Plant Growth-Promoting Fungi (PGPF): Phytostimulation and Induced Systemic Resistance

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Abstract

The associations between plants and multipurpose plant growth-promoting fungi (PGPF) have been proven extremely to be beneficial to plants. This review describes new knowledge about the interactions between plants and their associated PGPF in determining improved plant growth and induced systemic resistance (ISR) to invading pathogens. It has been shown that fungi of heterogeneous classes and habitats function as PGPF. The well-known fungal genera *Aspergillus*, *Fusarium*, *Penicillium*, *Piriformospora*, *Phoma*, and *Trichoderma* are the most frequently reported PGPF. On comparing the results of different studies, it appears that plant-PGPF interactions can have positive effects on belowground and aboveground plant organs. The most commonly reported effects are significant improvement in germination, seedling vigor, biomass production, root hair development, photosynthetic efficiency, flowering, and yield. Some strains have the abilities to improve plant biochemical composition. It has now known that PGPF can also control numerous foliar and root pathogens by triggering ISR in the host plants. These capabilities are driven by their abilities to enhance nutrient uptake and phytohormone production as well as to reprogram plant gene expression, through differential activation of plant signaling pathways. The PGPF-triggered plant growth and ISR responses to pathogen attack may work through genetype-dependent manner in plants.

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6.1 Introduction

Fertilizers and pesticides are the integral parts of the modern crop production inputs. Adequate access to pesticides and fertilizers is a prerequisite for smooth agricultural production and growth. The benefits of synthetic fertilizer and pesticide use in the crop field have been immense. They reduce crop losses due to nutrient deficiencies, weeds, diseases, and insect pests. The crop losses due to pests and diseases for eight of the world's major crops are estimated at US$244 billion per annum, accounting for 43% of world production (Oerke 2006), and postharvest losses contribute a further 10% (Edwards and Poppy 2009). Thus, the collective effects of increased fertilizer and pesticide use coupled with improved varieties and irrigation have significantly contributed to the improvement of grain yields since the late 1960s (Otsuka and Larson 2013). Consequently, the grain production per capita and the food-population balance have substantially been improved in many low-income countries and lagging regions, especially in Asia. Despite this success, the Green Revolution has yielded a range of unintended negative consequences on environment. Excessive use of fertilizer and pesticides has been associated with potentially highly detrimental effects on nontarget species and soil and water quality. Moreover, continuous use of pesticides over a long period results in developing resistance of the pest (Aktar et al. 2009). Overcoming these widespread hazards is a major challenge in contemporary agriculture, and the problem must be seriously addressed before their impacts on environment become irremediable.

It is well known that farm practices define the level of food production and, largely, the state of the global environment. The resource intensive current firm practices have been proven costly, as the environmental and health costs associated with fertilizer and pesticide use are higher (Soares and de Souza Porto 2012). Such big costs have already raised questions about the sustainability of the current production system. Sustainability is important as it ensures social, environmental, and economic acceptability of the farm practices. A sustainable production system relies on firm practices that seek to protect the environment by making a significant reduction in environmentally detrimental amounts of chemical inputs to the crop fields, while ensuring higher firm returns. Needless to say, efforts must be given in favor of green strategies, which are characterized by the development and diffusion of nontoxic and/or least-toxic alternatives for plant disease and nutrient management. Environmentally friendly preparations of multipurpose beneficial microbes seem to be one of the major substitutes of chemical inputs in agriculture. Currently huge research inventiveness is underway for the identification and utilization of beneficial microbes for plant growth and disease control.

Rhizosphere, the narrow zone of soil surrounding and influenced by plant roots, is a natural habitat for numerous beneficial microorganisms and represents a biologically complex ecosystem on Earth (Mendes et al. 2013). This biologically active zone is critical for plant-microbe interactions and, as a consequence, for nutrient cycling, plant growth, and resistance of plants to diseases. During positive plant-microbe interaction, rhizosphere colonization by soil microorganisms is beneficial for both plant and the microorganisms. Both partners derive benefits from the intimate association and vitalize each other. The large amount of rhizodeposits released by the plant roots is a key determinant of microbial activity and community structure in the rhizosphere (Gahan and Schmalenberger 2014). The rhizosphere microbes utilize the rhizodeposit carbon as a major energy source for their growth and development (Denef et al. 2007). Consequently, plant roots can manipulate the rhizosphere microbiome to its own benefit by selectively stimulating microorganisms with traits that are beneficial to plant growth and health (Mendes et al. 2013). Mutual interdependence and interplay between the rhizosphere microbiome and the plant result in the overall quality of plant productivity (Lakshmanan et al. 2014).

The rhizospheric microbial forms vary in diversity, which includes bacteria, fungi, nematodes, viruses, arthropods, oomycetes, protozoa, algae, and archaea. Beneficial effect of number of rhizosphere fungi with respect to plant growth promotion has long been known (Hyakumachi 1994). These plant growth-promoting fungi (PGPF) include species of the genera *Aspergillus*, *Fusarium*, *Trichoderma*, *Penicillium*, *Piriformospora*, *Phoma*, and *Rhizoctonia*, which have the natural ability to stimulate various growth-related traits of plants (Hossain et al. 2007, 2014; Shoresh et al. 2010). Many studies in dicots and monocots have shown that PGPF mimic the well-studied plant growth-promoting rhizobacteria (PGPR) in their interaction with host plant. As examples, treating seeds with PGPF inoculum can improve germination and seedling vigor of different plants. They can also induce longer and larger shoots. Some may exert effect on root development and performance. There are PGPF that may stimulate early and vigorous flowering of plants. Photosynthetic ability of the plant can also be enhanced by PGPF inoculation. Some PGPF have the ability to increase crop yield. They have also the ability to stimulate production of host secondary metabolites. These abilities are important to agriculture.

It is now established that plant growth-promoting activities by PGPF are only a fragment of their abilities. They also have the abilities to protect plant against the deleterious microorganisms. Suppression of plant diseases by PGPF can be achieved in many ways. Some PGPF produce antibiotics, some are parasite, while others compete with pathogens for food and space. Along with these direct antagonistic effects against pathogens, PGPF also protect plants by inducing systemic resistance. Induced systemic resistance (ISR) can be defined as the phenomenon by which plant exhibits increased level of resistance to broad spectrum of pathogens in a plant portion distant from the area where PGPF is active, caused by the triggering of active plant defenses (Pieterse et al. 2014). PGPF reduce the impacts of various fungi (Fontenelle et al. 2011; Murali et al. 2013; Tohid and Taheri 2015; Nassimi

and Taheri 2017), bacteria (Hossain et al. 2008a; Yoshioka et al. 2012; Hossain and Sultana 2015), viruses (Elsharkawy et al. 2012), and nematodes (Gottlieb et al. 2003; Vu et al. 2006) by eliciting ISR. These plant growth-promoting and disease control abilities are frequently considered to be the basis for how PGPF expedite the beneficial effects on plant (Fig. 6.1).

Over recent decades, interdisciplinary researches have made significant advances in understanding how these microorganisms interact with the host plants. It has been revealed that various signaling cascades modulate interaction of plants with PGPF. Furthermore, transcript-profiling analysis shows that plant response to PGPF depends on the complete reprogramming of a high number of genes or proteins in plants. Current knowledge also suggests that genetic variability in plant genotypes determines the outcome of phytostimulation and ISR interactions with PGPF. These illuminate the intensity of the interaction between plant and PGPF and favor the plasticity of the plant response to fine-tune the precise mechanisms. This chapter describes recent knowledge regarding PGPF's abilities and the underlying mechanisms for induction of plant responses.

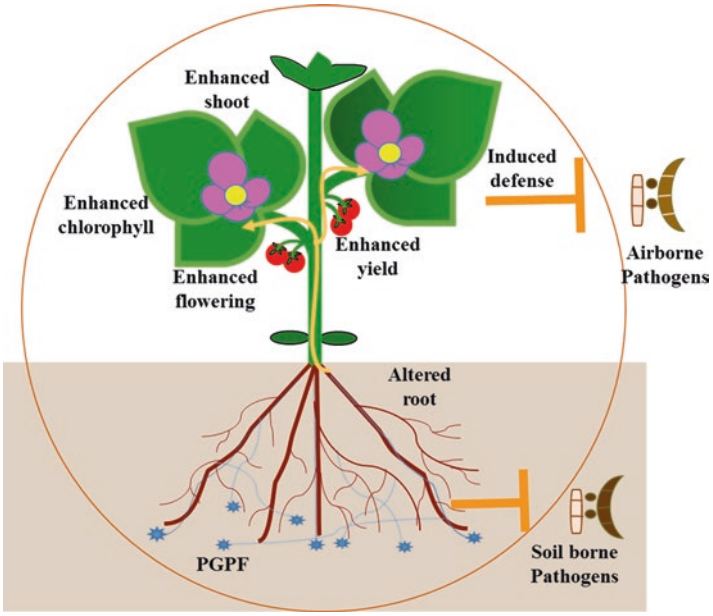

Fig. 6.1 Impact of plant growth-promoting fungi (PGPF) on plant growth promotion and disease suppression. PGPF stimulate shoot growth, root growth, photosynthetic efficiency, flowering, and yield. PGPF play a role in protection of plants against deleterious microorganisms by inducing systemic resistance

6.2 Nature and Diversity of Plant Growth-Promoting Fungi (PGPF)

Plant growth-promoting fungi (PGPF) are heterogeneous group of nonpathogenic fungi that are associated with plant and mediate improvements in plant growth and health. The classification of different fungi as PGPF does not represent any real biological similarity between fungi. Results from different studies indicate that the fungi under PGPF may differ distinctly from one another in taxonomy, in habitats, in physiology, and in their interaction with plants. Despite the name, PGPF do not always increase plant growth (Bent 2006). In reality, a fungus that promotes the growth of a given plant may not have same effect upon the growth of another plant, or the effect may vary under different set of environmental conditions. Similarly, not all fungi that promote plant growth are considered PGPF. For example, symbiotic mycorrhizal fungi are known to improve growth of the plants, but they are not considered as PGPF. Mycorrhizal fungi behave as obligate biotrophs and establish an intimate association with the roots of most host plants (Mehrotra 2005; Corradi and Bonfante 2012). On the other hand, PGPF are nonsymbiotic saprotrophic fungi that live freely in the root surface or the interior of the root itself or the rhizosphere. Therefore, the term PGPF is not any absolute term, rather it is an operational term (Bent 2006).

Microorganisms identified as PGPF have diverse taxonomy. According to the reported literatures, majority of true fungi characterized as PGPF primarily belongs to the phylum *Ascomycota* (*Aspergillus*, *Aureobasidium*, *Chaetomium*, *Cladosporium*, *Colletotrichum*, *Exophiala*, *Penicillium*, *Trichoderma*, *Fusarium*, *Gliocladium*, *Phoma*, *Phomopsis*, *Purpureocillium*, and *Talaromyces*), and a few of them belongs to *Basidiomycota* (*Limonomyces*, *Rhodotorula*, *Rhizoctonia*, and sterile fungi) and *Zygomycota* (*Mucor* and *Rhizopus*) (Table 6.1). A small number, like *Fusarium oxysporum*, *Colletotrichum*, and binucleate *Rhizoctonia*, is phylogenetically much related to plant pathogens but lack functional virulence determinants for many of the plant hosts from which they can be recovered. PGPF in mycelial fungi that do not produce any spores are known as sterile fungi. Most members in the *Oomycota* are usually virulent plant pathogens, while a few are nonpathogenic (Thines and Kamoun 2010). The nonpathogenic oomycetes *Pythium oligandrum* and *Phytophthora cryptogea* colonized the root ecosystems and acted as PGPF (Attitalla et al. 2001; Benhamou et al. 2012).

Species of PGPF are ubiquitous saprobes. Most PGPF have origin either in the soil or in the roots of large host range. On average 44% of the rhizosphere fungal isolates were PGPF (Hyakumachi 1994). This suggests that large portions of rhizospheric microorganisms are PGPF. However, the frequency of PGPF occurrence in the rhizosphere varies with crop plants. Some of the fungi that live inside root tissues or endophytes have also diverse positive effects on plant growth and are PGPF (Waqas et al. 2015). The most dominant endophyte appears to be *Fusarium* (25%), followed by *Penicillium* (12.5%) and *Alternaria* (7.5%) (Khalmuratova et al. 2015). Subsequent studies have also demonstrated the potential of phyllosphere fungi as PGPF (Limtong and Koowadjanakul 2012; Voříšková and Baldrian 2013), although the vast majority of studies have focused on phyllosphere bacteria and, to a lesser

Table 6.1 Different fungi reported as plant growth-promoting fungi (PGPF) with their original source of isolation

Systematics	PGPF strain(s)	Original source of isolation	References
Ascomycota	*Alternaria* sp.	Flower roots (*Rosa rugosa*, *Camellia japonica*, *Delonix regia*, *Dianthus caryophyllus*, and *Rosa hybrid*)	Zhou et al. (2014)
	Aspergillus sp.	Chili (*Capsicum annuum*)	Islam et al. (2014a)
	As. fumigatus	Soybean roots (*Glycine max*)	Hamayun et al. (2009a), and Khan et al. (2011a)
	As. niger	Tropical and subtropical soil, chickpea (*Cicer arietinum*) rhizosphere soil	Chuang et al. (2007), and Yadav et al. (2011)
	As. terreus	*Elymus mollis* roots	Waqas et al. (2015)
	As. ustus	Potato (*Solanum tuberosum*)	Marina et al. (2011)
	Aureobasidium pullulans	Dark Chestnut soil	Ignatova et al. (2015)
	A. pullulans	Golder shower tree leaves	Limtong and Koowadjanakul (2012)
	Candida maltosa	Unknown plant leaves	
	Chaetomium globosum	Pepper (*Capsicum annuum*) roots	Khan et al. (2012)
	Cladosporium sp.	Cucumber (*Cucumis sativus*) roots, flower roots (*Rosa rugosa*, *Camellia japonica*, *Delonix regia*, *Dianthus caryophyllus* and *Rosa hybrid*)	Hamayun et al. (2010), and Zhou et al. (2014)
	Colletotrichum sp.	Flower roots (*Rosa rugosa*, *Camellia japonica*, *Delonix regia*, *Dianthus caryophyllus* and *Rosa hybrid*)	Zhou et al. (2014)
	Exophiala sp.	Cucumber (*C. sativus*) roots	Khan et al. (2011b)
	Fusarium sp.	Bermuda grass (*Cynodon dactylon*)	Islam et al. (2014b)
	F. equiseti	Zoysiagrass (*Zoysia tenuifolia*) rhizosphere, *Lygeum spartum* roots	Kojima et al. (2013), and Maciá-Vicente et al. (2009)
	F. oxysporum	Cooking banana (*Musa* sp.) roots, diverse environment	Waweru et al. (2014), Bitas et al. (2015)
	Penicillium sp.	Halophyte roots	You et al. (2012)

	Penicillium koreense sp. *nov*	Rhizosphere soils of various Korean regions	You et al. (2014)
	Pe. chrysogenum	Rhizosphere soil and vegetables, sunflower, legumes, and cereal roots	Jogaiah et al. (2013)
	Pe. citrinum	Chickpea (*C. arietinum*) rhizospheric soil	Yadav et al. (2011)
	Pe. citrinum	*Ixeris repenes* (L.) roots, *Elymus mollis* roots	Khan et al. (2008), Waqas et al. (2015)
	Pe. janthinellum	*Zoysiagrass (Z. tenuifolia)* rhizosphere	Hossain et al. (2008a)
	Pe. kloeckeri	Soil	Yamagiwa et al. (2013)
	Pe. menonorum	Crop field soil	Babu et al. (2015)
	Pe. resedanum	*Capsicum annuum* roots	Khan et al. (2013)
	Pe. simplicissimum	Zoysiagrass (*Z. tenuifolia*)	Hossain and Sultana (2015)
	Pe. viridicatum	Zoysiagrass (*Z. tenuifolia*)	Hossain et al. (2014)
	Phoma sp.	Zoysiagrass *(Z. tenuifolia)* rhizosphere, flower (*Rosa rugosa*, *Camellia japonica*, *Delonix regia*, *Dianthus caryophyllus*, *Rosa hybrid*) roots	Sultana et al. (2008), and Zhou et al. (2014)
	Phoma herbarum	Soybean (*G. max*) roots	Hamayun et al. (2009b)
	Phoma multirostrata	Rhizosphere soil and vegetables, sunflower, legumes, and cereal roots	Jogaiah et al. (2013)
	Phomopsis sp.	Flower (*Rosa rugosa*, *Camellia japonica*, *Delonix regia*, *Dianthus caryophyllus*, *Rosa hybrid*) roots	Zhou et al. (2014)
	Phomopsis liquidambari	Inner bark of *Bischofia polycarpa*	Siddikee et al. (2016)
	Purpureocillium lilacinum	Soil	Cavello et al. (2015)
	Talaromyces wortmannii	Soil	Yamagiwa et al. (2011)
	Trichoderma asperellum	Soil	Yedidia et al. (2001)

(continued)

Table 6.1 (continued)

Systematics	PGPF strain(s)	Original source of isolation	References
	T. atroviride	Soil	Contreras-Cornejo et al. (2011)
	T. hamatum strain	Soil	Shaw et al. (2016)
	T. harzianum	Soil, rhizosphere soil, Zoysiagrass (*Z. tenuifolia*) rhizosphere, vegetables, sunflower, legumes, and cereal roots	Hyakumachi (1994), Brotman et al. (2013), Jogaiah et al. (2013), and Akhter et al. (2015)
	T. longibrachiatum	Soil	Zhang et al. (2016)
	T. pseudokoningii	Decorticated wood	Lee et al. (2016)
	T. viride (BBA 70239)	Water-damaged building	
	T. virens Gv. 29-8	Soil	Contreras-Cornejo et al. (2009)
Basidiomycota	Non-sporulating sterile fungi *Limonomyces roseipellis* SRF1	Wheat (*Triticum aestivum*) root	Andjic et al. (2005)
	Non-sporulating sterile fungi	Zoysiagrass *(Z. tenuifolia)* rhizosphere, wheat (*T. aestivum*) roots	Sultana et al. (2008), Andjic et al. (2005)
	Rhizoctonia solani	Tomato (*Lycopersicon esculentum*) roots	Muslim et al. (2003)
	Piriformospora indica	Thar desert, India	Bhuyan et al. (2015)
	Rhodotorula mucilaginosa	Dark chestnut soil	Ignatova et al. (2015)
Zygomycota	*Mucor* spp.	Zoysiagrass (*Z. tenuifolia*) rhizosphere	Hyakumachi (1994)
	Rhizopus	Arsenic-contaminated soil	Srivastava et al. (2012)
Oomycota	*Phytophthora cryptogea*	Tomato (*L. esculentum*)	Attitalla et al. (2001)
	Pythium oligandrum	Soil	Benhamou et al. (2012)

extent, phyllosphere fungi (Vorholt 2012). However, there are fewer number of PGPF in the phyllosphere as opposed to the rhizosphere. This is because the phyllosphere is a short-lived habitat for microorganisms and, more importantly, the rhizosphere microbes have better nitrogen capacity than those at the phyllosphere (Mwajita et al. 2013).

6.3 Impact of the PGPF on Plant Growth and Development

Plant growth-promoting fungi are generally believed to be beneficial for all plant species they associate with, because of their conserved beneficial abilities. PGPF directly and indirectly influence the growth and productivity of a wide range of host plants. The reported benefits derivable from plant-PGPF interactions include the improvements in seed germination rate, seedling vigor, root development and morphogenesis, shoot growth, yield, photosynthetic efficiency, flowering, and plant composition (Table 6.2). Recent studies have reported that certain PGPF strains promote plant growth through the production of plant growth-promoting compounds such as phytohormones and volatiles (Harman et al. 2004; Naznin et al. 2013). Plant growth promotion by PGPF may also variously arise from enhanced nutrient availability, amelioration of abiotic stresses, and antagonism to phytopathogens (Wakelin et al. 2007; Hossain et al. 2014). PGPF, most likely, stimulate plant growth through one or more of these remarkably diverse arrays of mechanisms.

6.3.1 Seed Germination and Seeding Vigor

The beneficial effects of PGPF are observed from the very early stage of plant development influencing germination and seedling growth. Various species of PGPF differ greatly in their effect on seed germination and seedling growth. Cucumber seeds sown in soil amended with *T. harzianum* propagules showed a ~ 30% increase in seedling emergence, 8 days after sowing (Yedidia et al. 2001). A significant increase in early seedling emergence and vigor was observed in tomato after seed priming with *T. harzianum* TriH_JSB27, *Phoma multirostrata* PhoM_JSB17, *T. harzianum* TriH_JSB36, and *Pe. chrysogenum* PenC_JSB41, *T. harzianum* Bi application (Jogaiah et al. 2013). Similarly, it was shown that treatment with *Trichoderma* spp. SL2 enhanced rice seed germination and vigor (Doni et al. 2014a). As per the findings of Mushtaq et al. (2012), presoaking of seeds in the culture filtrates of the nine *Penicillium* isolates was highly effective in significantly increasing seed germination in tomato when compared with the control seeds. Similar improvement in seed germination and seedling vigor in different plants was also found with treatment by other PGPF (Vujanovic and Goh 2012; Islam et al. 2014a, b) (Table 6.2).

PGPF colonization at the seed state has been proved to be beneficial for plant survival and timely seedling establishment (Baskin and Baskin 2004). Fungal isolates belonging to *Clonostachys rosea* controlled pre- and postemergence death caused by *A. dauci* and *A. radicina*, resulting in a higher number of healthy seedling

Table 6.2 Effect of different plant growth-promoting fungi on seed germination, plant growth, and yield in various plants

Growth traits	PGPF strain	Test crop	Specific effects	References
Germination and seedling vigor	*Talaromyces wortmannii* FS2	*Brassica campestris* L. var. *perviridis*	Enhanced seedling growth	Yamagiwa et al. (2011)
	Clonostachys rosea IK726	Carrot (*D. carota*)	Improved emergence and emergence time	Bennett et al. (2009)
		Onion (*Allium cepa*)		
	Cl. rosea	Carrot (*D. carota*)	Higher healthy seedling stand due to reduction in damping off caused by *A. dauci* and *A. radicina*	Jensen et al. (2004), and Szopińska et al. (2010)
	T. harzianum	Cucumber (*C. sativus*)	~ 30% increase in seedling emergence	Yedidia et al. (2001)
	Aspergillus spp. PPA1		Increased seed germination and seedling vigor	Islam et al. (2014a)
	Fusarium spp. PPF1	Indian spinach (*Basella alba*)	Higher germination percentage and increased vigor index	Islam et al. (2014b)
	T. harzianum	Maize (*Zea mays*)	Reduced *F. verticillioides* and fumonisin incidence and increased field emergence	Nayaka et al. (2010)
	T. harzianum Bi	Muskmelon (*C. melo*)	Augmented seed germination	Kaveh et al. (2011)
	Pe. chrysogenum, *Phoma* sp., and *T. koningii*	*Opuntia streptacantha*	Broke seed dormancy	Delgado-Sanchez et al. (2011)
	T. harzianum	Rice (*Oryzae sativa*)	Improvement in plant stand establishment	Rahman et al. (2015)
	Trichoderma spp. SL2		Increased seed germination and seedling vigor	Doni et al. (2014a, b)
	T. harzianum	Sunflower (*Helianthus annuus*)	Increased seed germination and seedling vigor	Nagaraju et al. (2012)
	Rhizopus sp.	*Thelocactus hexaedrophorus*	Broke seed dormancy	Arredondo et al. (2007)
	Penicillium spp.	Tomato (*Lycopersicon lycopersicum*)	Increased seed germination	Mushtaq et al. (2012)
	T. harzianum T-22		Under stress, treated seed germinated consistently faster and more uniformly	Mastouri et al. (2010)
	T. harzianum TriH_JSB27, TriH_JSB36		Enhanced early seedling emergence and seedling vigor	Jogaiah et al. (2013)
	Phoma multirostrata PhoM_JSB17			
	Pe. chrysogenum PenC_JSB41			

	Sphaerodes mycoparasitica	Wheat (*T. aestivum*)	Improved seed germination and seedling growth	Vujanovic and Goh (2012)
	Pi. Indica	Wheat (*T. aestivum*), chickpea (*Cicer arietinum*), bean (*Phaseolus vulgaris*)	Broke seed dormancy	Varma et al. (2012)
Shoot growth	*Pe. janthinellum* GP16-2	*Arabidopsis thaliana*	Increased shoot biomass and number of rosette leaves per plant.	Hossain et al. (2008a)
	Pe. simplicissimum GP17-2		~72% and 55% increase in shoot fresh and dry biomass, respectively, and one more rosette leaf per plant	Hossain et al. (2007)
	T. viride (BBA 70239)	*A. thaliana*, tomato (*L. lycopersicum*)	Increased fresh shoot weight	Lee et al. (2016)
	Fusarium oxysporum NRRL 38499, NRRL 26379, and NRRL 38335	*A. thaliana*, tobacco (*Nicotiana tabacum*)	~85% increase in shoot fresh and dry biomass	Bitas et al. (2015)
	T. virens Gv. 29-8	*A. thaliana*	Increased shoot biomass production	Contreras-Cornejo et al. (2009)
	Pe. citrinum IR-3-3	*Atriplex gemelinii*, *Waito-c* rice *(S. japonica)*	Enhanced shoot length	Khan et al. (2008)
	Preussia sp. BSL10	*Boswellia sacra*	Increased shoot length, number of internodes and leaf number	Khan et al. (2016)
	A. niger 1B and 6A	*Brassica chinensis*	Enhanced shoot biomass	Chuang et al. (2007)
	Pe. resedanum LK6	*Capsicum annuum* L.	Improved shoot growth	Khan et al. (2015)
	A. niger BHUAS01	Chickpea (*C. arietinum*)	Enhanced shoot length and shoot biomass	Yadav et al. (2011)
	Pe. citrinum BHUPC01			
	T. harzianum			

(continued)

Table 6.2 (continued)

Growth traits	PGPF strain	Test crop	Specific effects	References
	Pe. Menonorum	Cucumber (*C. sativus*)	~52% increase in shoot dry biomass	Babu et al. (2015)
	Pe. viridicatum GP15-1		Enhanced shoot length and shoot biomass	Hossain et al. (2014)
	Pe. simplicissimum GP17-2		Enhanced the plant shoot dry weight	Chandanie et al. (2009)
	T. harzianum GT3-2			
	F. equiseti GF19-1		Enhanced the shoot dry weight of cucumber plants	Saldajeno and Hyakumachi (2011)
	Aspergillus spp. PPA1		Augmented the shoot length as well as fresh and dry biomass	Islam et al. (2014a)
	Exophiala sp. LHL08		Enhanced shoot length, fresh weight, and dry weight	Khan et al. (2011b)
	Phoma sp. and sterile fungus		Increased shoot length, dry biomass, and number of leaves	Shivanna et al. (2005)
	Phoma sp.		Increased the shoot dry weight	Chandanie et al. (2005)
	T. harzianum T-22	GiSeLa6® (*Prunus cerasus* × *P. canescens*)	Improved shoot growth	Sofo et al. (2012)
	Fusarium spp. PPF1	Indian spinach (*Basella alba*)	Increased shoot length, shoot fresh and dry biomass	Islam et al. (2014b)
	F. oxysporum MSA 35	Lettuce (*Lactuca sativa*)	Increased shoot length (75.0%) and fresh weight (85.8%)	Minerdi et al. (2011)
	T. harzianum T-22	Maize (*Z. mays*)	Produced larger shoots	Harman et al. (2004)
	T. harzianum	Melon (*C. melo*)	Increased shoot fresh weight	Martínez-Medina et al. (2014)
	T. ghanense			
	T. hamatum			
	T. atroviride	*Miscanthus* × *giganteus*	Enhanced plant height	Chirino-Valle et al. (2016)
	Penicillium spp. NICS01 and DFC01	Sesame (*Sesamum indicum*)	Enhanced shoot length and biomass	Radhakrishnan et al. (2014)
	Aspergillus ustus	*Solanum tuberosum*, *A. thaliana*	Increased shoot fresh weight	Salas-Marina et al. (2011)

	Phoma herbarum TK- 2-4	Soybean (*Glycine max*)	Enhanced plant length and biomass	Hamayun et al. (2009b)
	A. fumigatus HK-5-2		Enhanced shoot length, shoot fresh and dry weight	Hamayun et al. (2009a)
	F. equiseti GF183	Spinach (*Spinacia oleracea*)	Improved shoot growth	Horinouchi et al. (2010)
	Alternaria sp. A7, A38	Tobacco (*N. tabacum*)	Increased shoot dry biomass and leaf area	Zhou et al. (2014)
	Phomopsis sp. H25			
	Cladosporium sp. B50			
	Cladosporium sp. MH-6	*Waito-c* rice *(Suaeda japonica)*	Improved shoot length, shoot fresh and dry biomass	Hamayun et al. (2010)
	Penicillium sp. Sj-2-2		Enhanced shoot length	You et al. (2012)
	A. niger NCIM	Wheat (*T. aestivum*)	~200% increase in shoot: Total length ratio	Gujar et al. (2013)
Root growth	*T. virens* Gv. 29-8	*Arabidopsis thaliana*	Induced production of lateral root (LR)	Contreras-Cornejo et al. (2009)
	P. indica		Increased number of RH	Peskan-Berghofer et al. (2004)
	As. ustus	*A. thaliana*, potato (*S. tuberosum*)	Increased root fresh weight and number of LR and RH	Salas-Marina et al. (2011)
	Ta. wortmannii FS2	*Br. campestris* L. var. *perviridis*	Increased root length (22.37%) and fresh biomass	Yamagiwa et al. (2011)
	T. harzianum T-22	Cherry rootstocks (*Prunus cerasus* x *P. canescens*)	Produced larger root	Sofo et al. (2011)
	Pi. indica	Chinese cabbage (*Brassica rapa*)	A twofold longer elongation zone, a 1.5-fold thicker epidermal and cortex layer, and a 1.4-fold higher biomass of the LR	Dong et al. (2013)
	Pi. indica	Chinese cabbage (*B. rapa*), *A. thaliana*	Promoted RH development	Lee et al. (2011)
	Pe. viridicatum GP15-1	Cucumber (*C. sativus*)	Enhanced fresh and dry weight and root length	Hossain et al. (2014)
	Epichloë festucae	*Festuca rubra*	Greater root biomass	Vázquez-de-Aldana et al. (2013)

(continued)

Table 6.2 (continued)

Growth traits	PGPF strain	Test crop	Specific effects	References
	T. harzianum T-22	GiSeLa6® (*Prunus cerasus* × *P. canescens*)	~76% increase in mean root length	Sofo et al. (2012)
	Fusarium spp. PPF1	Indian spinach (*Basella alba*)	Increased root length, root fresh and dry biomass	Islam et al. (2014b)
	F. oxysporum MSA 35	Lettuce (*Lactuca sativus*)	Increased root length and fresh weight	Minerdi et al. (2011)
	T. harzianum T-22	Maize (*Zea mays*)	Promoted deeper and robust roots with greater surface area	Harman et al. (2004)
	T. harzianum	Melon (*C. melo*)	Increased root fresh weight	Martínez-Medina et al. (2014)
	T. ghanense			
	T. hamatum			
	Dark spot endophytic fungus EF-37	*Saussurea involucrate*	Increased number of RH	Wu et al. (2010)
	Penicillium spp. NICS01 and DFC01	*Sesame (Sesamum indicum)*	Enhanced root length and biomass	Radhakrishnan et al. (2014)
	Mycocentrospora spp. (EF-37)	Snow lotus (*S. involucrate*)	Promoted root growth and number of RH	Wu et al. (2010)
	A. fumigatus HK-5-2	Soybean (*G. max*)	Enhanced root length, root fresh and dry weight	Hamayun et al. (2009a)
	F. equiseti	Spinach (*Spinacia oleracea*)	Improved root growth.	Horinouchi et al. (2010)
	M. robertsii	Switch grass (*Panicum virgatum*)	Increased root lengths, root hair (RH) density, and LR emergence	Sasan and Bidochka (2012)
		Haricot beans (*Phaseolus vulgaris*)		
	T. viride	Tomato (*L. lycopersicum*)	Enhanced LR development	Lee et al. (2016)
Photosynthetic efficiency	*T. viride* (BBA 70239)	*A. thaliana*, tomato (*L. lycopersicum*)	Increased chlorophyll content	Lee et al. (2016)
	Epichloë endophyte	*Achnatherum Inebrians*	Increased the chlorophyll content and net photosynthetic rate under *Blumeria graminis* infection	Xia et al. (2016)
	Pi. indica	*Aloe vera*	Increased Chl a, Chl b, and total Chl under high salinity	Sharma et al. (2016)

	Preussia sp. BSL10	*Boswellia sacra*	Enhanced photosynthetic pigments	Khan et al. (2016)
	Pe. menonorum	Cucumber (*C. sativus*)	Increased leaf chlorophyll contents	Babu et al. (2015)
	F. oxysporum MSA35	Lettuce (*L. sativa*)	~68% increase in leaf chlorophyll content	Minerdi et al. (2011)
	T. hamatum DIS 219b	Maize (*Z. mays*)	Increased chlorophyll contents in the drought-tolerant plant	Bae et al. (2009)
	T. virens		Increase photosynthetic rate	Vargas et al. (2009)
	T. atroviride TaID20G		Improved the chlorophyll under drought stress	Guler et al. (2016)
	Epichloë typhina	Orchard grass (*Dactylis glomerata*)	Improved chlorophyll b contents, abundance of LHCI and LHCII proteins and photosynthesis efficiency	Rozpądek et al. (2015)
	Metarhizium anisopliae LHL07	Soybean (*G. max*)	Higher chlorophyll contents and photosynthetic rate under salt stress	Khan et al. (2012)
	Pe. funiculosum LHL06		Chlorophyll contents in soybean plant under Cu stress	Khan and Lee (2013)
	As. fumigatus sp. LH02		Increased leaf area, chlorophyll contents, and photosynthetic rate	Khan et al. (2011a)
	Alternaria sp. A7, A38	Tobacco (*N. tabacum*)	Increased leaf chlorophyll content	Zhou et al. (2014)
	Phomopsis sp. H25			
	Cladosporium sp. B50			
Flowering	*Pe. chrysogenum*, *Saccharomyces cerevisiae*, *Pe. Aurantiogriseum*	*A. thaliana*	Promoted flowering	Sánchez-López et al. (2016)
	Pochonia chlamydosporia		Led to accelerated flowering	Zavala-Gonzalez et al. (2017)
	T. viride	*A. thaliana*, *C. forskohlii*	Showed robust and early flowering phenotype	Hung et al. (2014)
	Pi. indica	*Coleus forskohlii*	Induced early and vigorous flowering	Das et al. (2012)
	Sebacina vermifera	*Nicotiana attenuate*	Flowered earlier, produced more flowers, and matured more seed capsules	Barazani et al. (2005)

(continued)

Table 6.2 (continued)

Growth traits	PGPF strain	Test crop	Specific effects	References
	T. harzianum	Periwinkle (*Catharanthus roseus*), alyssum (*Lobularia maritima*), and marigold (*Tagetes erecta*)	Enhanced numbers of flower buds in chrysanthemum and petunia	Chang et al. (1986)
			Early flowering occurred in periwinkle, alyssum, and marigold	
	Pochonia chlamydosporia	Tomato (*L. lycopersicum*)	Led to accelerated flowering	Zavala-Gonzalez et al. (2015)
	T. viride (BBA 70239)		Acceleration of flower and fruit development	Lee et al. (2016)
	T. harzianum TriH_JSB27, and *Pe. Chrysogenum* PenC_JSB41		Induced early flowering	Jogaiah et al. (2013)
	Trichoderma spp.	*Verbena*, *Petunia*	Enhanced numbers and weight of flowers in verbena and numbers of flowers and buds in petunia	Ousley et al. (1994)
Crop yields	*Pochonia chlamydosporia*	*A. thaliana*	Increased seed production per plant	Zavala-Gonzalez et al. (2017)
	F. oxysporum V5 W2, Eny 7.11o, and Emb 2.4o	Banana (*Musa* sp.)	Up to ~20 to ~36% yield increase	Waweru et al. (2014)
	Pi. indica	Barley (*Hordeum vulgare*)	Increased grain yield	Waller et al. (2005)
	T. harzianum T-75	*Chickpea* (*Ci. arietinum*)	Enhanced grain yield in the field	Hossain et al. (2013)
	Phoma sp. and sterile fungus GU21-2	Cucumber (*C. sativus*)	Enhanced number and fresh biomass of marketable cucumbers	Shivanna et al. (2005)
	Pe. menonorum		Enhanced yield	Babu et al. (2015)
	T. harzianum	Mustard (*B. nigra*), Tomato (*L. lycopersicum*)	Enhanced yield	Haque et al. (2012)
	T. harzianum T-3	*Pea (Pisum sativum)*	Enhanced grain yield in the field	Akhter et al. (2015)
	T. viride	Sugarcane (*Saccharum officinarum*)	Increased cane yield	Yadav et al. (2009)
	T. harzianum		Increased millable canes, yield, and commercial cane sugar (CCS t/ha)	Srivastava et al. (2006)
	T. viride			
	Pi. indica	Thyme (*Thymus vulgaris*), *Foeniculum vulgare*	Increased essential oil yield	Dolatabadi et al. (2011)
	Sebacina vermifera			

	Po. chlamydosporia	Tomato (*L. lycopersicum*)	Increased number of marketable fruits, and fruits per plant, total fruit weight, and mature fruit weight per plant	Zavala-Gonzalez et al. (2015)
	T. viride (BBA 70239)		Enhanced tomato fruit yield	Lee et al. (2016)
	R. solani		Higher marketable and total yield	Muslim et al. (2003)
Photosynthetic and bioactive compounds	*Pi. indica*	*Aloe vera*	Higher phenol, flavonoid, flavonol, aloin contents, and radical scavenging activity at different salinity concentrations	Sharma et al. (2016)
	Pi. indica	*Artemisia annua* L.	Enhanced artemisinin content	Sharma and Agrawal (2013)
	Gilmaniella sp. AL12	*Atractylodes lancea*	Higher Sesquiterpenoid content	Wang et al. (2012)
	T. viride	*Coleus forskohlii*	Enhanced forskolin yield in roots	Boby and Bagyaraj (2003)
	Pi. indica	*Centella asiatica*	Enhanced asiaticoside content	Satheesan et al. (2012)
	Pi. indica	*Chlorophytum* sp.	Enhanced saponin content	Gosal et al. (2010)
	Pi. indica	*Coleus forskohlii*	Enhanced *p*-cymene in aerial parts	Das et al. (2012)
	Pe. menonorum	Cucumber (*C. sativus*)	Enhanced starch and protein content in leaves	Babu et al. (2015)
	Pi. indica	Fennel (*Foeniculum vulgare*)	Increased anethole level in fruit	Dolatabadi et al. (2011)
	Sebacina vermifera			
	Pi. indica	*Linum album*	Enhanced production of podophyllotoxins in *L. album* cells	Baldi et al. (2010)
	Neotyphodium lolii	*Lolium perenne* cv SR4000	Higher accumulation of soluble sugars in leaves under mild drought stress and starch under severe drought stress	Ren et al. (2006)
	Westerdykella aurantiaca FNBR-3	Rice (*O. sativa* L. var. IR-36)	Enhanced carotenoid and protein content	Srivastava et al. (2012)
	T. longibrachiatum FNBR-6	Pea (*P. sativum* L. var. PG-3)		
	T. atroviride D16	*Salvia miltiorrhiza*	Higher tanshinone I (T-I) and tanshinone IIA (T-IIA) content	Ming et al. (2013)
	Pi. indica	*Spilanthes calva*	Increase in spilanthol content	Rai et al. (2004)

(continued)

Table 6.2 (continued)

Growth traits	PGPF strain	Test crop	Specific effects	References
	T. harzianum	Sunflower (*H. annuus*)	Starch, total soluble sugars, reducing sugar, phenol, lipid and linoleic acid content	Lamba et al. (2008)
	Pi. indica	Thyme (*Thymus vulgaris*)	Enhanced level of thymol in fruit	Dolatabadi et al. (2011)
	Se. vermifera			
	As. niger	Tomato (*L. lycopersicum*)	Increased accumulation of salicylic acid, total phenolic and chlorophyll contents of plant, as well as lycopene, ascorbic acid (Vitamin C), and Brix index of fruit	Anwer and Khan (2013)
	T. longibrachiatum T6	Wheat (*T. aestivum*)	Higher soluble sugar and protein content	Zhang et al. (2016)

stand in carrot (Jensen et al. 2004; Szopińska et al. 2010). Priming seed with the same fungus also improved rate and time of seedling emergence in carrot and onion (Bennett et al. 2009). Maize seed treated with *T. harzianum* reduced the *F. verticillioides* and fumonisin incidence and increased the field emergence (Nayaka et al. 2010). Rahman et al. (2015) reported that *T. harzianum* seed treatment significantly contributed to the improvement of plant stand establishment in rice. These demonstrate that PGPF facilitate seed germination by nullifying adverse effects of dangerous seed-borne pathogens (Szopińska et al. 2010). Some PGPF may also function to overcome seed dormancy. Seed treatment with *P. indica* culture filtrate was effective in breaking the seed dormancy of *Triticum aestivum*, *Cicer arietinum*, and *Phaseolus vulgaris* (Varma et al. 2012). Arredondo et al. (2007) found that *Rhizopus* sp. was moderately effective in breaking dormancy of *Thelocactus hexaedrophorus* seeds. Olvera-Carrillo et al. (2009) observed that 7-month-old exhumed seeds of *Opuntia tomentosa* were colonized by fungal hyphae that penetrated the funicular envelope through the openings and favored germination of the weak embryo. Delgado-Sánchez et al. (2011) reported that inoculation of *O. streptacantha* seed with *P. chrysogenum*, *Phoma* sp., and *T. koningii* helped to break seed dormancy. Scanning electron microscopy revealed that these fungi had been able to erode the funiculus, thus reducing its resistance to germination. It may be possible that enzyme production by the fungal hyphae assists in seed stratification or replacement of scarification process. Fungi may also grow on the testa and erode or crack the hard stony endocarp. Consequently, they can potentially reduce mechanical resistance to germination (Morpeth and Hall 2000). The other possibilities are production of germination-inducing volatiles and degradation of water-soluble germination inhibitors associated with the outer surface of the seed (de Boer et al. 2005).

Orchid seeds also need a fungus for germination in nature. Orchid seeds lack endosperm and no significant food reserves. Exogenous supply of carbohydrates is required for orchid seed germination. After the formation of the protocorm, additional development does not occur until sugar molecules are supplied. Symbiotic fungi are the main source of sugars. When hyphae are broken, sugars are released into the orchid cells. The most common genus of fungi that stimulates germination of orchids and promotes growth of protocorms and seedlings is *Rhizoctonia* (Chou and Chang 2004). In addition, *Penicillium*, *Chaetomium*, *Choanephora*, and some other fungi are also known to stimulate germination in orchid seeds (Baskin and Banskin 2014). This improvement in germination and seedling vigor is attributed to the provision of compounds essential to germinating seeds and young plants by PGPF. Production of hormones such as gibberellins (GAs) and cytokinin (CK) by the fungi may also have a role in stimulating seed germination (Gupta and Chakrabarty 2013).

6.3.2 Shoot Growth

Although PGPF is restricted to roots, there are numerous changes in the phenotypic responses of shoots, indicating that the effects of these fungi are systemic. There are numerous field and growth chamber experiments, which have reported the shoot growth enhancement by PGPF. Members of the genus *Aspergillus*, *Fusarium*, *Trichoderma*, *Penicillium*, *Rhizoctonia*, *Exophiala*, *Phoma*, *Alternaria*, *Phomopsis*, *Cladosporium*, and *Colletotrichum* were often the most effective in eliciting their effects on shoot growth (Table 6.2). Shoot growth enhancement has been observed across a broad range of species, including Arabidopsis, tomato, tobacco, *brassica chinensis*, chilli, chickpea, cucumber, Indian spinach, lettuce, maize, melon, sesame, potato, soybean, spinach, wheat, etc. Reported studies have revealed that inoculation of these plants with PGPF promotes significantly greater shoot length and/or shoot biomasses in these plants. Application of root endophytic *Trichoderma* isolates significantly enhanced plant height of a second-generation energy crop *Miscanthus* × *giganteus* (Chirino-Valle et al. 2016). Similarly, inoculation with a *Pe. menonorum* isolate significantly increased the dry biomass of cucumber shoots (~52%) (Babu et al. 2015). Some species have been shown to produce large-leaved plants. Cucumber plants inoculated with a PGPF *Pe. simplicissimum* GP17-2 grew larger and produce ~1.5–2.0 times larger leaf than normal plants (Fig. 6.2). The results are in agreement with numerous growth chamber and field experiments, which have shown that PGPF inoculants can modulate plant shoot growth (Table 6.2).

Proteomes or genes triggered by PGPF in treated plants exhibit the mechanisms associated with the enhanced stem and leaf growth. Shoresh and Harman (2008)

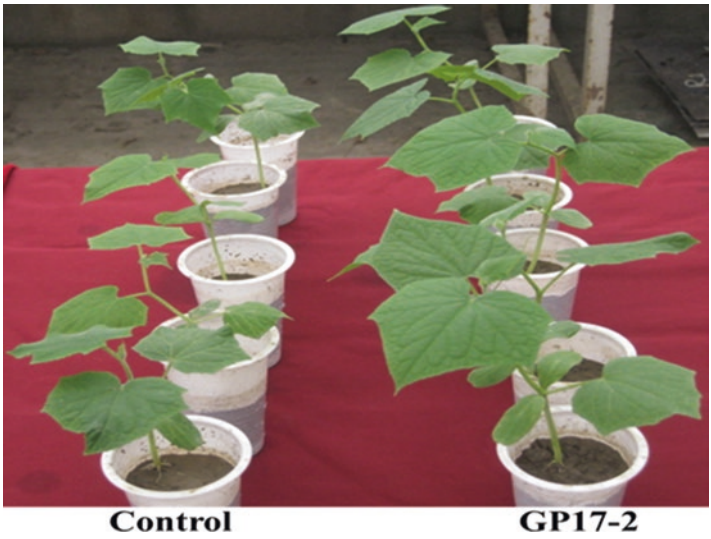

Fig. 6.2 Seedlings of cucumber cv. Baromashi (21 days old) grown in soil treated with (GP17-2) or without (control) a PGPF *Penicillium simplicissimum* GP17-2

revealed that proteins involved in carbohydrate metabolism were strongly affected in the shoots due to *Trichoderma* colonization of maize roots. The important identified proteins included fructokinase (FRK), Fru-bisphosphate aldolase (FBA), glyceraldehyde-3-P dehydrogenase (GAPDH), malate dehydrogenase (MDH), β-glucosidases, 3-phosphoglycerate kinase, and oxalate oxidases. FRK2 from tomato was shown to be expressed abundantly in leaves and essential for stem growth and vascular development (Odanaka et al. 2002; Damari-Weissler et al. 2009). Suppression or reduced expression of this gene resulted in smaller cell size in the xylem and phloem and much shorter plants (Odanaka et al. 2002; Damari-Weissler et al. 2009). Strong expression of FRK2 in stems confirms a similar role. Cotton plants transformed with a tomato fructokinase gene (*LeFRK1*) had larger leaf areas and stem diameters (Mukherjee et al. 2015). Increased FBA in plastids enhances growth of tobacco plants (Uematsu et al. 2012). As a member of the tricarboxylic acid cycle, MDH is involved in providing reducing power and is involved in photosynthetic fixation of CO_2 (Nunes-Nesi et al. 2005). Single- and double-knockout mutants of the mitochondrial MDH isoforms in Arabidopsis showed no detectable MDH activity, and the resulted plants were small and slow growing. These confirm that activation of carbohydrate metabolism in plants by PGPF contributes to the enhanced shoot growth.

Plant growth-promoting effect of PGPF is not necessarily limited to direct interaction of plants with fungi in the rhizosphere. Fungal elicitors such as culture filtrate produced by PGPF have also demonstrated a strong positive influence on the shoot growth of plants. Addition of *T. harzianum* culture filtrate in the growth medium of *Centella asiatica* resulted in significantly higher shoot dry weight (Prasad et al. 2012). Culture filtrate of *F. oxysporum* and *T. viridi* also significantly enhanced shoot growth of Arabidopsis and tomato, respectively (Bitas et al. 2015; Lee et al. 2016). The presence of gibberellic acids (GA4, GA9, and GA34), indole-3-acetic acid (IAA), and high concentrations of phosphate in the fungal culture filtrate is responsible for promoting host shoot growth (Khan et al. 2008; Kang et al. 2015). PGPF species are also abundant producers of small volatile metabolites. Co-cultivating plants with volatile-producing fungi or exposure of plants directly to volatile organic compounds (VOCs) induces shoot growth. Fungal VOCs emitted by different species and strains of *Trichoderma* augmented plant biomass and size of Arabidopsis (Lee et al. 2016). Similarly, tobacco plant growth was enhanced significantly, when they were grown in the presence of VOCs produced by *Phoma* sp. (Naznin et al. 2013). The PGPF VOCs have diverse chemical structures and are produced as mixture of hydrocarbons, ketones, amines, thiols, terpenes, alcohols, aldehydes, acids, ethers, esters, and their derivatives (Korpi et al. 2009; Lemfack et al. 2014; Lee et al. 2016). Their effects on plant growth depend on fungal species, culture conditions, plant developmental stage, and duration of the exposure (Hung et al. 2013; Lee et al. 2015). It is thought that promotion of plant growth by microbial VOCs is mainly due to CO_2 enrichment during co-cultivation (Kai and Piechulla 2009). However, Bitas et al. (2015) found no significant difference in CO_2 production among volatile-producing and neutral strains of *F. oxysporum*. Therefore, increased CO_2 production solely may not drive plant growth enhancement by PGPF VOCs.

6.3.3 Root Growth and Performance

The main functions of plant roots are to explore soil and acquire nutrients to support growth and development of the plant. The plant root system is in closest contact with soil microbial populations; therefore, the root system functions under the direct influence of microbial interaction. Many of the reported PGPF have long been known to significantly enhance the root growth. Plants inoculated with some PGPF had greater root biomass of the root system than the control plants (Zhang et al. 2012; Vázquez-de-Aldana et al. 2013; Hossain et al. 2014; Islam et al. 2014b). Other effects associated with PGPF colonization on roots were faster-growing roots and roots that grew for prolonged periods, causing the development of longer and larger root systems (Björkman et al. 1998; Hossain et al. 2014). Maize roots inoculated with *Trichoderma* were deeper, more robust, and had greater surface area (Harman et al. 2004). Similarly, the treatment of potting medium with barley grain inoculum of *Pe. simplicissimum* GP17-2 significantly increased root growth of cucumber plants, producing a longer and larger root system 3 weeks after planting (Fig. 6.3). There are also PGPF strains that can cause alterations in the root system architecture (RSA) of host plants. RSA is a complex notion that captures aspects of root structure and root shape (Pages 1992). The importance of RSA lies in the fact that it is a key determinant of nutrient- and water-use efficiency in plants. Moreover, RSA determines largely the extent of contact and interaction between the plant and the rhizosphere (Orman-Ligeza et al. 2013). The RSA is evolved from three main processes: (1) indeterminate growth of the main root, a process originated by the root meristem; (2) lateral root (LR) formation; and (3) root hair (RH) formation (Scheres et al. 2002). Each of the apparatuses that constitute the RSA has distinct roles. However, LR and RH constitute the most important traits of the root architecture that facilitate plant anchorage and increase the root's exploratory capacity for water and minerals. PGPF are well noted for their effects on LR and RH morphology.

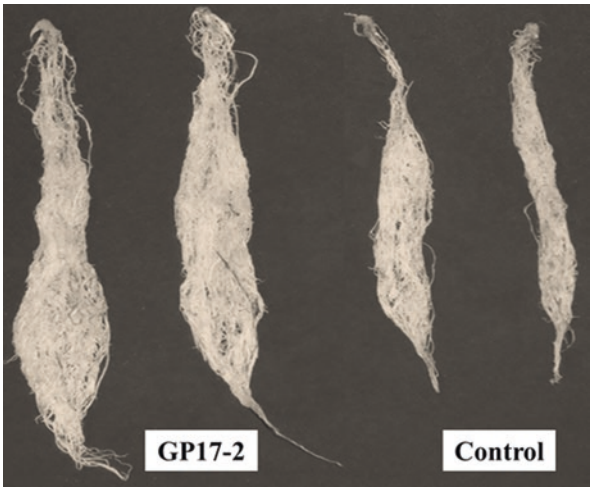

Fig. 6.3 Roots of cucumber cv. Baromashi (21 days old) grown in soil treated with (GP17-2) or without (control) a PGPF *Penicillium simplicissimum* GP17-2

Increased root branching via LR formation has been observed as a response to colonization by some PGPF species (Harrison 2005). *Trichoderma* spp. were highly efficient in inducing LR production in *A. thaliana* (Contreras-Cornejo et al. 2009). Inoculation of *As. ustus* on *A. thaliana* and *S. tuberosum* roots induced an increase in root growth and LR and RH numbers (Salas-Marina et al. 2011). The dark spot endophytic fungus EF-37 increased the RH number in *Saussurea involucrata* (Wu et al. 2010). RH development was strongly promoted in Chinese cabbage and *A. thaliana* by *Pi. indica* (Lee et al. 2011). On average, *Pi. indica* colonization resulted in a ~ 2-fold longer elongation zone, a ~ 1.5-fold thicker epidermal and cortex layer, and a ~ 1.4-fold higher biomass of the lateral roots, compared with the uncolonized control (Dong et al. 2013). This basidiomycete alters root growth in a number of other plant species (Varma et al. 1999; Peskan-Berghofer et al. 2004). Other endophytic fungi also cause similar changes in LR and RH (Malinowsky et al. 1999; Sasan and Bidochka 2012). There are also fungi that stimulate lateral root formation and increase root hair length through release of VOCs (Felten et al. 2009).

The mechanisms by which PGPF alter root systems have recently been started to be dissected at the genetic and molecular levels (Contreras-Cornejo et al. 2009). Stimulation of LR development seems to be an early phase of interaction in nonphytopathogenic, root-colonizing fungi (Felten et al. 2009). Microbial-induced increase in the number and/or length of LR and RH is thought to be caused by reduction in growth rate of the primary root (Contesto et al. 2008; Combes-Meynet et al. 2011; Chamam et al. 2013). Signals originating from the fungi target primarily the meristematic elongation zone in roots and activate the growth-stimulating programs (Dong et al. 2013). Auxin has a critical role during this developmental process from founder cell specification to LR emergence (Dubrovsky et al. 2008). However, high fungal IAA (auxin) production does not always lead to the highest rooting frequency (Niemi et al. 2002). Similarly, exogenous application of auxin did not stimulate the morphological changes in Chinese cabbage roots, which were observed after *Pi. indica* colonization (Lee et al. 2011). These observations are in line with a study by Hilbert et al. (2012) which have also demonstrated that production of indole derivatives by the fungus is not required for growth promotion of barley root. Therefore, the root-stimulating effects are suggested to be mediated by auxin of plants and not fungal auxin (Lee et al. 2011).

A decrease in CK content was induced by the isolates of *Trichoderma* that promoted the root growth of melon plants (Martínez-Medina et al. 2014). Sofo et al. (2011) also observed a significant decrease in trans-zeatin and in dihydrozeatin, two of the most active CKs in plants shoots and roots, following the inoculation with *T. harzianum* T-22. This indicates that CK has an opposing role in root development, although major sites of CK synthesis are considered to be root tips (Aloni et al. 2005). Exogenous application of CK at physiological concentrations suppresses root growth and reverses the IAA effects (Lloret and Casero 2002). A low CK level in CK-deficient transgenic plants overexpressing the CK oxidase/dehydrogenase (*CKX*) genes is seen to cause an enlarged root meristem, formation of LR closer to the root apical meristem, increased root branching, and promotion of adventitious root formation (Lohar et al. 2004). Similarly, abscisic acid (ABA) and ethylene (ET)

cascades share some common features in terms of mediation of root growth. The concentration of ABA and the ET precursor 1–aminocyclopropane-1–carboxylate (ACC) was decreased by isolates of *T. harzianum* (T-4, T-7, and T-22) (Martínez-Medina et al. 2014). A low concentration of both promotes root growth, and high concentrations inhibit root growth (Joshi-Saha et al. 2011; Arc et al. 2013). Previous studies have demonstrated root that growth inhibition by high concentrations of ABA requires ET signaling components but not ET production (Beaudoin et al. 2000; Ghassemian et al. 2000). This discussion implies that, as for other physiological processes, root growth is usually not regulated by hormonal levels per se but rather the complex balances between various hormones (Müller and Leyser 2011).

6.3.4 Photosynthetic Efficiency

The main source of carbon for green plants is photosynthesis. Higher photosynthetic potential may result in increased carbon assimilation in plants, which is the basis for faster development and higher biomass production. It has been reported that many of the studied PGPF clearly influence photosynthesis-related mechanisms in plant allowing to meet elevated energy demands. The changes in leaf architecture, leaf numbers, leaf chlorophyll levels, and photosynthetic rate are often the effects associated with plant's response to PGPF colonization. According to earlier reports, Arabidopsis plants treated with *Pe. simplicissimum* GP17-2 and *Pe. janthinellum* GP16-2 increased number of rosette leaves per plant (Hossain et al. 2007, 2008a), while soybean plants inoculated with *As. fumigatus* sp. LH02 significantly increased leaf area, chlorophyll contents, and photosynthetic rate as compared to non-inoculated plants (Khan et al. 2011b). Similar increases in the content of photosynthetically active pigments as well as the photosynthesis efficiency were reported in plants upon different PGPF colonization (Babu et al. 2015; Rozpądek et al. 2015; Khan et al. 2016; Per et al. 2016). Additionally, the abundance of light-harvesting chlorophyll a−/b-binding proteins LHCI and LHCII was significantly higher in *Epichloë typhina*-treated orchard grass (Rozpądek et al. 2015).

Many of these studies also show that PGPF is utilized to enhance photosynthesis under suboptimal conditions. Bae et al. (2009) observed increased chlorophyll contents in the drought-tolerant *T. hamatum* DIS 219b–colonized seedlings. *Metarhizium anisopliae* LHL07-inoculated soybean plants showed significantly higher chlorophyll contents, transpiration rate, photosynthetic rate, and leaf area, under salt stress as compared to non-inoculated control plants (Khan et al. 2012). Similarly, *Pe. funiculosum* LHL06 symbiosis increased chlorophyll contents in soybean plan under Cu stress (Khan and Lee 2013). Root colonization with *T. atroviride* TaID20G improved the chlorophyll and carotenoid synthesis in maize seedlings, contributing to the alleviation of the drought stress (Guler et al. 2016). PGPF also increase the chlorophyll content and photosynthetic rate in host plant under pathogen stress (Vargas et al. 2009; Xia et al. 2016). Loss of chlorophyll and carotenoid contents under biotic and abiotic stress regimes are frequently the primary causes of inactivation of photosynthesis (Xia et al. 2016). Hence, the positive effects of PGPF on

photosynthesis in plants can be ascribed, at least partially, to very efficient use of light as a consequence of enhanced accumulation of photosynthetic pigments and improved net photosynthetic rate (Sánchez-López et al. 2016).

Until recently, little is known about the molecular mechanisms of PGPF-mediated photosynthesis improvement in plants. PGPF may have the ability to switch the cellular mechanisms in the shoot, in consequence increasing photosynthetic efficiency. In order to elucidate the key changes in photosynthesis-related protein levels in plant shoots, Shoresh and Harman (2008) have examined the expression of proteins in maize shoot after root colonization by *T. asperellum* T-22. Upregulation of four spots associated with photosynthesis, including two forms of Rubisco large subunit, Rubisco, and PSII oxygen-evolving complex protein 2, were observed in shoots of *T. harzianum* T-22-treated plants. Similarly, Vargas et al. (2009) detected the transcriptional upregulation of two photosynthetic genes, rubisco small subunit (*rbc*S) and the oxygen-evolving enhancer 3–1 (*oee3–1*), in leaves of maize plants inoculated with *T. virens.* Upregulation of *rbc*S was also identified in the leaves of *Trichoderma*-challenged common bean plants (Pereira et al. 2014). The increased expression of these photosynthesis genes is suggestive of a higher photosynthetic rate in PGPF treated than control plants. Moreover, photosynthesis is generally subject to feedback inhibition by elevated sugar levels in plants (Rolland et al. 2006). Degradation of sucrose inside fungal cells might have a positive effect on the photosynthesis, as it reduces sugar levels. Vargas et al. (2009) demonstrated that the upregulation of the photosynthetic genes and photosynthetic rate in leaves were dependent on sucrose degradation in *T. virens* cells during mutualistic association. Consequently, when *Trichoderma* colonizes roots, the increased demand of photoassimilates alters the carbon partitioning toward the organs, causing a stimulation of the photosynthetic process in leaves (Vargas et al. 2013). On the contrary, *Alternaria alternata* VOC-promoted enhancement of photosynthesis was accompanied by accumulation of high levels of soluble sugars in the leaves (Sánchez-López et al. 2016). The lack of photosynthetic inhibition by high sugar content in leaves of VOC-exposed plants might be due to enhanced CK production, as CKs and sugars work antagonistically in gene-regulated responses (Kushwah and Laxmi 2014).

6.3.5 Flowering

The application of some PGPF strains seems to influence phenotypic plasticity of flowering, an important ecological trait for plants and their communities (Forrest and Miller-Rushing 2010). Although flowering phenology is known to be under strong genetic control, it also responds to different stimuli including temperature (Aikawa et al. 2011), water availability (Crimmins et al. 2013), herbivory (Brys et al. 2011), and pathogen infection (Korves and Bergelson 2003). Similarly, PGPF have also been found as a possible driver of flowering phenology in plants. It has shown that root inoculation with PGPF may stimulate flowering time, flower numbers, and/or size in the host plant (Table 6.2). Early reports of the effects of the *Trichoderma* spp. on floricultural crops indicated that when the fungus was applied

to soil as a peat-bran formulation, the numbers of flower buds were enhanced in chrysanthemum and petunia, while early flowering occurred in periwinkle, alyssum, and marigold (Chang et al. 1986). Similarly, adding *Trichoderma* as dried fermenter to the growing medium of flower plants enhanced the numbers and weight of flowers in verbena and the numbers of flowers and buds in petunia (Ousley et al. 1994). Early and vigorous flowering was also observed in *C. forskohlii* after inoculation of its root with *Pi. indica* (Das et al. 2012). Under greenhouse conditions, two PGPF *T. harzianum* TriH_JSB27 and *Pe. Chrysogenum* PenC_JSB41 induced early flowering in tomato (Jogaiah et al. 2013). The root-colonizing nematophagous fungus *Pochonia chlamydosporia* hastened flowering in tomato and Arabidopsis (Zavala-Gonzalez et al. 2015). Plants grown in the presence of VOCs emitted by different fungal species have also been reported to show robust and early flowering phenotype. Arabidopsis plant exposed to VOCs emitted by phylogenetically diverse fungi such as *T. viride*, *Pe. chrysogenum*, *Saccharomyces cerevisiae*, and *Pe. aurantiogriseum* had increased number of flowers in Arabidopsis (Hung et al. 2014; Sánchez-López et al. 2016).

Plants often exploit various interconnecting mechanisms, including photoperiod, vernalization, hormone biosynthesis, nutrient uptake, and aging pathways to shorten the vegetative growth period and hasten flowering (Song et al. 2013). Enhancement of flower production in PGPF-treated plant may be due to an increase in plant nutrient (especially K+) uptake in combination with one or more of the abovementioned mechanisms (Perner et al. 2007). Hormones, such as GAs, are involved in the regulation of bud production and early flowering in plants (Zhang et al. 2014). Higher levels of K+ in the plant are responsible for faster transport of GAs (Das et al. 2012). Some studies have emphasized the importance of phosphorus on the impact on bud formation and development and the number of flowers (Poulton et al. 2002). Furthermore, CKs also play important roles in flowering by stimulating floret primordia differentiation and ovule development (Riefler et al. 2006; D'Aloia et al. 2011; Zhang et al. 2014). In contrast, nitric oxide (NO) is known to participate in plant flowering repression (Shi et al. 2012). Fungal VOC-promoted early flowering involves suppression of NO action through the scavenging of NO molecules by CKs (Sánchez-López et al. 2016). It is likely that PGPF may utilize one or more of these flowering mechanisms.

6.3.6 Crop Yields

Global yields of many crops have been somewhat static during the last two decades (Gopalakrishnan et al. 2015). Many studies have proposed to use PGPF as an eco-friendly and sustainable tool to enhance the yield of different crop plants (Table 6.2). Commercial trials on several *T. harzianum* T-22-treated hybrids and inbred lines have revealed the yield increases in most genotypes (Harman et al. 2004). Application of *T. harzianum* and *T. viride* was significantly effective in improving millable canes (~5–30%), yield (~6–38%), and CCS (commercial cane sugar) t/ha (~30–34%) over the control in plant cane (Srivastava et al. 2006). Similarly, application of 50% N fertilizer

along with 50% *Trichoderma*-enriched biofertilizers has resulted in ~ 108% and ~203% yield increase in mustard and tomato, respectively, over the control (Haque et al. 2012). In strawberry, lettuce, chickpea, and pea, crop yields were also increased significantly following the application of *Trichoderma* spp. (Elad et al. 2006; Bal and Altintas 2006; Hossain et al. 2013; Akhtar et al. 2015). Treatment with *Pe. menonorum* was useful in increasing the yields of cucumber plants (Babu et al. 2015). Inoculation of banana plants with *F. oxysporum* strains resulted in up to ~20 to ~36% yield increase (Waweru et al. 2014). Root colonization by *Pi. indica* results in an overall increase in grain yields in barley (Waller et al. 2005) and oil yields in *Thymus vulgaris* and *Foeniculum vulgare* as compared with non-colonized plants (Dolatabadi et al. 2011). Application of HBNR isolates to tomato plants in greenhouses resulted in consistent and higher marketable and total yields, which were ~70–73% higher than untreated plants (Muslim et al. 2003). These examples are a few of many that demonstrate the yield benefit from plant-PGPF interactions (Table 6.2).

The exact reason for increased yields seems to be unclear yet, but in most cases, it is probably due to greater supply of nutrients by PGPF to plants. Yedidia et al. (2001) suggested that presence of PGPF in the rhizosphere increases root surface area allowing the roots to explore larger volumes of soil; thus, more nutrients become available to the plants especially under nutrient-stressed soil environments. In vitro studies have shown that micronutrients and insoluble phosphates become soluble and available by PGPF treatments, therefore useful to the roots interacting with PGPF in the root zone (Waklin et al. 2007). PGPF also have the ability to increase nitrogen-use efficiency in crops (Alberton et al. 2013) and to ameliorate biotic and abiotic stresses (Shoresh et al. 2010). Some PGPF strains show abilities to improve photosynthetic efficiency (Babu et al. 2015). All of these capabilities singly or in combination contribute to improve crop yield.

6.3.7 Photosynthetic and Bioactive Compounds

Positive effects of PGPF are not always limited to the growth and yields; rather many species of PGPF are associated with the biochemical changes in the colonized plants. It is believed that some PGPF are quality enhancers and treatment with them alters the photosynthetic product content in plants (Table 6.2). The application of *T. harzianum* and *Ps. fluorescens* led to increases in starch, total soluble and reducing sugar, and phenol contents in leaves of sunflower (*Helianthus annuus*). There was also a significant increase in seed lipid content and the proportion of linoleic acid (Lamba et al. 2008). In a greenhouse study, plants inoculated with inocula of *Westerdykella aurantiaca* FNBR-3 and *T. longibrachiatum* FNBR-6 significantly improved total carotenoid and protein contents of the plant leaves in rice and pea (Srivastava et al. 2012). Application of isolates of *As. niger* significantly caused higher accumulation of total phenolic, salicylic acid, and chlorophyll contents of plant, as well as lycopene, ascorbic acid (vitamin C), and Brix index of tomato fruit compared to untreated control (Anwer and Khan 2013). PGPF inoculation also improve the levels of different photosynthetic compounds under stress and help the

plants ameliorate oxidative stress resulting from high stress. Under mild drought stress, endophyte fungus *Neotyphodium lolii* enhanced the accumulation of soluble sugars in *Lolium perenne* cv SR4000 plants to improve their osmotic ability (Ren et al. 2006). When stress have been intensified, the improvement by endophyte no longer sustained, but other photosynthetic products such as starch were accumulated in the endophyte-infected plants to survive through the undesirable conditions. Similarly, application of *T. harzianum* T6 increased the soluble sugar and protein contents in the wheat seedlings grown under salt stress, compared to the control (Zhang et al. 2016). Sharma et al. (2016) investigated the effect of *Pi. indica* inoculation on salinity stress tolerance of *Aloe vera* plant and observed significantly higher phenol, flavonoid, flavonol, and aloin contents as well as improved radical scavenging activity in the inoculated plantlets as compared to non-inoculated controls at all salinity concentrations. The increased accumulation of these compounds in plants usually indicates a highly protective mechanism against oxidative damage caused by high stress in the plant environment (Bartels and Sunkar 2005). Accordingly, PGPF-inoculated plants are likely to recover from undesirable conditions more rapidly than non-inoculated plants.

Many of the PGPF have developed the ability to enhance the production of bioactive substances originated from the host plants. In addition to their role in conferring fitness benefits to host plants, many of these secondary metabolites have interesting applications in industry. For example, *Coleus forskohlii* is a perennial medicinal shrub of the mint family (Lamiaceae) and has been used in traditional medicine for treating a broad range of human health disorders (Lukhoba et al. 2006). The main active compound of *C. forskohlii* is forskolin, which is known for its broader pharmacological activities (Li and Wang 2006; Wagh et al. 2012). The forskolin concentration in roots of *C. forskohlii* was enhanced by dual inoculation with *Glomus mosseae* and *T. viride* (Boby and Bagyaraj 2003). Others report that the effect of bioinoculation on the production of secondary metabolites was negative. For example, Das et al. (2012) found the reduced contents of forskolin in *Pi. indica*-colonized plants as compared with the non-colonized plants. Singh et al. (2012) reported that it is not the forskolin content of the root, rather the forskolin yield which is increased significantly by treatment with bioinoculants. Another essential oil, p-cymene, is frequently utilized in pharmaceuticals or in fine chemical industries for syntheses of fragrances, p-cresol, flavorings, herbicides, non-nitrated musks, etc. (Martín-Luengo et al. 2008). The level of p-cymene increased in the aerial parts of the *Pi. indica*-colonized *C. forskohlii* plants as compared with the non-colonized plants (Das et al. 2012). Likewise, inoculation of *Sebacina vermifera* and *Pi. indica* significantly increased the level of thymol in thyme, anethole in fennel, and podophyllotoxin and 6-methoxypodophyllotoxin in *Linum album* as compared to non-inoculated control plants (Baldi et al. 2010; Dolatabadi et al. 2011). Similar cases of enrichment of bioactive compounds such as artemisinin in *Artemisia annua* L. shoots (Sharma and Agrawal 2013), spilanthol in *S. calva* (Rai et al. 2004), saponin from *Chlorophytum* sp. (Gosal et al. 2010), and asiaticoside from *Centella asiatica* (Satheesan et al. 2012) were also reported in earlier studies with *P. indica* treatment. As biotic elicitors, PGPF or constituents of their cells can equally be used to stimulate the

secondary metabolite production in plant cells. As reported by Ming et al. (2013), both the mycelial extract and the polysaccharide fraction produced by *T. atroviride* D16 could stimulate the biosynthesis of tanshinones in hairy roots of *Salvia miltiorrhiza*. The data presented here show that PGPF can increase industrial advantages of the host plants by producing scarce and valuable bioactive compounds for human use. Moreover, understanding the effects of PGPF on plant secondary metabolite production may help produce targeted drugs through bioengineering.

6.3.8 Plant Signaling Pathways Leading to Enhanced Growth

The interaction between host plant and PGPF involves the exchange of signal molecules by the two partners. This initial exchange leads to recognition of the appropriate partner and thus plays an integral role in establishing successful association. Plant responses to microbial association are translated into massive changes in biochemical reactions, metabolic adjustments, and physiological state. With current advances in molecular biology, many components of the signal transduction pathways in beneficial plant-microbe interaction have now been characterized. It has now become obvious that plant signaling pathways leading to enhanced growth by PGPF rely on endogenous regulators, such as auxin, ET, and CKs. Other plant hormones such as GAs and ABA represent additional classes of signaling molecules that influence beneficial plant-PGPF interactions.

As noted earlier, plant-PGPF interactions can employ direct or indirect influences on belowground and aboveground plant structures. The frequently reported effects are enhanced biomass production, flowering, root hair development, and increased yield (Björkman et al. 1998; Harman et al. 2004; Contreras-Cornejo et al. 2009). Several interesting studies have pointed to the role of auxin as plant signaling hormones in plant responses to PGPF and especially describing their participation in controlling shoot and root development. Wild-type Arabidopsis seedlings inoculated with *T. virens* showed augmented biomass production and lateral root development (Contreras-Cornejo et al. 2009). The inoculated plants exhibited the expression of auxin-regulated genes. As it was expected, mutations in genes involved in auxin transport or signaling, *AUX1*, *BIG*, *EIR1*, and *AXR1*, reduced the plant growth-promoting and root developmental effects of *T. virens* inoculation in Arabidopsis. These results indicate that plant growth promotion by *T. virens* operates through the classical auxin response pathway (Contreras-Cornejo et al. 2009). Similarly, *Pi. indica*-induced expression of auxin-regulated genes was reported in barley (Schäfer et al. 2009) and in Chinese cabbage (Lee et al. 2011), and their induction was instrumental for the strong growth-promoting effect by the fungus. It is assumed that microbial auxin may have a role in altering auxin biosynthesis or signaling in the host (Sukumer et al. 2013). Previously, Sirrenberg et al. (2007) have noted that the phenotype obtained from interactions of Arabidopsis with *Pi. indica* is mimicked by an external application of IAA, at a concentration lower than produced by the fungus, suggesting a role for exogenous auxin. Similarly, Contreras-Cornejo et al. (2009) showed that treatment with IAA and indole-3-acetaldehyde was found to

rescue the root hair-defective phenotype of *rhd6* mutant. This result may imply that the microbial auxin may take part in suppressing the root hair formation defects of *rhd6.* Therefore, auxin can act as a reciprocal signaling molecule in plant-microbe interaction.

Ethylene, the gaseous phytohormone, is important for plant growth and development as well as plant response to environmental signals (Vandenbussche et al. 2012). The growth-promoting endophytic fungus *Sebacina vermifera* significantly increases the growth of *Nicotiana attenuata*. When the *N. attenuata* plant was transformed to silence ET production, growth promotion effect by the fungus was not observed (Barazani et al. 2005). DNA microarray-based gene expression analysis revealed a differential induction of genes related to ET synthesis and signaling in barley roots colonized by endophytic fungus *Pi. indica* (Schäfer et al. 2009). Mutants *etr1*, *ein2*, and *ein3/eil1* impaired in ET signaling showed compromised or inhibited growth and seed production responses by this fungus compared with the wild type. These results are the indication of involvement of ET signaling in the beneficial interaction between the two symbionts (Camehl et al. 2010). Impaired ET signaling resulted in reduced root colonization by the fungus, while Arabidopsis mutants exhibiting constitutive ET signaling and synthesis or ET-related defense were hypersusceptible to *Pi. indica* (Khatabi et al. 2012). This suggests that ET signaling influences plant growth by affecting fungal colonization on the roots.

Although several VOCs from PGPF are known to affect plant growth, the signaling pathways mediating VOC sensing are not fully understood. The major natural antifungal VOC isolated from *Trichoderma* was 6-pentyl-2H-pyran-2-one (6-PP) (Lee et al. 2016) which induces *A. thaliana* root morphogenesis via auxin transport and signaling and the ET-response modulator EIN2 (Garnica-Vergara et al. 2016). Ryu et al. (2003) reported that CK signaling plays a role in growth promotion with exposure to *Bacillus subtilis* GB03 VOCs. CKs are also essential for *Pi. indica*-induced growth promotion in Arabidopsis (Vadassery et al. 2008). Moreover, in response to *Pi. indica* colonization, the ABA pathway was proposed to enhance plant growth via cellular [Ca^{2+}] elevations, phosphoinositide, and particular protein kinases (Vadassery et al. 2009; Camehl et al. 2011). Additional phytohormones synthesized or manipulated by the growth-promoting fungi include GAs and brassinosteroids (Schäfer et al. 2009). In summary, almost the whole phytohormone signaling networks appear to be involved in generating compatible interactions between the fungus and host, which lead to growth promotion and finally to greater biomass.

6.3.9 Plant Genetic Variability Affecting Induced Plant Growth

The expected beneficial effects of microbial application are frequently influenced by treated plant genotype. While plant growth promotion by PGPF has been well documented, this trait rarely occurs across all plant-PGPF combinations. It is assumed that a preferential interaction exists between strains of PGPF and a

particular host. Similarly, plant-dependent differences in response to PGPF inoculation may also occur at the cultivar level. Both fungi and plant cultivars have their own sets of characteristics that ultimately define the intimate interaction between them and the beneficial outcomes resulting from the developed interaction. There are cultivar genotypes for which the use of particular PGPF strain may be either endorsed or contraindicated. The use of a responsive cultivar may help maximize the efficacy of PGPF, and new inducer strains should be explored for the less responsive cultivars. Despite the obvious significance for agriculture, there are still a few studies on how the plant response to PGPF is influenced by plant genotypes in terms of growth promotion.

Earlier, Shivanna et al. (1994) tested seven zoysiagrass sterile fungal isolates and a wheat rhizosphere isolate (K-17) on two wheat varieties in field conditions. The growth of one variety was enhanced by most of the isolates, except K-17, while only a few isolates increased the growth of the other variety. There are at least four PGPF isolates which increased yields of both varieties. The authors concluded that the effectiveness of PGPF isolates in terms of plant growth promotion depends on the crop variety besides their inherent growth promotion abilities. In another study, Shivanna et al. (2005) examined the ability of a few of *Phoma* sp. isolates and one non-sporulating fungal isolate to promote plant growth of four cucumber cultivars: Aodai kyuri, Jibai, Ochiai fushinari, and Shogoin fushinari. All isolates enhanced plant length in cucumber cv. Shogoin fushinari, while nine isolates except the sterile fungal isolate GU21-1 improved the plant length in cv. Aodai kyuri. On the contrary, stimulated plant length was not observed in cucumber cv. Jibai and Ochiai fushinari, when the plants were treated with one (GS6-4) and five fungal isolates (GS6-1, GS7-4, GS8-6, GS10-2, and GU21-2), respectively. These results also suggest that the tested PGPF isolates caused cultivar-specific plant length promotion in cucumber. Harman (2006) reported that maize inbreeds treated with T-22 strain of *T. harzianum* showed three different types of growth responses such as strongly positive, little effect, and negative. Thus, there clearly are strong genetic components to the response of maize to T-22. Further, analysis of T-22-induced growth responses of hybrids derived from parent with dissimilar growth responses suggests that the T-22 responses in maize are largely conditioned by dominant genes (Harman 2006). In a growth chamber study, Tucci et al. (2011) demonstrated that substantial differences in the growth response to the symbiotic interaction with two selected strains of *Trichoderma* spp. occurred when different tomato varieties were tested. Consequently, the plant response to *T. harzianum* T-22 or *T. atroviride* P1 is affected by plant genetic variability and thus is under genetic control in tomato. Since plant response to PGPF is a heritable trait (Harman 2006), its extrapolation to crop plants by breeding would be significant for plant improvement. The possible mechanisms that underlie plant genetic control of the interaction may include the genotype ability to support and sustain root colonization by the PGPF, different sensitivities to the effectors produced by the fungus, variability in the perception and signal transduction of any of the hormones whose concentrations are controlled by it, and so on (Tucci et al. 2011).

6.4 Induction of Systemic Resistance by PGPF

Additional interests in the biological control of soil-borne diseases of plants led to the useful discovery of a specialized type of induced resistance as resulting effects of the colonization of plant roots by certain PGPR, referred to as induced systemic resistance or ISR (van Loon et al. 1998). ISR is known to reduce the incidence and/or severity of various fungal, bacterial, viral, nematode, and oomycete diseases on a diversity of plants (Walters et al. 2013). In contrast to constitutive defense, ISR is considered cost saving. ISR reduces physiological costs of the plants by better matching between resource investment into defense and potential threats (Gómez et al. 2007). Therefore, ISR could offer the most efficient means of defense against invading pathogens.

Research in the last decade in plant-fungal biocontrol agent interactions has made it clear that elicitation of ISR is a widespread phenomenon. It is not limited only for PGPR but also for a variety of other microorganisms including PGPF. PGPF of different taxa have been found as potential inducers of systemic resistance against pathogens. Among them, members of *Trichoderma* (Shoresh et al. 2005), *Penicillium* (Hossain et al. 2007; Hossain et al. 2008a), nonpathogenic *Fusarium* (Kojima et al. 2013), *Piriformospora* (Stein et al. 2008), *Pythium* (Hase et al. 2008), *Sebacinales* (Waller et al. 2008), *Phoma* (Sultana et al. 2009), and sterile fungi (Sultana et al. 2008) are well studied for their roles as elicitors of ISR (Table 6.3). The classical biocontrol agents *Trichoderma* spp. have frequently been shown to suppress the severity of diseases, particularly those caused by soil-borne plant pathogens through mycoparasitism and antibiosis (John et al. 2010; Akhter et al. 2015). However, *T. virens* mutants deficient in mycoparasitic ability and/or inability to produce antibiotics had no effect on the biological activity of these strains. Instead, there seemed to have a very strong correlation between the abilities of these strains to trigger terpenoid phytoalexin defense in cotton seedlings and control of *R. solani* (Howell et al. 2000). These examples clearly demonstrate the importance of ISR by PGPF. The ability of *Trichoderma* spp. to trigger ISR has been shown in agriculturally important crops such as rice, wheat, bean, maize, cucumber, lettuce, cotton, tobacco, and tomato and *Rhododendron* against fungi to oomycetes to bacteria and even virus (Ahmed et al. 2000; Koike et al. 2001; Yedidia et al. 2001; Howell 2003; Harman et al. 2004; Shoresh et al. 2005; Hoitink et al. 2006; Saksirirat et al. 2009; Elsharkawy et al. 2014; Vitti et al. 2016). Several *Penicillium* spp. have also been extensively tested for their ability to elicit ISR in plants and were very much effective against fungi (Hossain et al. 2014), bacteria (Hossain and Sultana 2015), and viruses (Elsharkawya et al. 2012). *Phoma* sp. and sterile fungi have similar capabilities (Hossain et al. 2008b; Sultana et al. 2008; Sultana et al. 2009). ISR has been reported to be a mechanism of action for some nonpathogenic strains of *F. oxysporum*. ISR by *Fusarium* isolates have been reported against root-knot nematodes (Dababat and Sikora 2007) and *Radopholus similis* in banana (Athman et al. 2006); *Pythium ultimum* infection in cucumber (Benhamou et al. 2002); *Verticillium* wilt in eggplant (Ishimoto et al. 2004); *Fusarium* wilt in watermelon (Larkin and Fravel 1999), sweet potato (Ogawa and Komada 1986), and tomato (Patil et al.

Table 6.3 Induction of systemic resistance by different plant growth-promoting fungi against diverse pathogens in various plants

Host Plant	PGPF	Pathogen	Effect	References
Arabidopsis (A. thaliana)	*Ampelomyces* sp., *Cladosporium* sp.	*Pseudomonas syringae* pv. *tomato* DC3000	Reduction in disease severity and pathogen proliferation	Naznin et al. (2014)
	Aspergillus ustus	*Botrytis cinerea*	Reduction in disease incidence	Salas-Marina et al. (2011)
		Ps. s. pv. *tomato* DC3000		
	Fusarium equiseti GF19-1	*Ps. s.* pv. *tomato* DC3000	Reduction in disease severity and pathogen proliferation	Kojima et al. (2013)
	P. simplicissimum GP17-2	*Ps. s.* pv. *tomato* DC3000	Reduction in disease severity and pathogen proliferation	Hossain and Sultana (2015)
	Pe. simplicissimum GP17-2	*Ps. s.* pv. *tomato* DC3000	Reduction in disease severity and pathogen proliferation	Hossain et al. (2007) and Hossain and Sultana (2015)
	Penicillium sp. GP16-2	*Ps. s.* pv. *tomato* DC3000	Reduction in disease severity and pathogen proliferation	Hossain et al. (2008a)
	Phoma sp. (GS6-2 and GS7-3) and sterile fungus (GU23-3)	*Ps. s.* pv. *tomato* DC3000	Reduction in disease severity and pathogen proliferation	Sultana et al. (2008)
	Phoma sp. GS8-1	*Ps. s.* pv. *tomato* DC3000	Reduction in disease severity and pathogen proliferation	Hossain et al. (2008b)
	Phoma sp. GS8-3	*Ps. s.* pv. *tomato* DC3000	Reduction in disease severity and pathogen proliferation	Sultana et al. (2009)
	Pi. indica	*Golovinomyces orontii*	Reduction in conidia per leaf fresh weight	Stein et al. 2008
	Rhizoctonia spp.	*Rhizoctonia* spp. isolate RS13	Increase plant survival	Sharon et al. (2011)
	T. asperellum SKT-1	*Cucumber mosaic virus* (*CMV-Y*)	Reduction in CMV symptoms	Elsharkawy et al. (2013)
	T. hamatum T382	*B. cinerea* B05-10	Reduction in average lesion diameter	Mathys et al. (2012)
	T. harzianum Tr6	*B. cinerea*	Reduction in disease incidence index	Alizadeh et al. (2013)
	T. harzianum Rifai T39	*B. cinerea* Strain B4	Reduction in percentage of mean lesion area	Korolev et al. (2008)

(continued)

Table 6.3 (continued)

Host Plant	PGPF	Pathogen	Effect	References
Cucumber (*C. sativus*)	*Alternaria cucumerina* *Cladosporium fulvum*	*Sphaerotheca fuliginea*	Reduction in number of powdery mildew colonies on each leaf	Reuveni and Reuveni (2000)
	Nonpathogenic *F.oxysporum* Fo47	*Py. ultimum*	Reduction in the number of root lesions	Benhamou et al. (2002)
	P. simplicissimum GP17-2	*C. orbiculare*	Reduction in the number and size of the lesions	Shimizu et al. (2013)
	Pe. chrysogenum	*Meloidogyne javanica*	Reduced root galling	Gotlieb et al. (2003)
	Penicillium sp. isolate GP15-1	*C. orbiculare*	Reduction in lesion number per leaf and total lesion area	Hossain et al. (2014)
		R. solani AG-4 RO2	Reduction in disease severity	
	Phoma sp. GS8-1	*Colletotrichum orbiculare*	Reduction in lesion area and lesion number	Elsharkawy et al.(2015)
	Sterile fungi GU21-2			
	T. asperellum T203	*Ps. s.* pv.*lachrymans*	Inhibited multiplication of bacterium	Shoresh et al. (2005)
	T. harzianum Tr6	*F. o.* f. sp. *radicis-cucumerinum*	Reduction in disease incidence index	Alizadeh et al. (2013)
	Trichoderma sp. GT3-2, *Fusarium* sp.GF18-3, *Penicillium* sp. GP17-2, *Phoma* sp. GS8-2, sterile fungus GU23-3	*C. orbiculare*	Reduction in total lesion area, lesion diameter, disease index and severity	Koike et al. (2001)
		F. oxysporum f. sp. *cucumerinum*		
		Ps. s. pv. *lachrymans*		
Rice (*O. sativa*)	*Meyerozyma guilliermondii* TA-2	*Magnaporthe oryzae*	Reduction in disease severity	Elsharkawy et al. (2015)
	Phoma spp.	*F. semitectum*	Reduction in disease severity	Elsharkawy et al. (2014)
	T. harzianum GT3-2	*Rhizopus* sp.		
		F. moniliforme		
	Pi. indica	*Magnaporthe oryzae*	Reduction in disease symptoms	Mousavi et al. (2014)
	Pi. indica	*F. proliferatum*	Reduction in *F. proliferatum* DNA in roots	Hajipoor et al. (2015)
	T. virens Gv29-8	*C. graminicola*	Reduction in lesion area	Djonović et al. (2006)

Maize (*Z. mays*)	*Pi. indica*	*R. solani* AG1-IA	Delayed the infection process of *R. solani* and decreased sheath blight severity	Nassimi and Taheri (2017)
	T. virens Gv29-8	*C. graminicola*	Reduction in lesion area	Djonović et al. (2007)
Wheat (*T. aestivum*)	*T. virens*	*Cochliobolus heterostrophus*	Reduction in lesion size	Gaderer et al. (2015)
	T. atroviride			
	Aureobasidium pullulans	*F. culmorum*	Reduction in *Fusarium* head blight severity	Wachowska and Głowacka (2014)
Barley (*H. vulgare*)	*Pi. indica*	*F. culmorum*	Reduction in *Fusarium*-induced shoot and root fresh weight loss	Waller et al. (2005)
		Blumeria graminis f. sp. *hordei*	Reduction in disease index	
Cabbage (*B. oleracea*)	*Meyerozyma guilliermondii* TA-2	*Alternaria brassicicola*	Reduction in disease severity and pathogen proliferation	Elsharkawy et al. (2015)
Banana (*M. acuminata*)	*F. oxysporum*	*Radopholus similis*	Reduction in root penetration rates by nematode	Vu et al. (2006)
	F. cf. *diversisporum*			
	F. oxysporum	*Radopholus similis*	Reduction in total number and percentage of *Ra. similis* attracted to banana root segments	Athman et al. (2006)
			Reduction in percentage of *Ra. similis* that migrated toward banana plants	
Tomato (*L. esculentum*)	*Fusarium* spp. UPM31P1	*F. o.* f. sp. *cubense* race 4	Reduction in disease incidence	Ting et al. (2010)
	Meyerozyma guilliermondii TA-2	*Ralstonia solanacearum*	Reduced symptom development, disease severity, and pathogen proliferation	Elsharkawy et al. (2015)
	Pe. chrysogenum	*Phytophthora infestans*	Reduction in development of necrotic leaf spot and leaf area	Unger et al. (2006)
	T. harzianum T-22	*Cucumber mosaic virus* (CMV)	Reduction in CMV infection severity and accumulation	Vitti et al. (2016)

(continued)

Table 6.3 (continued)

Host Plant	PGPF	Pathogen	Effect	References
	Pe. chrysogenum	*Me. javanica*	Reduced root galling	Gotlieb et al. (2003)
	Phy. cryptogea	*F. o.* f. sp. *lycopersici*	Reduction in disease incidence	Attitalla et al. (2001)
	Phy. cryptogea	*F. o.* f. sp. *lycopersici*	Reduction in disease incidence	Attitalla et al. (2001)
	R. solani AG 4	*R. solani*	Reduction in pre and post-emergence seedling mortality caused by *R. solani.*	Cardinale et al. (2006)
		B. cinerea	Reduction in *B. cinerea* lesion size	
	T. hamatum 382	*X. euvesicatoria* 110c	Reduction in disease severity	Alfano et al. (2007)
	T. harzianum	*Xanthomonas campestris* pv. *vesicatoria*	Reduction in spot numbers, disease severity and pathogen proliferation	Saksirirat et al. (2009)
	T. harzianum T-78	*B. cinerea*	Reduction in lesion size	Martínez-Medina et al. (2013)
Mustard (*B. campestris*)	*Talaromyces wortmannii* FS2	*C. higginsianum*	Reduction in infection frequency	Yamagiwa et al. (2011)
Cotton (*Gossypium barbadense*)	*Penicillium janczewskii*	*R. solani*	Reduction in the incidence of damping-off	Madi and Katan (1998)
	T. virens strain Gv29-8	*Colletotrichum* sp.	Reduction in lesion area	Djonović et al. (2006)
Melon (*C. melo*)	*Pe. janczewskii*	*R. solani*	Reduction in the incidence of damping-off	Madi and Katan (1998)
Pepper (*C. annuum*)	*T. harzianum* isolate 2413	*Phytophthora capsici*	Reduction in length of necrosis in the stem	Ahmed et al. (2000)
Kidney bean (*P. vulgaris*)	*R. solani* AG-Bb	*R. solani*	Reduction in disease severity	Tohid and Taheri (2015)

2014); *Phytophthora infestans* in potato (Quintanilla 2002); pea root rot pathogen (Peters and Grau 2002); and *Ps. syringae* in Arabidopsis (Kojima et al. 2013). The hypovirulent *Rhizoctonia* isolates protect bean and tomato (Cardinale et al. 2006), Arabidopsis (Sharon et al. 2011), and kidney bean (Tohid and Taheri 2015) against important pathogens through mechanisms associated with ISR. Evidence also suggests that *Pi. indica* induces systemic resistance in rice against bakanae disease caused by *F. proliferatum* (Hajipoor et al. 2015), leaf blast caused by *Magnaporthe oryzae* (Mousavi et al. 2014), and sheath blight caused by *R. solani* (Nassimi and Taheri 2017). The fungus reduces fusarium head blight severity in wheat (Rabiey and Shaw 2016) and powdery mildew disease caused by *Blumeria graminis* f. sp. *hordei* in barley (Waller et al. 2005; Harrach et al. 2013). These results show that PGPF strains can effectively enhance disease resistance of plants.

Colonization of plant roots by PGPF seems an essential step for eliciting ISR. However, studies revealed that culture filtrates of certain *Penicillium*, *Fusarium*, *Phoma*, and sterile fungi afforded better protection than living inocula, suggesting that not only the effect of root colonization but also the triggering of host defense mechanisms by certain chemical factors produced by fungi is responsible for the induction of resistance in plants against pathogens (Hossain et al. 2008a; Sultana et al. 2008; Kojima et al. 2013). Various microbial metabolic molecules such as protein with enzymatic activity, cell wall lipid, chitin oligomers, and glycopeptides have been described with elicitor activity. Hyakumachi (1997) revealed that the lipid fraction of mycelial cell walls of non-colonizing PGPF and the cell wall lipid fractions as well as polysaccharides of root colonizing PGPF were effective in eliciting a resistance response. Koike et al. (2001) reported that both the MW 12,000 D fraction and the lipid fraction of culture filtrate of *Pe. simplicissimum* GP17-2 induce resistance, lignification at the site of pathogen infection, and generation of reactive oxygen species. The peptaibols (peptide antibiotics) and the small protein Sm1 produced by *T. virens* have been shown to be responsible for the systemic activation of the defense responses against *Colletotrichum graminicola* and *Cochliobolus heterostrophus* in maize leaves (Djonović et al. 2007; Viterbo et al. 2007; Gaderer et al. 2015). Similarly, its homologue Epl1 from *T. atroviride* induces plant resistance responses to a lesser extent against *Cochliobolus heterostrophus* (Gaderer et al. 2015). Recent studies have also revealed that VOCs emitted by some PGPF strains can effectively enhance disease resistance. A terpenoid-like volatile β-caryophyllene emitted by *Talaromyces* wortmannii FS2 significantly enhanced the resistance to *Colletotrichum higginsianum* (Yamagiwa et al. 2011). Two VOC blends extracted from *Ampelomyces* sp. and *Cladosporium* sp. containing m-cresol and methyl benzoate (MeBA) as major active volatile compounds, respectively, were found to elicit ISR in Arabidopsis plants against *Ps. s.* pv. *tomato* DC3000 (Naznin et al. 2014). These observations imply the use of VOCs emitted from beneficial fungi as a novel strategy for biocontrol. However, they are difficult to apply in the field because of their high evaporative nature, and additionally, their efficacy seems to be low compared with other chemical elicitors (Naznin et al. 2014).

6.4.1 Defense Responses During PGPF-Mediated ISR

Plants defend themselves against phytopathogenic attacks by activating a wide spectrum of defense-related genes or compounds that enhance both cellular protection and disease resistance. Often, the induced effects of PGPF on the plant defenses are not limited to the root, but they are also exhibited in aboveground plant tissues (Martínez-Medina et al. 2010), providing the whole plant more resistance to a wide range of plant pathogens. Various transcriptomic studies have provided evidences that ISR may result in the direct activation of cellular defense responses in systemic tissue after local stimuli and/or of the priming, which involves activation of systemic responses, but only when the pathogen reaches these sites (Aranega-Bou et al. 2014). Some of PGPF-mediated ISR result from direct activation of defense genes than priming, while others are most frequently associated with priming for boosted defense rather than direct activation. There are also PGPF-mediated ISR which are partly associated with the direct activation of defense-related genes and partly associated with priming (Hossain et al. 2008a). These differential mechanisms of ISR by different PGPF could possibly be due to strain-specific differences in elicitor substances.

6.4.1.1 Direct Activation of Defense Responses

Direct activation of various defense responses and a significant reduction in pathogen growth are observed in different PGPF-mediated ISR. In a growth chamber study, examination of local and systemic gene expression revealed that *Pe. simplicissimum* GP17-1-mediated ISR is accompanied by direct activation of *PR-2* and *PR-5* genes in leaves and roots of Arabidopsis plants, while increased expression of *PDF1.2* was seen in the leaves of treated plants (Hossain et al. 2007). In another study, *Pe. chrysogenum* PenC_JSB4 and *T. harzianum* TriH_JSB27 treatments directly activated phenylalanine ammonia lyase (PAL) activity in tomato plant (Jogaiah et al. 2013). Similar results have been reported with increase in PAL activity in sunflower plants treated with *T. harzianum* (Lamba et al. 2008). Mathys et al. (2012) reported that addition of *T. hamatum* T382 to the roots of the plant triggers a clear and pronounced induction of *PR-1*, *PR-2*, and *PR-5* on the first 3 days of post-T382 inoculation, while the expression of the *PDF1.2a* was not affected in the leaves on the second day after the treatment. Moreover, comparing plants treated with *T. hamatum* T382 with mock-treated controls, they identified 2075 genes that are differentially expressed during T382-mediated ISR. Several other studies also suggested the direct activation of defense-related genes during *Trichoderma*-induced systemic resistance (Alfano et al. 2007; Salas-Marina et al. 2011; Morán-Diez et al. 2012). Root treatment with nonpathogenic *F. oxysporum* modulates the expression of systemic acquired resistance (SAR) marker genes in tomato (Duijf et al. 1998). Similarly, the onset of resistance induced by *F. equiseti* GF19-1 in the leaves of Arabidopsis plant was associated with a significant induction of *PR-1*, *PR-2*, and *PR-5* genes (Kojima et al. 2013). Not only the root colonization by PGPF but also the culture filtrates produced by them modulate the direct activation of defense genes, leading to enhanced resistance to invading pathogens (Hossain et al. 2008a; Sultana et al. 2009; Kojima et al. 2013; Shimizu et al. 2013). Enhanced expression

of *PR-1*, *PR-2*, *PR-5*, *ChitB*, and *Hel* genes was observed in Arabidopsis plants treated with culture filtrate of *Phoma* sp. GS8-1 (Hossain et al. 2008b). Two VOC blends extracted from *Ampelomyces* sp. and *Cladosporium* sp. containing m-cresol and MeBA induced *PR-1* and *PDF 1.2* genes in leaves of *A. thaliana* (Naznin et al. 2014). The correlation between ISR and presence of constitutive induction of defense genes postulates the assumption that constitutively activated defense responses are essential mechanisms in the PGPF-mediated ISR response of plants.

6.4.1.2 Priming (Sensitization) of Defense Responses During PGPF-Mediated ISR

There are PGPF, which are believed not to significantly alter gene expression upon treatment or show minimal induction of defense genes. Rather, they acquire a second line of defense, in which they prime or sensitize plants to express resistance response more rapidly and/or more robustly upon pathogen attack. Upon pathogen infection, there is an activation of cellular defense responses in attacked cells of both ISR-expressing and non-expressing plants. However, in case of ISR-expressing, cellular defense responses are induced more rapidly and stronger than in a non-induced plant. The primed state develops from the enhanced perception and/or amplification of defense signals (Aranega-Bou et al. 2014). Thus, ISR orchestrates an enhanced ability of the plant for the fast and effective activation of defense responses that are triggered not until challenged pathogen attack (Conrath 2009). This process of priming has been demonstrated in various plant species protected by ISR triggered by PGPF. Hossain et al. (2008a) analyzed the expression of a set of defense-related genes, locally, in roots as well as, systemically, in the leaves of *Penicillium* spp. GP16-1-colonized plants. The leaves and roots of the GP16-2-treated plants did not show enhanced expression of any of the genes studied over untreated plants. However, upon infection with *P. syringae* pv. *syringae*, activation of the *ChitB* gene was greatly enhanced in GP16-2-treated plants. Despite no induction of the *Vsp* gene was observed in *Pe. simplicissium* GP17-2-treated plants before pathogen inoculation, transcript levels accumulated to greater levels in these plants at 4 and 6 days post-infection by *P. s.* pv. *syringae* (Hossain et al. 2007). Likewise, although systemic induction of three defense genes (*PI II*, *PS*, and *MC* coding for the proteinase inhibitor II, prosystemin, and multicystatin) was relatively weak in plant colonized by *T. harzianum*, the expression of these genes has been boosted in the induced plants, upon *Botrytis cinerea* infection (Martínez-Medina et al. 2013). Similar activation of a priming state in plants by *Trichoderma* has been observed previously in Arabidopsis, tomato, and grapevine plants (Segarra et al. 2009; Tucci et al. 2011; Perazzolli et al. 2012; Alizadeh et al. 2013). These solid evidences substantiate that priming is a major defense mechanism in PGPF-mediated ISR. PGPR and SAR activators have also been demonstrated to enhance the plant's defense capacity by priming for potentiated expression of defense genes (Verhagen et al. 2004; Tjamos et al. 2005; Conrath et al. 2006). Ryu et al. (2004) demonstrated that some PGPR can even induce priming by the release of volatiles. This indicates that priming is, indeed, a very common mechanism underlying plant's various induced responses (Bruce et al. 2007). From an economic context,

priming appears to offer an overall advantage to plant over the direct induction of the plant defense responses. Direct induction of defense mechanisms is known to seriously affect the growth and seed set, while priming had only marginal effects (van Hulten et al. 2006). Priming conditions plants to trigger appropriate set of defenses without misuse of resources in every situation and reduces trade-offs between defenses against various pathogens. Biochemical and histological changes characteristic of ISR-expressing plants become apparent only in plant organs where an effective resistance is essential.

6.4.2 Plant Signaling Pathways Leading to ISR

SAR and ISR are two classes of inducible resistance where plant defense systems are sensitized by prior infection or treatment with a stimulus that triggers putative resistance against succeeding challenge inoculation by a pathogen (Choudhary et al. 2007). These different forms of resistance are usually associated with the generation of defense-eliciting signals that stimulate a series of downstream events. The key downstream elements of defense signal transduction that warrants particular importance are SA, jasmonic acid (JA), and ET. SA signaling through NPR1 is necessary to trigger SAR (Withers and Dong 2016). Different from SAR, ISR elicited from *Ps. fluorescens* colonization is independent of SA accumulation but requires responsiveness to JA and ET. Besides SAR, NPR1 is also needed for ISR triggered by rhizobacteria (Pieterse et al. 1996, 2009). Some studies have indicated that similar signaling pathways of PGPR-mediated ISR are likely to have required in PGPF as well. ISR triggered by *Trichoderma* spp. involves responsiveness to JA and ET pathways (Shoresh et al. 2005; Segarra et al. 2009; Perazzolli et al. 2011; Tucci et al. 2011). Similarly, ET- and JA-signaling pathways with mediation of NPR1 are key players in the regulation of ISR elicited by *Penicillium* sp. GP16-2 (Hossain et al. 2008a). However, others have disputed this generalization (Hossain et al. 2007; Korolev et al. 2008; Niu et al. 2011), an indication that is established by the results of many studies. As examples, ISR mediated by *Pe. simplicissimum* GP17-2 against *P. syringae* pv. *tomato* only partially requires the SA pathway, while it shows complete independency on the JA and ET pathways (Hossain et al. 2007). The same PGPF elicits resistance to *cucumber mosaic virus* (CMV) in Arabidopsis independent of SA, JA, and ET pathways (Elsharkawya et al. 2012). Although ISR elicited by *Penicillium* spp. GP16-2 against *P. syringae* pv. *tomato* follows JA- and ET-dependent pathways, its cell-free filtrate mediates resistance independent of SA, JA, and ET pathways (Hossain et al. 2008a). Similarly, differences from the reported pathways were noted with mycelial extract of *Pe. chrysogenum* and culture filtrate of *Phoma* sp. (Thuerig et al. 2006; Hossain et al. 2008b; Sultana et al. 2008).

It has been proven that other forms of induced resistance exist. A study by Korolev et al. (2008) using multiple mutant lines of Arabidopsis has shown that the induction of resistance by *T. harzianum Rifai* T39 against *B. cinerea* requires responsiveness to JA, ET, and ABA signalings. Stein et al. (2008) showed that induction of systemic resistance in Arabidopsis by *Pi. indica* to powdery mildew

(*Golovinomyces orontii*) requires JA signaling and function of NPR1. Mathys et al. (2012) reported a role of the SA pathway in *T. hamatum* T-382-induced ISR against *B. cinerea* in Arabidopsis. Similarly, the phenotypic analysis of disease development in the JA (*def1*)- and SA (*Nah*G)-impaired mutants demonstrated that *T. harzianum*-induced systemic resistance against *B. cinerea* requires not only the JA but also the SA signaling pathways (Martínez-Medina et al. 2013). Investigation of ISR in various signaling mutants and transgenic plants showed that the induced protective effect conferred by *F. equiseti* GF19-1 against *P. s.* pv. *tomato* requires responsiveness to an SA-dependent pathway (Kojima et al. 2013). The examination of plant hormones revealed that treating tomato plants with *T. harzianum* T-22 before or simultaneously to CMV infection leads to a systemic resistance that requires JA/ET and SA signaling pathways. Conversely, systemic resistance occurs in an ABA-dependent manner when T-22 treatment was administered after the CMV infection (Vitti et al. 2016). Therefore, the role of plant signaling pathways in the regulation of ISR is complex. The nature and composition of signaling pathways and the regulated defenses during PGPF-mediated ISR distinctively depend on the tripartite combination plant-PGPF-pathogen, and the overlap between SAR and ISR is very common.

6.4.3 Plant Genetic Variability Affecting Induced Systemic Resistance

In nature, plants within a population generally vary in different traits, which include yield potential, large seed, disease resistance, etc. Natural variation in plants is prerequisite for biological effects of genetic diversity and for the adaptive potential of a species to environments that vary in space and time (Shindo et al. 2007; Hossain and Sultana 2015). From the very beginning of modern agriculture, breeders make use of the trait diversities in plant population to develop new and improved cultivars with desirable characteristics. These improved cultivars have been crucial in producing surplus food for growing populations. ISR has been emerging as an important mechanism, which allows conditioning of plant defense system by rhizosphere microorganisms to promote desirable traits in plant. Exploitation of this mechanism is extremely valuable in reducing yield losses to diseases in susceptible crops in a cost-efficient way. So far, various application methods have been attempted to integrate ISR into conventional agriculture and in a few cases with improved efficacy (Hossain and Sultana 2015). Existing data support the heritability in the ISR and a link between basal and induced resistance (Ton et al. 2001a). Therefore, breeding efforts to add ISR to commercial cultivars could be a feasible option that, overall, would have much significant impact on resistance breeding.

The variation in morphological and physiological traits among plant genotypes is known to affect relative benefits and efficacy of induced resistance (Tucci et al. 2011). Walters et al. (2011) have examined the effect of host genotype on the expression of chemical elicitor-induced resistance in barley to foliar pathogens and noticed that manifestation of induced resistance differed widely across a range of spring

barley varieties. This implies that genetically different genotypes vary in the extent to which induced resistance is expressed. Until now, only a few studies have examined the genotypic effects of plants on PGPF-mediated ISR. In tomato, genetic variability among cultivated and wild lines influenced the consequence of the interaction with strains of *T. harzianum* and *T. atroviride*, with ISR to *B. cinerea* being observed in some, but not all, tomato lines examined (Tucci et al. 2011). In table and wine grapes, treatment with *T. harzianum* T39 reduced downy mildew symptoms, but the degree of efficiency varied greatly among grapevine cultivars (Banani et al. 2013). In Arabidopsis, Hossain and Sultana (2015) investigated the variation in basal as well as *Pe. simplicissimum* GP17-2-mediated resistance to *P. s.* pv. *tomato* among a worldwide collection of 75 Arabidopsis accessions. A wide variation was observed in basal as well as induced resistance among the accessions infected with the bacterium. Only 49 accessions manifested GP17-2-mediated ISR to the pathogens, while 26 accessions were non-responsive to GP17-2 treatment. This indicates that the observed GP17-2-mediated ISR is ecotype specific in Arabidopsis. Interestingly, accessions non-inducible to GP17-2 treatment appeared to be marked with higher basal resistance to infection by *P. syringae* pv. *tomato* (Hossain and Sultana 2015). Hence, GP17-2-ISR in Arabidopsis does not require components of the basal resistance pathway. Future study with these parental lines could be undertaken to map and introgress major trait loci responsible for PGPF-mediated ISR in plant.

6.5 Conclusion and Future Perspectives

Understanding the induction of plant responses by PGPF is essential for developing new strategies for managing plant growth and diseases. The enormous benefits of their exploitation are related to their use as innovative microbial sources for plant growth promotion and induced resistance to a diverse range of pathogens. Some of these fungi are already being used successfully in a number of countries, and this practice is expected to grow. However, practical use of PGPF is often hindered by inconsistency and relatively poor plant growth and disease control compared with their chemical alternatives, and as such, their effects are greatly influenced by genotype, environment, and other factors. Eventually, for PGPF to gain widespread use in farmer fields, a number of issues should be addressed. It is crucial to develop effective and practical techniques for mass culture, storage, shipping, formulation, and application of these fungi. More importantly, effort is needed to convince the growers that PGPF can provide a useful addition to their existing crop management programs.

Recent advances in molecular tools continue to give more insight into the cellular process and signaling mechanisms, related to growth and defense, resulting from plant-PGPF interactions. The current demand for high-performing PGPF could be achieved by applying innovative biotechnology to generate genetically modified strains with improved characteristics. Likewise, PGPF genes can be expressed functionally in plants to confer beneficial properties. Concern exists about the nontarget activities of the genetically modified plant or microbes, which needs to be carefully

and thoroughly assessed in non-field studies. Moreover, market failure of the developed products illustrates one aspect of the problem of externalities. Active and justified participation of private industry in product research and development may help overcome the problem.

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