herbarum TK-2-4	Plant length	[41]
Triticum aestivum	*T. harzianum, T. koningii*	Plant biomass, root-shoot growth.	[4]
	Sphaerodes mycoparasitica	Seed germination, seedling growth	[12]
	A. niger NCIM	Shoot and total plant length ratio	[76]
Vinca minor	*T. harzianum*	Flowering, plant height, weight	[77]
Zea mays	*T. harzianum* T22	Shoot growth, area and size of main and secondary roots	[78]

Table 2.
Effect of different plant growth promoting fungi (PGPF) on seed germination, plant growth and yield in various plants.

by *Talaromyces wortmannii* in cabbage [40], *Chaetomium globosum* in chili [23], *Colletotrichum* sp. in tobacco and *Exophiala* sp. in cucumber [26]. The results from these studies are consistent with numerous field and growth chamber experiments that have shown that PGPF inoculants can mediate shoot growth improvement.

4.3 Impact of PGPF on photosynthesis

The plant growth promotion in some plant-PGPF interaction is occasionally associated with improvement in state and function of the photosynthetic apparatus of plants. Treatment with *T. longipile* and *T. tomentosum* increased leaf area of cabbage by 58–71% in glasshouse trials [57]. Tomato plants grown with HBNR isolates had significantly higher leaf fresh weight than control plants in greenhouse [13]. Arabidopsis grown in soil amended with *Pe. simplicissimum* GP17-2 and *Pe. janthinellum* GP16-2 were more greener and had approximately 1 more leaflet per plant than control plants 4 weeks after treatment [9]. *Penicillium* spp. also enhanced leaf chlorophyll content in cucumber and chili [36, 39]. Soil amendment with *Aspergillus* spp. PPA1 and *Fusarium* spp. PPF1 significantly increased leaf area and leaf chlorophyll content in cucumber and Indian spinach, respectively [27]. Improvement in leaf number, leaf area and leaf chlorophyll levels would contribute to increases in photosynthesis rate and net accumulation of carbohydrate in plants.

4.4 Impact of PGPF on root growth and architecture

Roots are vital plant organs that remain below the surface of the soil. The root system is important for plant fitness because it facilitates the absorption of water and nutrients, provides anchorage of the plant body to the ground and contributes to overall growth of plants. Root functions as the major interface between the plant and the microbes in the soil environment. The bulk of previous studies have evidenced the immense ability of PGPF in enhancement of root growth in different plants (**Table 2**). Plants forming association with PGPF show faster and larger root growth resulting in a rapid increase in the root biomass [27, 35, 50, 57]. Moreover, root length, root surface area, root diameter and branch number are under direct influence of intimate interaction with PGPF. Application of *T. virens* ZT05 increased root length, root surface area, average root diameter, root tip number and root branch number of pines by 25.11, 98.19, 5.66, 45.89 and 74.42%, respectively [72]. *A. ustus* is known to cause alterations in the root system architecture by promoting the formation of secondary roots in Arabidopsis and potato [20]. In maize (*Zea mays*), *Trichoderma* inoculation enhanced root biomass production and increased root hair development [78]. The abundance in root hair formation significantly increases root surface area, suggesting that PGPF inoculants could enhance the potential for plant roots to acquire nutrients under nutrient-limited conditions.

4.5 Impact of PGPF on flowering

The application of PGPF may influence the number, size and timing of flower in flowering plants. *Tagetes* (marigolds) grown with companion of *Pe. simplicissimum* flowered earlier and had greater flower size and weight [80]. Steamed or raw soil infested with *T. harzianum* hastened flowering of periwinkle and increased the number of blooms per plant on chrysanthemums [77]. Under greenhouse conditions, *T. harzianum* TriH_JSB27 and *Pe. Chrysogenum* PenC_JSB41 accelerated the flowering time in tomato [34]. Similarly, root colonization by the nematophagous fungus *Pochonia chlamydosporia* hurried flowering in *Arabidopsis thaliana* [81]. Root colonization by *Piriformospora indica* also results in early flowering in *Coleus forskohlii*, bottle gourd and *Nicotiana tabacum* [82]. Flowering time has commercial significance for crops and ornamental plants by shortening crop duration and improving productivity. A short duration crop would have several advantages over a long duration crop, even with equal total yields such as require less water, expose less to stresses and

increase the availability of the land for subsequent cropping. This indicates that PGPF improve the plasticity of complex plant traits.

4.6 Impact of PGPF on yield

PGPF show promising ability to promote growth through extensive improvements and betterment of fundamental processes operating in the plants, all of which directly and indirectly contributes to the crop yield increase. Inoculation of banana (cv. Giant Cavendish and Grand Nain) with *F. oxysporum* resulted in 20–36% yield increase in the field [29]. Soil treatment with *T. harzianum* alone or in combination with organic amendment and fungicide significantly improved seed yield in pea [83] and chickpea [58]. Similarly, soil treatment with *T. viride* produced significantly the highest number of fruits per plant, number of seeds per fruit, fruit weight and dry weight of 100 seeds as compared to untreated control [84]. The beneficial association of plants with nonpathogenic binucleate *Rhizoctonia* spp. resulted in increase in yield of carrot, lettuce, cucumber, cotton, radish, wheat, tomato, Chinese mustard and potato [13, 45, 46]. These results demonstrate that PGPF hold great promise in the improvement of agriculture yields.

5. Duration of sustained plant growth promotion effect by PGPF

The duration of biofunctional activities of PGPF in plants is a key factor for their effective application in the field. Naturally, a legitimate question may arise whether PGPF isolates that have shown promising effects on early growth stage of plants, could also affect the middle or late ontogenetic stages and ultimately contribute to yield increases at harvest. As for potato, an increase in leaf, shoot, and tuber weight was observed by a nonpathogenic isolate (No. 521, AG-4) of *Rh. solani* 63–70 days after planting, while it was not expressed in yield at harvest [85]. Conversely, increased growth responses of wheat plants treated with PGPF were observed during seedling (2 weeks after sowing), vegetative (4 weeks), preflowering (6 weeks), flowering (10 weeks) and seed maturation stages (14 weeks) [4]. The isolates of *Phoma* sp. (GS6-1, GS7-4) and non-sporulating fungus (GU23-3), increased plant height, ear-head length and weight, seed number and plant biomass at harvest [79]. Again, isolates of *Phoma* sp. and non-sporulating fungus significantly increased plant length, dry biomass, leaf number and fruit number of cucumber cv. Jibai until 10 weeks post planting in greenhouse trials [62]. These isolates were equally effective in promoting growth and increasing yield of cucumber at 6 and 10 weeks post planting in the field [62]. There are other PGPF, which as well have shown the ability to confer long-term growth benefits to different plants. Rice and pea plants inoculated with *Westerdykella aurantiaca* FNBR-3, *T. longibrachiatum* FNBR-6, *Lasiodiplodia* sp. FNBR-13 and *Rhizopus delemar* FNBR-19 showed a stimulatory increase of growth for 8 weeks in the greenhouse [86]. Similarly, a single inoculation with inoculum of *Penicillium* and *Pochonia* affected the whole life cycle of tomato and Arabidopsis, respectively, accelerating the growth rate, shortening their vegetative period and enhancing seed maturation [34, 81]. As such, majority of PGPF strains are able to induce sustained beneficial effects on plant growth. The basis of sustained effects of PGPF on plants is not fully understood. One possibility is that the fungus continues to colonize the root system and establishes a life-long colonization with crop roots. The ability of PGPF to confer sustained benefit to plant is of great agriculture importance in terms of improving crop yield.

6. Host specificity of the plant growth-promoting cooperation

Although plants harbor a diverse community of fungi, a preferential interaction exists between certain PGPF and a particular host. Once a particular host mutualizes this fungus, it undergoes host-specific adaptations. The outcome of such adaptations is a highly specialized and finely tuned mutualism, leading to improved responsiveness to each other needs. Evidences show that PGPF that induce growth in one plant species do not necessarily have the same effect in other species [5]. Some PGPF exert general growth promotion effects in several plant species, other fungi only do so in specific host plant. A field study showed that most of eight non-sporulating PGPF isolates enhanced the growth of one wheat variety, whereas a few isolates enhanced the growth of the other variety [87]. Moreover, at least four isolates increased yields of both varieties. Thus, the efficacy of the PGPF isolates depended upon the wheat variety in addition to their inherent growth promoting abilities. Similarly, many of the zoysiagrass PGPF isolates promoted growth of bentgrass [4], in contrast to a few isolates enhanced growth in soybean [88]. Similarly, nine isolates belonging to *Phoma* sp. and one non-sporulating fungus caused consistent plant length enhancement in cucumber cv. Shogoin fusiharii compared to nine isolates except the non-sporulating fungus in cv. Aodai Kyuri. Again, plant length enhancement in cv. Jibai was shown by eight *Phoma* sp. and one non-sporulating fungus compared to five *Phoma* sp. isolates in cv. Ociai fushinari [62]. Identically, *Pe. simplicissimum* GP17-2 and *F. equiseti* 19–1 demonstrated sufficient growth-promoting effects on different host plants [4, 9, 60], but did not have effect on *Lotus japonicas* [89]. The outcome of the plant-PGPF interaction, therefore, depends on the plant and PGPF species. It is likely that the specific interaction develops during long-term co-evolution, as it has been observed for compatible and incompatible interactions of pathogens with plants [90]. Moreover, certain components of root exudates may attract and interact microbe specifically and allow it colonize the roots.

7. Mechanisms of plant growth promotion

The course of plant growth promotion by PGPF is complex and often cannot be attributed to a single mechanism. Various mechanisms that are known to modulate plant growth and development can be either direct or indirect. Direct growth promotion occurs when substances produced by the fungi or nutrient available by them facilitate plant growth. On the other hand, the ability of fungi to suppress plant pathogens and to ameliorate stress are considered major indirect mechanisms of plant growth promotion by PGPF. A particular PGPF may affect growth and development of plants using one or more of these mechanisms (**Table 3**).

7.1 Phosphate solubilization

Phosphorus is the second most important and frequently limiting macronutrient for plant growth and productivity. It is an important component of the key macromolecules in living cells and thereby, required for wide array of functions necessary for the survival and growth of living organisms. Despite the abundance of phosphorus in agricultural soils, the majority occurs in an insoluble form. Phosphorus forms complex compounds by reacting with iron, aluminum or calcium depending on the soil types and becomes insoluble and unavailable to plants [102]. To circumvent this problem, phosphate-solubilizing PGPF can play an important role dissolving insoluble P into the soluble form and making it available for plants. PGPF produce

Mechanisms	Specific activities	PGPF strain	References
Phosphate solubilization	Solubilized P by acid phosphatase and alkaline phosphatase	*F. verticillioides* RK01, *Humicola* sp. KNU01	[30]
	Solubilized P from rock phosphate and Ca-P by organic acid	*A. niger* 1B and 6A	[56]
	Solubilize P from tricalcium phosphate (TCP)	*A. niger* BHUAS01, *Pe. citrinum* BHUPC01, *T. harzinum*	[16]
	Solubilized P by organic acid activities	*Pe. oxalicum* NJDL-03, *Aspergillus niger* NJDL-12	[91]
	Phytase-mediated improvement in phytate phosphorus	*A. niger* NCIM	[76]
	Increased HCO_3-extractable P (23% increase)	*Pe. bilaiae* RS7B-SD1	[92]
Mineralization of organic substrate	Increased production of NH4-N and NO_2-N in soil	*T. harzianum* GT2-1, *T. harzianum* GT3-1	[4]
	Increased availability of ammonium nitrogen from barley grain	*Phoma* sp.GS6-1, GS6-2, GS7-3, GS7-4, GS8-6, GS10-1, GS10-2, sterile fungus GU23-3	[87]
	Solubilize minerals such as MnO_2 and metallic zinc	*T. harzianum* Rifai 1295-22	[93]
	Increased availability of ammonium nitrogen from barley grain	*Phoma* sp. GS8-1, GS8-2, GS8-3, Sterile fungus GU21-1	[62]
	Increased concentration of Cu, P, Fe, Zn, Mn and Na in roots Increased concentration of Zn, P and Mn in shoot	*T. harzianum* strain T-203	[47]
	Increased soil organic carbon, N, P and K content	*T. viride*	[73]
	Increased availability of macro and micronutrients and organic carbon	*T. harzianum* strain Th 37	[94]
Phytohormone and enzyme production	Auxin-related compounds (indole-3-acetic acid, IAA)	*T. virensGv. 29-8*	[48]
	Gibberellins (GA1 and GA4) production	*A. fumigatus* HK-5-2	[65]
	GAs production	*Pe. resedanum* LK6	[39]
	GAs production	*Penicillium* sp. Sj-2-2	[38]
	GAs production	*Cladosporium* sp.MH-6	[24]
	GAs production	*Pe. citrinum* IR-3-3	[37]
	GAs and IAA production	*Chaetomium globosum*CAC-1G	[23]
	GAs production	*Exophiala* sp. *LHL08*	[26]
	GAs production	*Phoma herbarum* TK-2-4	[41]
	GAs production	*A. fumigatus* HK-5-2	[65]
	GAs production	*A. fumigatus* LH02	[18]
	IAA production	*T. harzianum* T-22	[64]
	Zeatin (Ze), IAA, 1-aminocyclopropane-1-carboxylic acid (ACC)	*T. harzianum*	[95]

Mechanisms	Specific activities	PGPF strain	References
Suppression of deleterious pathogens	Suppressed damping off caused by *Pythium irregular, Pythium* sp., *Pythium paroecandrum, Pythium aphanidermatum* and *Rhizoctonia solani* AG4	Sterile fungus GSP102, *T. harzianum* GT3-2, *F. equiseti* GF19-1, *Pe. simplicissimum* GP17-2	[4]
	Induced systemic resistance against *Colletotrichum graminicola*	*T. harzianum* T22	[78]
	Suppressed bacterial wilt disease caused by *Ralstonia solanacearum*	*T. harzianum* TriH_JSB27, *Phoma multirostrata* PhoM_JSB17, *T. harzianum* TriH_JSB36, *Pe. chrysogenum* PenC_JSB41	[34]
	Suppressed Fusarium wilt caused by *Fusarium oxysporum* f. sp. *ciceris*	*T. harzianum* T-75	[58]
	Suppressed *Fusarium graminearum*	*Sphaerodes mycoparasitica*	[12]
	Suppressed damping off caused by *Rhizoctonia solani* AG4	*Pe. viridicatum* GP15-1	[35]
	Suppressed nematodes *Pratylenchus goodeyi* and *Helicotylenchus multicinctus*	*F. oxysporum* V5W2, Eny 7.11o and Emb 2.4o	[29]
	Suppressed seedling mortality by *Rhizoctonia solani*	*T. harzianum* isolate T-3	[83]
Amelioration of abiotic stress	Increased tolerance to salt stress	*T. harzianum* T-22	[69]
	Mitigation of oxidative stress due to NaOCl and cold stress	*T. harzianum* Rifai strain 1295-22	[96]
	Enhanced maize seedling copper stress tolerance	*Chaetomium globosum*	[97]
	Minimized Cu-induced electrolytic leakage and lipid peroxidation	*Pe. funiculosum* LHL06	[98]
	Increased tolerance to drought stress	*T. atroviride ID20G*	[99]
Volatile organic compounds (VOCs)	Produced abundant classes of VOCs (sesquiterpenes and diterpenes)	*F. oxysporum* NRRL 26379, NRRL 38335	[28]
	Produced mainly terpenoid-like volatiles including β-caryophyllene	*Talaromyces wortmannii* FS2	[40]
	Produced 2-methyl-propanol and 3-methyl-butanol	*Phoma* sp. GS8-3	[100]
	Produced abundant amount of isobutyl alcohol, isopentyl alcohol, and 3-methylbutanal	*T. viride*	[101]

Table 3.
Different mechanisms of plant growth promotion used by various plant growth promoting fungi (PGPF).

phosphate-solubilizing enzymes such as phytases and phosphatases and organic acids, which liberate P from insoluble phosphates. The most efficient phytase and phosphatase producing PGPF belong to the genera *Aspergillus, Trichoderma,* and *Penicillium* [103]. The order in terms of phytate hydrolysis efficacy was *Aspergillus* > *Penicillium* > *Trichoderma* [104]. *Fusarium verticillioides* RK01 and *Humicola* sp. KNU01 solubilized phosphate by increasing activities of acid phosphatase and alkaline phosphatase, and promoted soybean growth significantly [30]. The phosphate solubilizing fungi possess greater phosphorus solubilization ability than bacteria,

especially under acidic soil conditions [105]. The main reason is most fungi are eosinophilic, and have relatively higher growth in acidic environments than bacteria [106]. The acidity has significant influence on organic acid-mediated phosphate solubilizing activities of *Pe. oxalicum* NJDL-03 and *A. niger* NJDL-12 [91]. However, acidification is not always the major mechanism of P solubilization by *T. harzianum* Rifai 1295-22 (T-22), where pH of cultures never fell below 5.0 and no organic acids were detected [93]. Some of the reported PGPF such as *Aspergillus niger* has twin abilities of P mineralization and solubilization [104]. The fungus releases P both from organic and inorganic sources. These suggests that specific PGPF may have specific activity in solubilizing phosphate and making it available for crop growth.

7.2 Substrate degradation (mineralization)

Microorganisms primarily mediate soil nutrient pathways. Microbial mineralization of nutrients from organic matter is crucial for plant growth. Some PGPF promote plant growth, but do not produce plant hormones or solubilize fixed phosphate. Among *Pe. radicum*, *Pe. bilaiae* (strain RS7B-SD1) and *Penicillium* sp. strain KC6-W2, the strongest growth promotion in wheat, medic, and lentil was shown by *Penicillium* sp. KC6-W2, while the only significant P increase (~23% increase) was found in *Pe. bilaiae* RS7B-SD1-treated plants [92]. Similarly, seven *Trichoderma* isolates significantly improved the growth of bean seedlings; despite some of them do not possess any of the assessed growth-promoting traits such as soluble P, indole acetic acid (IAA) and siderophores [107]. These PGPF are believed to encourage plant growth by accelerating mineralization in the soil. Fungi have better substrate assimilation efficiency than any other microbes and are able to break down complex polyaromatic compounds such lignin and humic or phenolic acids [108]. A close relationship was found between the cellulose and starch degradation activity of PGPF for decomposing barley grain and their subsequent growth promotion effect in plants [109]. Application of *T. harzianum* strain Th 37 increased the availability of macro and micronutrients and organic carbonate in the ratoon initiation stage in sugarcane [94]. Colonization of *T. harzianum* in cucumber roots enhanced the availability and uptake of nutrients by the plants [47]. Cucumber plants grew better and produced more marketable fruits due to an increase in soil nutrients caused by PGPF, and accumulated more inorganic minerals like Ca, Mg, and K in aerial shoots [62]. PGPF are also directly involved the degradation of the nitrogenous organic materials through ammonization and nitrification. Formation of NH_4-N and NO_2-N in soil was accelerated during soil amendment with PGPF-infested barley grains [109]. More interestingly, the fungal entomopathogen *Metarhizium robertsii,* when established as a root endophyte, was shown to translocate nitrogen from a dead insect to a common bean plant host, suggesting this PGPF's potential to acquire mineral nutrients from organic matter and promote plant growth [54]. Nutrient release by mineralization could explain why PGPF other than mycorrhizae improve plant growth when added to soil.

7.3 Phytohormone production

Phytohormones are involved in many forms of plant-microbe interactions and also in the beneficial interactions of plants with PGPF. The commonly recognized classes of phytohormones produced by PGPF are the auxins (IAA) and gibberellins (GAs) (**Table 3**). IAA, the most studied auxin, regulates many aspects of plant growth, in particular, root morphology by inhibiting root elongation, increasing lateral root production, and inducing adventitious roots [48]. The *T. harzianum* T-22-mediated root biomass production and root hair development in maize is

believed to operate through a classical IAA response pathway [78]. Similarly, a direct correlation exists between increased levels of fungal IAA and lateral root development in *Arabidopsis* seedlings inoculated with *T. virens* [48].

GAs are well known for their role in various developmental processes in plants, including stem elongation. Shoot elongation of waito-c rice seedlings by culture filtrates of *Pe. citrinum* IR-3-3 and *A. clavatus* Y2H0002 was attributed to the activity of physiologically active GAs existing in the culture filtrates [19, 37]. Biochemical analyses of *Penicillium* sp. LWL3 and *Pe. glomerata* LWL2 culture filtrates that enhanced the growth of Dongjiin beyo rice cultivar and in GA-deficient mutant *Waito-C* revealed the presence of IAA and various GAs [110]. Similarly, production of bioactive GAs correlated with enhanced growth of *Waito-C* under salinity by *Penicillium* sp. Sj-2-2 [38]. GA also played key roles during root colonization by *P. indica* in pea roots [111].

Another phytohormone through which PGPF mediate plant growth is cytokinin, especially the Zeatin. Zeatin production has been documented in *Piriformospora indica, T. harzianum* and *Phoma* sp., and the fungi that also produce other phytohormones [95, 112, 113]. *P. indica* produces low amounts of auxins, but high levels of cytokinins. *Trans*-Zeatin cytokinin biosynthesis was found crucial for *P. indica*-mediated growth stimulation in Arabidopsis [112]. This evidence suggests that PGPF often mediate the various growth and developmental processes in plants by influencing the balance of various plant hormones.

7.4 Microbial ACC deaminase

PGPF produces a crucial enzyme ACC (1-aminocyclopropane-1-carboxylic acid) deaminase. ACC deaminase cleaves the ethylene precursor, I-aminocyclopropane-1-carboxylic acid (ACC), into NH_3 (ammonia) and α-ketobutyrate [114]. The ACC deaminase regulates the plant growth by cleaving ACC produced by plants and thereby minimizing the ethylene level in the plant, which when present in high concentrations can lead to a reduced plant growth [115]. ACC deaminase is an inducible enzyme encoded by *acdS* genes of fungi and bacteria [116]. ACC deaminase appears to be central to the functional interactions of some plant-PGPF. *T. asperellum* T203 produced high levels of ACC deaminase and showed an average 3.5-fold induction of the *acds* gene [117]. When ACC deaminase expression is impaired in the fungus *T. asperellum* T203, the plant growth promotion abilities of this organism are also decreased [51]. The root colonizing bacteria *T. harzianum* T22 no longer promote canola root elongation after its *acdS* gene is knocked out [64]. Production of ACC deaminase was reported in some other fungi, which include *Issatchenkia occidentalis* [118], and *Penicillium citrinum* and a stramnopile, *Phytophthora sojae* [119, 120]. The ACC deaminase-producing microbes have competitive advantages in the rhizosphere over nonproducing microorganisms because the enzyme acts as a nitrogen source for them [116]. Moreover, bacteria and fungi that express ACC deaminase can lower the impact of a range of different stresses that affect plant growth and development [114]. These show that ACC deaminase is not only related to plant growth promotion abilities of the microbes, but also play additional roles in the rhizosphere.

7.5 Suppression of deleterious microorganisms by PGPF

The key indirect mechanism of PGPF-mediated plant growth promotion is through their activities as biocontrol agents. PGPF protect and empower plants to resist harmful pathogens and ensure their better growth. The mechanisms by which PGPF suppress growth or activity of invading pathogens in crop plants

include antibiosis, competition for nutrient and space, mycoparasitism and induced systemic resistance (ISR) [121]. PGPF of diverse genera promoted growth of field-soil grown cucumber by counteracting damping off pathogen *Pythium* sp. through microbial antagonism [4]. Banana plants inoculated with PGPF *F. oxysporum* significantly suppressed nematode pathogens *Pratylenchus goodeyi* and *Helicotylenchus multicinctus* resulting in up to ~20 to 36% increase in banana yields [29]. The mycoparasite *Sphaerodes retispora* has been reported to improve the plant dry weight and to decrease plant mortality in the presence of *F. oxysporum* [122]. Similarly, under phytotron conditions, seed germination, root biomass, total biomass, root length, and total length of *F. graminearum*-infected wheat were noticeably increased with the treatments of *S. mycoparasitica* and *T. harzianum*, as compared to inoculation with *F. graminearum* alone. Both mycoparasites prevented colonization and reduction in root growth by the pathogen [12]. PGPF compete with the pathogen for colonization niche on roots [79]. Other mechanisms of disease suppression by PGPF are, therefore, likely to include competition with pathogens for infection sites on the root surface. Moreover, there is a long and growing list of PGPF such as *Trichoderma, Penicillium, Fusarium, Phoma*, and non-sporulating fungi, which can protect crop plants against pathogens by eliciting ISR [14, 31, 123, 124]. Although many fungal strains to act as PGPF and elicit ISR, it is not clear how far both mechanisms are connected. These microbes may use some of the same mechanisms to promote plant growth and control plant pathogens.

7.6 Rhizoremediation and stress control

The microbial association of plants has a major influence on plant adaptation to abiotic stresses such as salinity, drought, heavy metal toxicity, extreme temperatures and oxidative stress. Recent studies indicate that fitness benefits conferred by certain PGPF contribute plant adaption to stresses [125]. There are reports of enhanced plant growth because of the association of PGPF with plants, even when plants are under suboptimal conditions [126]. Root colonization by *T. atroviride* ID20G increased fresh and dry weight of maize roots under drought stress [99]. Supplementation of *T. harzianum* to NaCl treated mustard seedlings showed elevation by 13.8, 11.8, and 16.7% in shoot, root length and plant dry weight, respectively as compared to plants treated with NaCl (200 mM) alone [127]. The fungus *Pe. funiculosum* significantly increased the plant biomass, root physiology and nutrients uptake to soybean under copper stress [98]. These fungi have been known to produce plant growth regulators (like GAs and auxins) and extend plant tolerance to abiotic and biotic stresses [23, 125]. Recurrently, *T. harzianum* T22 has little effect upon seedling performance in tomato, however, under stress; treated seeds germinate consistently faster and more uniformly than untreated seeds [69]. A few other fungi like *Microsphaeropsis, Mucor, Phoma, Alternaria, Peyronellaea, Steganosporium*, and *Aspergillus* are known to grow well in polluted medium and protect plants from adverse effects of metal stress [128]. There are numerous similar examples of PGPF ameliorating abiotic stresses and promoting plant growth. Despite significant differences between different stresses, cellular responses to them share common features. Enhanced resistance of PGPF-treated plants to abiotic stresses is explained partly due to higher capacity to scavenge ROS and recycle oxidized ascorbate and glutathione [99, 127]. The increase in proline content is found to be very useful in providing tolerance to these plants under stress [129]. Both enzymatic (peroxidase, catalase, superoxide dismutase, ascorbate peroxidase, monodehydroascorbate reductase, dehydroascorbate reductase, glutathione reductase, glutathione S-sransferase and gaucol peroxidase), and non-enzymatic (ascorbic acid, reduced glutathione, oxidized glutathione) antioxidants are induced by PGPF further

enhance the synthesis of these phytoconstituents and defend the plants from further damage [127].

7.7 Production of volatile organic compounds (VOCs)

Microorganisms produce various mixtures of gas-phase, carbon-based compounds called volatile organic compounds (VOCs) as part of their normal metabolism. The comparative analysis of experimental data has shown that volatile metabolites make a much greater contribution to the microbial interactions than non-volatile ones [130]. Recent studies reveal that VOC emission is indeed a common property of a wide variety of soil fungi, including PGPF. Some of these VOCs produced by PGPF exert stimulatory effects on plants. A PGPF, *Talaromyces wortmannii* emits a terpenoid-like volatile, β-caryophyllene, which significantly promoted plant growth and induced resistance in turnip [40]. The identified VOCs emitted by *Phoma* sp. GS8-3 belonged to C4-C8 hydrocarbons, where 2-methyl-propanol and 3-methyl-butanol formed the main components and promoted the growth of tobacco seedlings [100]. These two components were also extracted from PGPR [131]. On the other hand, 3-methyl-butanal has been reported from *T. viride* [101]. The other most abundant VOCs from *T. viride* were isobutyl alcohol, isopentyl alcohol, farnesene and geranylacetone. Arabidopsis cultured in petri plates in a shared atmosphere with *T. viride*, without direct physical contact was taller with more lateral roots, bigger with augmented total biomass (~45%) and earlier flowered with higher chlorophyll concentration (~58%) [101]. Moreover, volatile blends showed better growth promotion than individual compounds [132]. Volatile compounds produced by PGPF are also heavily involved in induce systemic resistance toward pathogens [100].

8. Pattern and process of root colonization by PGPF

Root colonization is considered as an important strategy of PGPF for plant growth promotion. Root colonization is the ability of a fungus to survive and proliferate along growing roots in the presence of the indigenous microflora over a considerable period [35]. The fungus that colonizes plant root effectively is more rhizosphere competent than others [107]. Rhizosphere competence is a necessary condition for a fungus to be an efficient PGPF. Re-isolation frequency of the fungus from the colonized roots is an indirect measure of its root colonizing ability and thereby, its rhizosphere competence. In such studies, *Pe. simplicissimum* GP17-2 and *Pe. viridicatum* GP15-1 were re-isolated from *Arabidopsis* Col-0 roots 3 weeks after planting at high frequencies which were found to be >90% (**Figure 2**). Similarly, the re-isolation frequency of *Pe. janthinellum* GP16-2 from the roots of Col-0 plants was recorded to be, on average, 85% [33]. *Aspergillus* spp. PPA1 was re-isolated from the roots of cucumber plants at a frequency of 95–100% 3 weeks after planting [17], indicating a rapid and efficient root colonization by the PGPF. However, a slow root colonization by PGPF was also reported, as it was the case with *Phoma* sp. GS8-2, which achieved maximum colonization on cucumber roots at 10 weeks [62]. The relative growth rate of the fungi and roots seems to determine the length of time required for maximum root colonization.

Some PGPF selectively colonize host roots and promote growth. Isolates of *Phoma* and sterile fungi showed poor ability to colonize the soybean roots and were unable to enhance the growth of soybean [79]. Similarly, *T. koningi* colonized roots and enhanced growth of *Lotus japonicas,* but *Pe. simplicissimum* and *F. equiseti* did not [89]. It was observed that *T. koningi* induced a transient and decreased level of defense gene expression in *L. japonicas* during its entry into the roots, while a

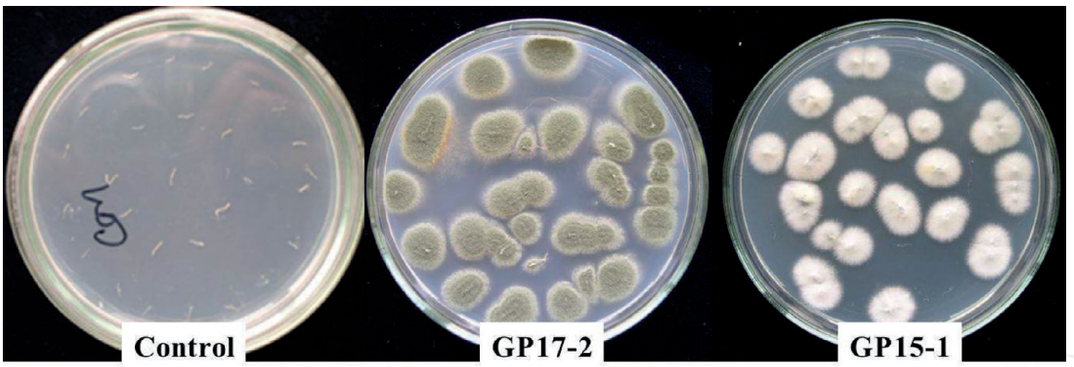

Figure 2.
Re-isolation of Penicillium simplicissimum *GP17-2 and* Penicillium viridicatum *GP15-1 at higher frequencies from colonized roots of* Arabidopsis thaliana *ecotype Col-0 3 weeks after sowing.*

stimulated expression of these genes was induced by *Pe. simplicissimum* and *F. equiseti* [89]. *T. koningi* resembles symbiotic fungi, while *Pe. simplicissimum* and *F. equiseti* act similar to fungal pathogens in activating host defense. This shows that legumes selectively avoid some PGPF and thus allow only specific PGPF to interfere.

There are also PGPF, in particular, the non-sporulating sterile fungi that lack root colonization ability, but they are able to promote growth and yield of plants [62, 133]. This indicates that root colonization is not an indispensable condition for growth promotion by all PGPF. Some chemical factor(s) produced by them might be responsible for growth promotion.

The colonization of the root system of by PGPF is not always homogenous; the density of PGPF varies in different parts of the root system. The colonization of roots by the majority of PGPF appears to be higher in the upper than in the middle and lower root parts of roots, [35, 133]. The lower part was always less colonized by PGPF, especially during first 2 weeks of colonization. This is probably due to the faster growth of the roots than of the hyphae. Moreover, the main zone of root exudation is located behind the apex [134]. However, some PGPF can keep up with root growth and colonize the entire root system [35]. Only fungi with large nutrient reserves can move to the root and along the root over larger distances [135].

Anatomical data show that PGPF may colonize root tissues internally and establish a mutualistic relationship with host. *F. equiseti* GF19-1 produced abundant hyphal growth on the root surface, formed appressoria-like structures and grew in the intercellular space, not inside the cell [31]. *T. harzianum* CECT 2413 exhibited profuse adhesion of hyphae to the tomato roots and colonized the epidermis and cortex. Intercellular hyphal growth and the formation of plant-induced papilla-like hyphal tips were also observed [136]. Hyphae of *T. koningi* penetrated the epidermis and entered the intercellular inner cortex tissues [89]. Sterile red fungus has been also demonstrated to invade the inner root regions that helped plants derive nutrients from the soil and protected roots from pathogens [137].

9. Formulation of PGPF

PGPF, especially *Trichoderma*, have many success stores as plant growth promoting agents and appear to have much potential as a commercial formulation. Different organic and inorganic carrier materials have been studied for effective delivery of bioinoculants. A talc-based formulation was developed for *T. harzianum* to supply concentrated conidial biomass of the fungus with high colony forming units (CFU) and long shelf life [138]. The concentrated formulation provided an extra advantage of smaller packaging for storage and transportation, and low

product cost as compared to other carriers such as charcoal, vermiculite, sawdust and cow dung. Seed application of the formulation recorded significant increase in growth promotion in chickpea [138]. Corn and sugarcane bagasse were used as potential carriers for *Trichoderma* sp. SL2 inoculants. The corn formulation of SL2 significantly enhanced rice seedlings root length, wet weight and biomass compared to inoculum mixed with sugarcane bagasse and control [139]. A spray-dried flowable powder formulation was developed for biostimulant *Trichoderma* strains using a CO_2 generating dispersant system, based on polyacrylic acid, citric acid and sodium bicarbonate, polyvinyl alcohol as adhesives and lecithin as wetting agent [140]. Hydrolytic amino acids derived from pig corpses were used in the preparation of *T. harzianum* T-E5-containing bioorganic fertilizer. The resulting bioorganic fertilizer supported higher densities of *T. harzianum* T-E5 and substantially enhanced plant growth when applied as a soil amendment [141]. A composted cattle manure-based *Trichoderma* biofertilizer was developed and tested in the field. Plots fertilized with biofertilizer had the greatest aboveground biomass of any treatment and were significantly more productive than non-amended plots and plots fertilized with any rate of organic fertilizer [142]. Effective formulation of *P. indica* was prepared in talcum powder or vermiculite with 20% moisture. The talcum-based formulations performed significantly better as bioinoculant over vermiculite-based formulations in glasshouse experiments [143]. These show the feasibility of commercial level production and applicability of different PGPF formulations for plant growth promotion in the field.

10. Conclusions

Because of current concerns over the adverse effects of agrochemicals, there is a growing interest in improving our understanding of the role and application of beneficial microbes in agriculture. The plant-associated growth promoting fungi show excellent potential for wider use in sustainable agriculture as they improve plant growth and yield in an ecofriendly and cost-effective manner. However, the PGPF continue to be greatly underutilized, primarily due to some practical problems such as the inconsistency in field performance, which appears to be the greatest challenge in the development of microbial inoculants for plant growth until now and well into the future. If our understanding of complex rhizosphere environment, of the mechanisms of action of PGPF and of the practical aspects of mass production, inoculant formulation and delivery increase, more PGPF products will become available. Knowledge of multiple microbial interaction with different or complementary mode of actions is also of extreme value for development of bio-formulation.

Recent advances in biotechnological tools and reliable transformation system could be useful in engineering of the PGPF to confer improved benefits to the crop. Genetic transformation and overexpression of one or more of the plant growth promoting traits that act synergistically may lead to enhanced performance by the inoculant. Research may be required periodically in order to evaluate the genetic stability and ecological persistence of the genetically modified strain. Efforts should be strengthened to foster linkage between investigators and entrepreneurs in facilitating technology transfer, promotion and acceptance by end users.

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