Harnessing Plant-Microbe Interactions for Enhanced Protection Against Phytopathogens

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Abstract

Beneficial plant-microbe interactions have utmost importance for enhancing plant growth, improving soil structure, and managing plant diseases. Not surprisingly, such mutual interactions, where plants provide nourishment to rhizospheric microbes and in return microbes help in facilitating plant growth and stress amelioration, actually lay the foundation of sustainable agriculture. To cope with the major challenge of pathogen attack, beneficial rhizospheric microbes have proven their efficacy by induced systemic resistance (ISR). Therefore, such microbes are increasingly used in the form of biofertilizers and biopesticides. Moreover, such plant-microbe interactions elicit a range of defense-responsive activities in order to combat the pathogen challenge. The main microbes-mediated defense strategies adopted by plants include activation of antioxidant status of the plant by reprogramming defense-related enzymes, modulation of quorum sensing phenomenon, and activation of phenylpropanoid pathway leading to phenolics production, lignin deposition, and transgenerational defense response. In this chapter, we highlight the relevance of beneficial interactions between plant and microbes in enhancing plants' innate immune system against pathogen attack. This review provides a better understanding of the recent advances and major outcome of positive plant-microbe interactions and linking their relevance to plant defense response.

Introduction

Plants are the basis of life on earth that provide carbon source for all non-photosynthetic organisms. However, ~300,000 plant species are attacked by a huge number of detrimental organisms including pathogens and insects (Pieterse and Dicke 2007). Such biotic factors tremendously

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influence the plant growth and limit total agricultural production. Hence, sustainable approach of enhancing plant growth and managing plant diseases is being integrated to achieve higher crop yield. Plants in nature interact with wide range of beneficial and detrimental microorganisms providing baseline for linking aboveground and belowground community members (Van der Putten et al. 2001; Pineda et al. 2010).

The successful establishment of plant-microbe interaction depends on the ability of roots to interact with microbes as rhizosphere is the main zone where such interactions take place. The rhizospheric interaction could directly affect the plant growth by exerting either beneficial, neutral, or detrimental effects. Beneficial plant-microbe interactions require involvement of plant growth-promoting rhizobacteria (PGPR), endophytes, and mycorrhizal fungi that enhance plant growth by improving nutritional status for plants and helping the plants to combat abiotic and biotic stresses (Harrison 2005; Berendsen et al. 2012). In contrary, the detrimental interaction is imparted by pathogenic microorganisms resulting into various kinds of plant diseases. In the crowd of mixed population of beneficial and detrimental microbes residing in the rhizospheric region, the selection of potent biocontrol microbes is necessary to eliminate the pathogens and to combat the challenge imposed by pathogens. Moreover, plants also develop strategies spontaneously to recognize biotic and abiotic interactions and further translate the signal into defense response (Pei et al. 2000; Jones and Dangl 2006; Dicke and Hilker 2003).

Interestingly, plant-microbe interaction is regulated through signal-transduction pathways allowing plants to prioritize defense responses following stress conditions. It is well known that plants' response to pathogen attack is regulated by jasmonic acid (JA) and salicylic acid (SA)-dependent pathways effective against necrotrophic and biotrophic pathogens, respectively (Pieterse et al. 2012). The induced resistance imparted by these pathways represents two distinct responses: systemic acquired resistance (SAR) and ISR (van Loon et al. 1998). SAR is mediated by SA which is frequently produced following pathogen infection (Park and Kloepper 2000; Jeun et al. 2004). In contrary, JA- and ethylene (ET)-

dependent ISRs are activated by beneficial microbes proven to produce antimicrobial compounds, siderophores, O-antigen of lipopolysaccharides (LPS) and salicylate. Moreover, ISR leads to the expression of pathogenesis-related (PR) proteins such as PR-1, PR-2, chitinases, and some peroxidases (POxs) (van Wees et al. 2000; Silva et al. 2004; Jetiyanon 2007). Considering the importance of ISR, recently, noteworthy consideration is being given to exploiting the beneficial soil microbes for enhancing plants' immunity against pathogen attack. Moreover, microbe-mediated suppression of plant diseases provides eco-friendly and sustainable approach of plant disease management. It is believed that such beneficial microbes can enhance the plant's innate immunity level against the invading pathogens by inducing an array of defense responses that include enhancement in antioxidant status of the plant by reprogramming defense-related enzymes, modulation of quorum sensing activities, and activation of phenylpropanoid pathway leading to phenolics production and lignin deposition.

Microbe-Mediated Antioxidants Status in the Host

Successful pathogen infection in plants results into oxidative burst that lead to production of reactive oxygen species (ROS) causing oxidative destruction of the cell (Asada 1999; Dat et al. 2000). These ROS are formed as a result of excitation of O_2 to singlet form of oxygen or via formation of a superoxide radical (O_2^-), hydrogen peroxide (H_2O_2), or a hydroxyl radical (HO^-). The enhanced production of ROS after pathogen infection acts as cellular indicator of stress conditions and is triggered by the activity of NADPH oxidases (Cazale et al. 1999; Pei et al. 2000). However, recently, it has been investigated that apart from NADPH oxidases, the other sources such as amine oxidases and cell wall-bound POxs also participate in the formation of ROS during programmed cell death and pathogen defense (Dat et al. 2000; Grant and Loake 2000). It is interesting to note that though the elevated level of ROS imposes threat condition to the cells, it also acts as a signal for commencement of stress

Table 5.1 Major ROS scavengers in plants

Scavengers	Localization	Target ROS
Superoxide dismutase	Chl, Cyt, Mit, Per, Apo	O_2^-
Ascorbate peroxidase	Chl, Cyt, Mit, Per, Apo	H_2O_2
Catalase	Per	H_2O_2
Glutathione peroxidase	Cyt	H_2O_2, ROOH
Peroxidases	CW, Cyt, Vac	H_2O_2
Thioredoxin peroxidase	Chl, Cyt, Mit	H_2O_2
Ascorbic acid	Chl, Cyt, Mit, Per, Apo	H_2O_2, O_2^-
Glutathione	Chl, Cyt, Mit, Per, Apo	H_2O_2
α-Tocopherol	Membranes	ROOH, O_2^1
Carotenoids	Chl	O_2^1

Apo apoplast, *Chl* chloroplast, *CW* cell wall, *Cyt* cytosol, *Mit* mitochondria, *Per* peroxisome, *Vac* vacuole

response and defense pathways (Desikan et al. 2001). The steady-state level of ROS in plant cells should always be under control as their over accumulation eventually result in cell death as a consequence from various kinds of oxidative processes, viz., lipid peroxidation, protein oxidation, nucleic acid damage, and enzyme inactivation.

In order to cope with the detrimental effects of elevated level of ROS, plants are bestowed with efficient antioxidant enzymes that contribute to ROS-scavenging mechanisms of plants. Major ROS scavengers in plants are reported to be superoxide dismutase (SOD), ascorbate peroxidase (APX), and catalase (CAT) (Mittler 2002) (Table 5.1). To maintain the balance of superoxide radicals in cells, the activities of SOD and APX or CAT enzymes play crucial role as this balance avert formation of hydroxyl radical via the metal-dependent Haber–Weiss or the Fenton reactions (Asada and Takahashi 1987; Bowler et al. 1991). Moreover, the key pathways of ROS scavengers in plants include SOD present in more or less all cellular compartments. The major threat to plant system is instigated by various kinds of plant pathogens which upon infection lead to rapid formation of ROS. Plants generally increase their tolerance against invading pathogens by elevating activities of antioxidant enzymes.

The major defense strategy adopted by plants is phenylpropanoid pathway catalyzing transformation of L-phenylalanine into trans-cinnamic acid (Dixon and Paiva 1995) which play an important role in the biosynthesis of phenolics having strong antimicrobial properties (Nicholson and Hammerschmidt 1992). Interestingly, activation of the phenylpropanoid pathway also leads to deposition of lignin and induction of antioxidant enzymes including SOD and peroxidase (POx) (Silva et al. 2004; Singhai et al. 2011). It is interesting to note that beneficial soil microflora in rhizosphere provide supportive environment for the plants by augmenting the antioxidant status. Such microbe-mediated ISR protects the plants from various plant pathogens. Earlier reports have revealed significant role of many microbes in enhancing antioxidant enzymes in plants contributing to their resistance against pathogens (Table 5.2). Previously, rhizobacterial strains and *Serratia marcescens* were reported to enhance activities of POx, phenylalanine ammonia lyase (PAL), polyphenol oxidase (PPO), and lipoxygenase (LOX) in betelvine and tomato after pathogen attack by *Phytophthora nicotianae* and *Pseudomonas syringae*, respectively. Modulation of such antioxidant status in plants treated with beneficial rhizobacteria enhanced disease resistance against pathogen attack (Diallo et al. 2011). Similar observation was recorded by Singhai et al. (2011) where pseudomonad strains were found to increase the level of POx and PAL in potato leading to tolerance against potato scab disease caused by *Streptomyces scabies*. Similarly, in another interesting study by Jain et al. (2012), the microbial consortium enhanced tolerance in pea plants against *Sclerotinia sclerotiorum* by inducing the level of PAL, POx, PPO, and SOD. Most recently, Singh et al. (2013) showed elevation of SOD and PO in *Sclerotium rolfsii* challenged chickpea plants treated with triple consortium of *Pseudomonas*, *Trichoderma*, and *Rhizobium*. Taken together, these reports clearly validate the importance of beneficial rhizosphere microbes in imparting tolerance to the plants against diverse range of pathogens by modulating their innate antioxidant status as shown in Fig. 5.1.

Table 5.2 Examples of microbe-mediated defense response in plants against pathogen infection

| Host plant	Microbes	Antioxidant enhanced	Pathogen	References
Chickpea	*Pseudomonas, Trichoderma, Rhizobium*	Superoxide dismutase, peroxidase	*Sclerotium rolfsii*	Singh et al. (2013)
Pea	*Pseudomonas, Trichoderma harzianum, Bacillus subtilis*	Phenylalanine ammonia lyase, peroxidase, polyphenol oxidase, superoxide dismutase	*Sclerotinia sclerotiorum*	Jain et al. (2012)
Potato	Pseudomonad strains	Peroxidase, phenylalanine ammonia lyase	*Streptomyces scabies*	Singhai et al. (2011)
Betelvine	*Serratia marcescens*	Phenylalanine ammonia lyase, peroxidase, polyphenol oxidase	*Phytophthora nicotianae*	Lavania et al. (2006)
Tomato	Rhizobacterial strains	Lipoxygenase, phenylalanine ammonia lyase, peroxidase	*P. syringae* pv. *tomato*	Silva et al. (2004)
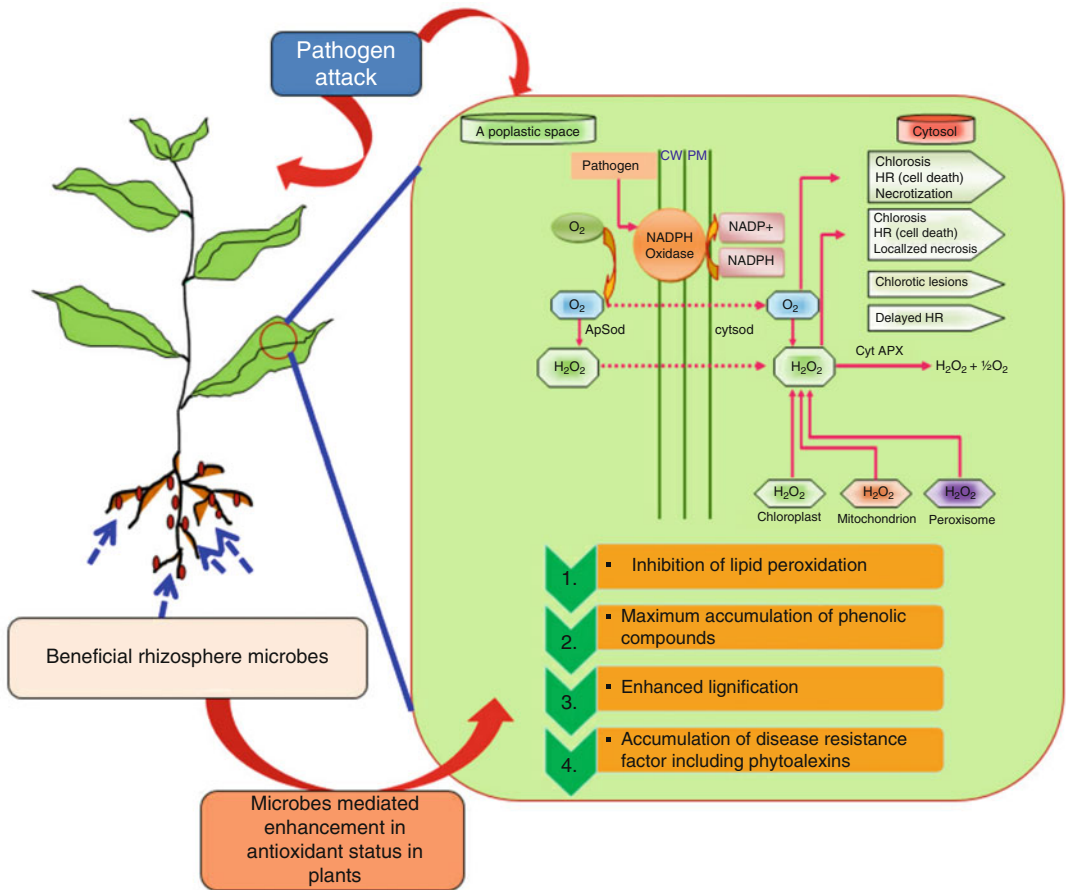
Fig. 5.1 Schematic diagram showing beneficial rhizosphere microbes mediated enhanced antioxidant activity contributing to their defense strategy against pathogen attack

Microbe-Mediated Activation of Phenylpropanoid Pathway

Soil is the locale of numerous microorganisms and can aptly be referred to as the mine of microorganisms. The rhizospheric regions of the plants inhabit most of the microbial communities in its vicinity, be it having beneficial or deleterious effects on the plant. Beneficial microorganisms may include PGPR and mycorrhizal fungi that induce systemic defense response in the host to preclude it from the chronic impairment of phytopathogens comprising of bacteria, fungi, viruses, and nematodes. To avoid the perplexity in the use of different terms for denoting the beneficial microbes, two new terms were proposed by Bashan and Holguin (1998): "biocontrol plant growth-promoting bacteria (PGPB)" that suppress plant diseases by enhancing the plant defense responses and "PGPB" that specifically play eminent role in augmenting plant growth. The upgradation of the conventionally used "PGPR" term coined by Kloepper et al. (1980) to "PGPB" would thereby include the useful microbes that do not inhabit the rhizospheric region of the soil yet enhance the vigor of plants against the phytopathogens.

Diverse interactions prevail between the microbial commune and plant roots, for instance, the symbiotic associations by mycorrhizal fungi that aid in the uptake of water and minerals (Harrison 2005), and the nodule-inhabiting *Rhizobium* bacteria that fix the atmospheric nitrogen for the plant (Spaink 2000). Several other types of beneficial microbes like PGPR and fungi are reported to suppress plant diseases (Van Loon et al. 1998; Harman et al. 2004; Kloepper et al. 2004) or insect herbivory (Van Oosten et al. 2008) by enhancing the defense response of the plant thereby resulting in overall increment in the plant growth parameters. The plethora of benefits endowed to the plants by the microbes can be attributed to either direct effect through mycoparasitism of soil-borne pathogens or indirectly by eliciting the plant defense mechanisms thereby fortifying the plant immune system against the invading pathogens (Van Loon et al. 1998; Pozo and Azcon-Aguilar 2007).

Several microbial determinants are related with the elicitation of defense responses in plant system. Most commonly studied and well associated as the inducers of host immune response conferred by rhizobacteria are the microbe-associated molecular patterns (MAMPs). Also, LPS and flagellin found at the cell surfaces of rhizobacteria are found to be potent in inducing defense response of the associated host against phytopathogens (Bakker et al. 2007). Another important mechanism employed by beneficial microbes in disease suppression is to create competition for iron by forming low molecular weight iron chelators known as siderophores (Meziane et al. 2005). Important chemicals that act as elicitors for the defense response are the variously secreted antibiotics by the rhizobacteria and fungi (Ran et al. 2005); surfactin, a lipoprotein secreted by *Bacillus subtilis* (Ongena et al. 2007); biosurfactant massetolide A from *P. fluorescens* (Tran et al. 2007); N-alkylated benzylamine (Ongena et al. 2005); N-acyl-L-homoserine lactone (Schuhegger et al. 2006); and volatile organic compound 2, 3-butanediol by *Bacillus* spp. (Ryu et al. 2004). Fungal proteins like endochitinase secreted by *Trichoderma* spp. have been shown to enhance plant defense-related proteins (Harman and Shoresh 2007; Keswani et al. 2014). A small protein SM1 produced by strains of *Trichoderma virens* can induce terpenoid phytoalexin biosynthesis and POx activity as studied in cotton plants and other systems as well (Djonovic et al. 2006, 2007). Another class of proteins associated with the immune system of the plants is the products of avirulence like (Avr) genes, produced not only by the phytopathogens but also by the beneficial microbes. They generally function as pathogen-specific elicitors of the hypersensitive responses in plants containing the corresponding resistance (R) gene (Woo et al. 2006). Small secondary metabolites produced by *Trichoderma* species have also been reported to possess defense response induction activity mainly via eliciting the expression of PR proteins on application to plants causing both local and

systemic disease suppression (Vinale et al. 2008; Keswani et al. 2014).

Plant defense response gets activated by the metabolism of phenyl propanoid (PP) pathway in which PAL catalyzes the first important step of the general PP metabolism. Further, the pathway leads to the synthesis of other important compounds having indispensible role in providing plant defense including cell wall strengthening and repair (lignin and suberin), antimicrobial activity (pterocarpan, isoflavonoid phytoalexins), and signaling SA (Hummerschmidt 1999). Beneficial microbes like *Trichoderma* spp. have been reported to trigger the terpenoid phytoalexin defense compounds in cotton seedlings thereby controlling *Rhizoctonia solani* infestation apart from the conventional mycoparasitic mode exhibited by the species of the genus (Howell et al. 2000). Also, biocontrol of *Pythium ultimum* on *Arabidopsis* seedlings by *T. harzianum* strain T22 reported the elevated expression level of *NPR1* gene which is the main gene involved in disease resistance (Shoresh et al. 2010). Recently, the concept of using two or three compatible beneficial microbes has been proposed for better management of disease. It has been shown that significant enhancement of PP activity is recorded in chickpea plants treated with the triple consortium developed using *Trichoderma*, *Bacillus*, and *Rhizobium* spp. when challenged with *S. rolfsii* (Singh et al. 2013). Similar results were previously reported by Jain et al. (2012) where the consortium of beneficial microbes (*Trichoderma* spp., *Pseudomonas* spp., *Bacillus* spp.) were reported for the increment of various defense-related enzymes in pea plants against *S. sclerotinia* challenge. Another class of beneficial fungi *Piriformospora indica* has also been reported to cause elevation of defense response in plants against soil-borne pathogens (Serfling et al. 2007; Stein et al. 2008) showing its mechanism to be related with the upregulation of JA-mediated pathway.

A complex cross talk subsists between the plant and the beneficial microbes in response to the pathogenic microbes. The advancement in the research related to the responses triggered in plants against the pathogens by the beneficial microbes demonstrates the involvement of specific MAMPs analogous to the MAMPs of the pathogen highlighting the extensive coordination prevailing between different defense pathways involved.

Microbe-Mediated-Induced Lignification

Tertiary structure of lignin results from the polymerization of polyphenols and free radicals p-coniferyl, coumaryl, and sinapyl alcohols within the plant cell wall. This polymerization also results in the formation of covalent cross links with polysaccharide and protein moieties framing a tremendously resistant cell wall towards mechanical and enzymatic disruption against various classes of plant pathogens, insects, and herbivores (Bernards and Lewis 1998; Sederoff et al. 1999; Davin and Lewis 2000; Hatfield and Vermerris as 2001; Boerjan et al. 2003). Thus, lignin serves as physical defense shield in plant defense. Modifications in lignin composition, content, and distribution affect the strength of the shield which ultimately influences the agro-industrial pertinence of the plant material (Lewis and Yamamoto 1990).

Lignification obstructs phytopathogen growth on plant surface by a pentagonal approach (Ride 1978) as mentioned below:

1. Lignin deposition shields the plant tissue surface from enzymatic hydrolysis and mechanical penetration of phytopathogens by intensifying compressive forces between lignin layers preventing cellular penetration of phytopathogens.

2. Lignification of walls hinders the mobility of water and electrolytes between plant cells and phytopathogens facilitating pathogen killing by starvation.

3. Chemical modification of cell wall components is an effective strategy for disguising the pathogen enzymes. Coniferyl alcohol and ferulic acid covalently bound to cell wall glycoproteins and esterification of cell wall polysaccharides with cinnamic acid derivatives evidently reduces the cell wall damage

due to unavailability of substrates (Friend 1976; Whitmore 1978).

4. Generation of free radicals and low molecular weight phenolic precursors produced during polymerization of lignin may directly inactivate pathogens' membranes, enzymes, toxins, and elicitors.

5. Fungal walls contain chitin, cellulose, and hydroxyproline-rich proteins which can serve as matrices for lignin polymerization. Consequently, the hyphal tips become lignified and lose plasticity necessary for growth and penetration (Gottlieb and Pelczar 1951).

Among various mechanisms of plant defense, lignification is a strong structural defense strategy employed by plants to prevent pathogen penetration, and this relationship of lignification and disease resistance in plants is clearly witnessed in various studies. Comparatively, rapid lignin accumulation and deposition is observed in resistant cultivars than susceptible varieties (Vance et al. 1976; Yates et al. 1997; Durrant and Dong 2004). Not much is known about the role of rhizospheric microbes in strengthening plant's cell wall towards various biotic stresses. A recent study aimed to determine the efficacy of a triple microbial consortium of fluorescent *Pseudomonas* PHU094, *Trichoderma* THU0816, and *Rhizobium* RL091 strain on physiological defense responses in chickpea against the collar rot pathogen *S. rolfsii*. The result clearly illustrates the profound variation of lignin deposition in chickpea infected with *S. rolfsii*, which is attributed to different combinations of plant beneficial microbes to trigger lignification process. Interestingly, on treatment with triple consortium, uniform and maximum lignin deposition in the intrafascicular cambial cells was clearly observed and the phloem cells also displayed an enhanced lignification in sclerenchyma cap. Thus, claiming that beneficial rhizospheric microbes when employed in synergistic consortium can enhance the physical strength and durability of the cell wall towards cell wall-degrading phytopathogen (Singh et al. 2013).

In another study, alterations in phenolic metabolism and lignin deposition were analyzed in the roots of tomato plants after elicitation with *Fusarium* mycelium extract (FME), *Fusarium* culture filtrate (FCF), chitosan (CHT), and *Trichoderma* mycelium extract (TME). Maximum lignin synthesis was observed in plants treated with FME followed by CHT. Lignin deposition in the root cell walls increased to 5.7 times within 24 h after elicitation with FME. Similarly, CHT increased lignin deposition to almost five times, 24 h after elicitation. Thus, it was concluded that cell wall strengthening by lignin deposition was preceded by elicitation of lignin synthesizing enzymes revealing its essential role in defense response of tomato plants in response to various elicitors including one derived from *Fusarium oxysporum* f. sp. *lycopersici*, the causal organism of *Fusarium* wilt of tomato (Mandal and Mitra 2007).

Microbe-Mediated Quorum Sensing in Pathogen Management

The phenomenon of quorum sensing (QS) depicts the bacterial cell-cell communication and is generally cell density dependent. This cell-cell communication network is mediated by signal molecules (also called autoinducers), for example, oligopeptides and N-acylhomoserine lactones (AHL) in Gram-positive and Gram-negative bacteria, respectively. The QS plays a significant role in biofilm formation and in determining virulence factor in pathogenic bacterial species (Gram et al. 2002). In contrary, the phenomenon of antiquorum sensing (anti-QS) also exists where autoinducers interrupt with QS and thereby reducing the pathogenicity in several bacterial species (Truchado et al. 2012). Since QS contribute significantly in regulating virulence factor in many plant pathogens, anti-QS could be of great interest for decreasing pathogenic behavior and in developing innovative approach of disease control (Alvarez et al. 2012).

Considering the importance of anti-QS, presently, this phenomenon is getting noteworthy attention in plant disease management using bacterial biosensors and indicators. Interestingly, the cloning of *aiiA* gene (from *Bacillus* sp.) into transgenic potato and tobacco for enhancing

disease resistance against *Erwinia carotovora* is perhaps the very first example (Dong et al. 2001). Expression of this gene resulted in the production of AHL-lactonase in transgenic plants that interrupt with the QS systems arresting the virulence factor of *E. carotovora* leading to reduced disease incidence. Likewise, another example is the generation of transgenic tobacco lines using *expI* (*E. carotovora* AHL gene) which, after expression in plants, trap the pathogen in premature stage when it is unable to cause infection (Mäe et al. 2001). It is interesting to note that the autoinducer molecule AHL also contributes to the production of antimicrobial compounds in nonpathogenic *Pseudomonas chlororaphis* which has been successfully employed in suppressing plant diseases (Pierson et al. 1998a, b). Molina et al. (2003) evaluated the biocontrol potential of AHL-degrading *Bacillus* sp. A24 and genetically engineered AHL-degrading strain P3/pME6863 against soft rot in potato caused by *E. carotovora*. Recently, the novel approach of disrupting QS using structural analogs stimulating AHL-degradative microflora has been investigated by some researchers (Crépin et al. 2012a, b). In conclusion, these studies altogether clearly validate that the QS inhibition of phytopathogenic bacteria could be successfully employed for plant disease management. Hence, more focused researches are needed towards this approach.

Microbe-Mediated Nutrient Uptake and Defense

Fifty years back, the drive required for feeding the surplus population gave birth to the much talked about "Green Revolution" in India, leading to tremendous increase in food production. The unremitting use of fertilizers and pesticides has undoubtedly contributed to the increment in the food production but had led to the slow death of the soil microflora and fertility as well. In order to resolve the burning issue of deposition of toxic residues leading to biomagnifications in the food web, urgent need of using eco-friendly alternatives is required. Biopesticides comprising of microbial inoculants have emerged as a silver line

for the current scenario with multifaceted benefits like safer approach both to the environment and to human kind, more targeted activity, low dose effectiveness, easily decomposable, natural propagation, and multiplication along with fortifying the plants' immune system (Berg 2009).

A constant conversation exists between the plants and the microbes in its vicinity. The plant-microbe interaction persists owing to the beneficial mutualism between the two partners which upshot various remuneration to plants as well as microbial commune. Positive effect on the growth and health of plants, enhanced stress tolerance, induction of disease reduction, biodiversity enrichment with ability to foster nutrient availability and uptake are the consequence of the interface between plant and microbes (Lugtenberg et al. 2002; Morrissey et al. 2004). These interactions are specific in terms of the host colonization due to the specific secondary metabolism and morphology (Berg and Smalla 2009). However, plant growth promotion and disease reduction or control have been the most noteworthy consequence of this interaction. Growth promotion in plants can be mediated through direct mechanisms by the microbes and also through indirect means through their antagonistic properties thereby reducing disease incidence allowing the healthy proliferation of the plants.

The competence of the microbes to colonize plant habitats is one of the crucial requirements for an effective plant-microbe interaction (Kamilova et al. 2005). Recognition, adherence, invasion (in case of endophytes and pathogens), colonization, and growth are the essential steps required for successful colonization apart from the various strategies employed by the microbial commune to establish the interaction. However, the initiation is executed by the plant itself by releasing signals recognized by the microbes which reciprocate the signals to initiate the colonization (Bais et al. 2006). Generally, motile organisms are preferred to participate and react in this cross talk (Lugtenberg et al. 2002).

Basically, three main types of interactions are related to the increment of plant growth mediated by beneficial microbes (Fig. 5.2). The most commonly known type of interaction is the
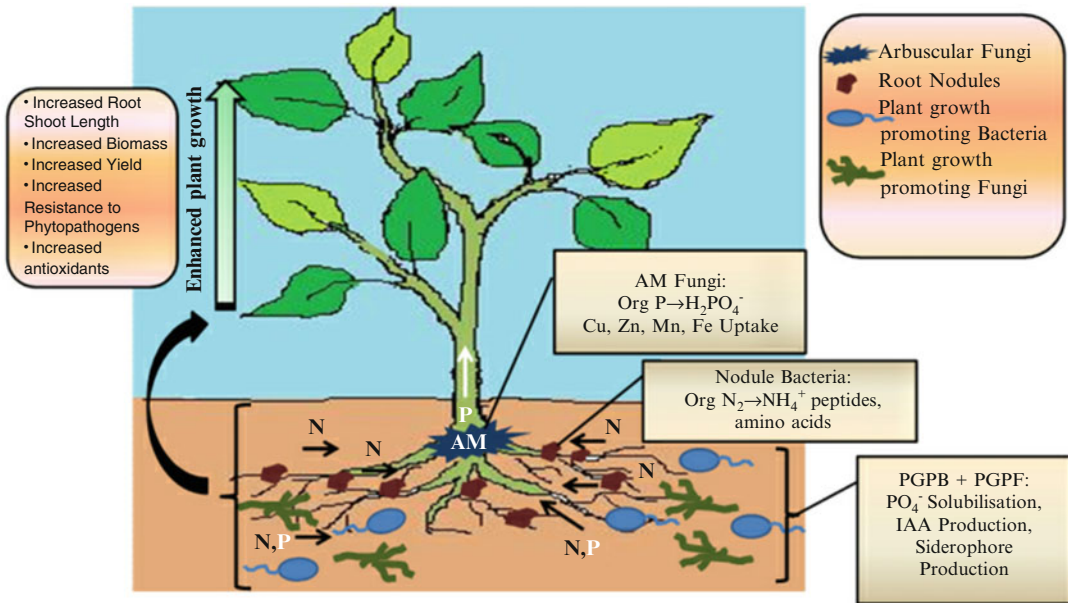
Fig. 5.2 An overview of microbe-mediated nutrient uptake in plants

symbiosis by *Rhizobium* species in fixing atmospheric nitrogen into ammonia in specific organs called nodules, found in leguminous plants (Van Rhijn and Vanderleyden 1995). Other important interaction is that of higher plants, commonly terrestrial flowering plants, with arbuscular mycorrhiza (AM) fungi which facilitate the absorption and translocation of phosphate from the soil (Harrison 1999). Lastly, the outcome of the numerous beneficial microbes that aid in mineralization of organic matter, thereby producing available nitrogen and phosphorous forms along with numerous micronutrients, provides the platform for the third type of interaction prevailing between plants and microbes (Hayatsu et al. 2008).

Phytohormones like indole-3-acetic acid (IAA), ET, cytokinins, and gibberellins are crucial for plant growth. Plants can obtain these hormones by either synthesizing themselves or by obtaining these from the microbes which can even alter the hormonal balance of the plant thereby causing alterations in the growth of the plants. Plant-associated bacteria have been shown to decrease the endogenous ACC levels thereby leading to increased root growth (Glick 2005). ACC deaminase-producing bacteria have also been reported to provide abiotic and biotic stress tolerance to plants thereby protecting them

from the unfavorable conditions (Saleem et al. 2007). Seed treatment with auxin-producing *Pseudomonas fluorescens* has been reported to show stimulation of root growth, due to the production of nine times more tryptophan in root exudates of radish plants (Kamilova et al. 2006). This could be directly related to the growth promotion ability as the root growth-promoting hormone auxin is generally found in the root exudate which is synthesized from the amino acid tryptophan. Certain microbes like *B. subtilis*, *B. amyloliquefaciens*, and *Enterobacter cloacae* are known to enhance plant growth by releasing volatiles like 2, 3-butanediol and acetoin (Ryu et al. 2003). Increased photosynthetic efficiency and chlorophyll content were recorded in *A. thaliana* on treatment with *B. subtilis* GB03 which could be possibly related with the modulation of glucose and abscisic acid signaling (Zhang et al. 2008). Apart from auxin-producing bacteria, beneficial fungi like *Trichoderma* have been shown to be responsible for plant growth increment via auxin signaling (Contreras-Cornejo et al. 2009). Nitrogen fixation by the symbiotically associated *Rhizobium* species in the root nodules of leguminous plants or by free living bacteria like *Azospirillum*, *Burkholderia*, and *Stenotrophomonas* (Dobbelare et al. 2003) has been a major example

for nutrient acquisition to plants by microbes. Bacterial indirect contribution to plant growth by liberating phosphorous from organic compounds such as phytates play an important role in providing the necessary phosphorous required for proper growth of the plant (Unno et al. 2005). Another important nutrient, sulfate, is also made available to plants through oxidation by bacteria (Banerjee and Yesmin 2002). Siderophores have also been an important mode for the uptake of important micro-elements like Fe and other poorly soluble inorganic nutrients. Also, relation of siderophore production has been reported with the antagonistic activity against pathogens. *P. fluorescens* CHA0 has been reported to produce gluconic acid which acidifies the surrounding environment and thereby solubilizes the mineral phosphate in the soil creating a nutrient-limited condition for the plant pathogens (De Werra et al. 2009). Fungal biocontrol agent *Trichoderma* and mycorrhizal fungus *P. indica* have been reported to produce siderophore as a mechanism to check the growth of pathogens by creating a competitive environment for the availability of iron (Shoresh et al. 2010). Phosphate absorption to plants by AM has been well reported (Smith et al. 2011; Balakrishnan and Subramanian 2012). Also, increment in Cu, Zn, B, Mn, and Fe uptake in plants has been attributed to AM (Lambert et al. 1980; Clark et al. 1999; Liu et al. 2000).

Other important microbes that have been well studied for their mode of action and regulation in promoting plant growth and antagonism are members of the genera *Azospirillum* (Cassan and Garcia 2008), *Serratia* (De Vleeschauwer and Hofte 2007), *Stenotrophomonas* (Ryan et al. 2009), and *Streptomyces* (Schrey and Tarkka 2008) along with fungal genera *Ampelomyces*, *Coniothyrium*, and *Trichoderma* (Harman et al. 2004).

Microbe-Mediated Transgenerational Defense

Plant-recruited beneficial microbes can also prime the plants for enhanced defense responses, and the effect of priming could be passed on to the next generations as well. Priming of plants leads to enhanced perception of MAMPs,

recognition of effector molecules secreted by pathogen, and recruitment of beneficial rhizospheric microbes (Conrath 2011). Recent understanding in the subject reflects that similar to animals, epigenetic inheritance in plants also takes place, and the epigenetic modifications of the chromatin as well as DNA methylation in plants could be well preserved in several subsequent generations (Pieterse 2012). Being sessile organisms, plants communicate with their offspring through this mechanism to "inform" the offsprings about the potential threats in their environment. Since, plants encounter potential biotic and abiotic threats from the environment at one or the other point of their life span, they are adapted to such mechanisms through the process of evolution for passing on the information to the next generation. Slaughter et al. (2012) demonstrated that the descendants of *A. thaliana* plants primed with an avirulent strain of *P. syringae* pv. *tomato* (PstavrRpt2) showed enhanced and rapid accumulation of defense-related gene transcripts associated with the SA signaling pathway. Further, the descendents also showed enhanced disease resistance against a virulent isolate of *P. syringae* and another oomycete pathogen *Hyaloperonospora arabidopsidis*. Interestingly, the progeny of transgenerationally primed plants when treated again with the priming agent displayed an even stronger primed phenotype. Recent evidences suggest that SA-mediated systemic resistance in plants also require chromatin remodeling and DNA methylation (Luna et al. 2012). Luna and Ton (2012) showed that transgenerationally acquired resistance was sustained through one stress-free generation, confirming epigenetic basis of the phenomenon. Failure of *non expressor of PR 1* (*npr1*) mutants to sustain transgenerationally acquired resistance in the progenies further signifies the SA-inducible pathway in this phenomenon and the central role of *NPR1*. Further, transgenerationally acquired systemic resistance was also demonstrated against biotrophic pathogens. A study on progenies obtained from diseased *Arabidopsis* also resulted in enhanced resistance towards the downy mildew pathogen (Luna and Ton 2012). Histone deacetylase 6 (HDA6) is a well-studied histone

deacetylase that has a prominent role in the silencing of genes. It was reported that HDA6 has also a significant role to play in the process of DNA methylation on its direct target locus. Thus, elucidation of the functions of HDA6 provided some very important clues of epigenetic regulation in plants (Kim et al. 2012). All these findings suggest the importance of transgenerationally acquired systemic resistance in plants and their potential role in managing plant diseases.

Future Prospects

The major challenge in the form of plant pathogens imposed to plant growth in natural and agricultural ecosystems urges for exploiting beneficial plant-microbe interactions. It is a well-known fact that microbial approach for plant disease management is necessary for maintaining the sustainability in agroecosystems. Therefore, it has been an emerging topic and gained considerable attention by many researchers. Though, various facets of plant-microbe interactions have long been studied, there is still a long way to go for achieving greater knowledge. The better understanding of plants' rhizosphere components is necessary to know the cross talk between plants and microbes. Linking this information to stress conditions would certainly provide a clue about developing a favorable and friendly environment for plant growth. Moreover, molecular approaches of studying the regulatory components of plant-microbe interactions can provide better understanding of improving such relationships by their manipulation.

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