Plant-Microbe Interactions: Current Perspectives of Mechanisms Behind Symbiotic and Pathogenic Associations

6

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Abstract

The phyllosphere and rhizosphere of plants have been a reservoir of microorganisms of both symbiotic and pathogenic nature. The interplay between plants and associated microbes involves complex and dynamic mechanisms, many of which are unexplored. The unraveling of these mechanisms is a big challenge for plant biologists. The consequence of such interactions may be beneficial, detrimental, or neutral for the hosts. There are many known mechanisms through which microorganisms especially bacteria support plant growth, i.e., fixation of atmospheric nitrogen, solubilization of inorganic phosphate, modulated phytohormones synthesis, production of stress-responsive enzymes like 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase, and biocontrol of many plant diseases. Both above- and underground plant organs are frequently exposed to a plethora of microorganisms, including viruses, bacteria, oomycetes, fungi, and eukaryotic protozoans. Phytopathogens defend their habitat and infect

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plants by a variety of compounds (toxins) that are broad spectrum in their activity. In response, plants initiate defensive mechanisms that resist pathogen penetration and subsequent infection. Thus, various events of molecular crosstalk take place between plants, and both friendly and hostile microbes trigger a series of highly dynamic plant cellular responses. Such mechanisms are very crucial for pathogen recognition and induction of adequate defense signal transduction cascades in the plant. More research insights are required to unravel the molecular basis behind these mechanisms. Also, to support the plant life, many complex mechanisms initiated after the association of symbiotic or pathogenic microorganisms need to be explored.

Keywords
Mechanisms • Plant-associated microbes • Symbiosis • Pathogenesis • Defense responses

6.1 Introduction

Plant-microbe interactions play a vital role to ensure sustainability in agriculture and ecosystem restoration (Badri et al. 2009). The interactions may be categorized as positive, negative, or neutral which largely depends on the nature of microorganisms associating the host. Positive interactions stimulate plant growth by conferring abiotic and/or biotic stress tolerance and help the plants for the revitalization of nutrient-deficient and contaminated soils. Negative interactions involve host-pathogen interactions resulting in many plant diseases and adverse effects and host life (Abhilash et al. 2012). Moreover, some microbes reside in the soil surrounding the plant roots just to obtain their nutrition from root exudates. They do not influence the plant growth or physiology in a positive or negative way, thus forming neutral interactions. Apart from that, the resource allocation between different plant parts is greatly affected by beneficial microorganisms. Also, many above- and belowground interactions with herbivores and other natural enemies of the plants are modulated by the microorganisms. In addition, the physicochemical and biological soil properties are modified in response to physiological, biochemical, and molecular dialogues between plants and associated microbes (Dubey et al. 2015). Plant root exudates are rich in low molecular weight compounds like amino acids, organic acids, polymerized sugars, root border cells, and dead root cap cells. Moreover, plant roots secrete many phyto-siderophores which sequester the metallic micronutrients from the soil, resulting in enhanced plant nutrition. Some secondary metabolites present in plant root exudates also play key role in plant-microbe communications (Bais et al. 2006). Different interfaces of rhizosphere, phyllosphere, and endosphere possibly exist in such complex and largely unexplored interactions. Thus, the complex and interconnected process that takes place at the abovementioned interfaces must be explored to understand the contribution of each and every player to the well-being of the ecosystem. Therefore, the complete

knowledge of mechanisms underlying plant-microbe communications is necessary to decipher the interfaces among host plant microorganisms for sustainable agriculture, increased biomass and bioenergy production, and restoration of soil properties (Saleem and Moe 2014). For microorganisms, colonization is a vital step for effective establishment leading to friendly or pathogenic relationship with plants (Kamilova et al. 2006; Lugtenberg et al. 2002). Successful colonization involves host cell surface recognition, adherence, invasion, growth, and multiplication along with several unexplored mechanisms. The crosstalk between plants and microbes is initiated by the production of plant signals that are perceived by the microbes and stimulate synthesis of chemicals for colonization (Ali et al. 2016; Bais et al. 2006). Motile microorganisms are best suited to participate actively in this crosstalk (Lugtenberg et al. 2002). Moreover, a confirmation of microbial structure greatly influences the intensity, duration, and outcome of plant-microbe interactions (Danhorn et al. 2004; Shahid et al. 2015). In this chapter, we attempted to highlight all the known mechanisms that drive strong association of microorganisms and hosts. The outcomes of these mechanisms on growth and physiology of plant have also been discussed.

6.2 Mechanisms Behind Plant-Symbiont Interactions

6.2.1 Biological Nitrogen Fixation

Plants uptake nitrogen either as inorganic form (NH_4^+ and NO_3^-) or as low molecular weight dissolved organic nitrogen (DON), particularly amino acids (Murphy et al. 2003; Streeter et al. 2000). Atmospheric dinitrogen (N_2) cannot be incorporated into plant metabolism until reduced to a more useable form like ammonia (NH_3) by some diazotrophic microorganisms (Rovira 1991). Nitrogen cycle also contains biological nitrogen fixation (BNF) as a vital process (Stevenson and Cole 1999). One type of nitrogen fixation that does not include any biological activity involves industrial fixation and fixation through natural lightening process, which converts atmospheric N_2 to NO_3^-. The other type, biological nitrogen fixation (BNF), is a process by which atmospheric N_2 is converted to NH_3, and this reaction is catalyzed by nitrogenase enzyme present in diazotrophic microorganisms. The later type contributes more than 2×10^{13} g nitrogen annually, worldwide. From this amount, 80% is contributed by symbiotic fixation, and the remaining 20% is made available by free-living or associative nitrogen-fixing systems (Falkowski 1997).

The ability to convert atmospheric N_2 into plant usable form exists only in bacteria and Archaea (Young 1992). For BNF, bacterial species of *Acinetobacter*, *Alcaligenes*, *Arthrobacter, Azotobacter*, *Azospirillum*, *Bacillus*, *Enterobacter*, *Burkholderia*, *Pseudomonas*, *Serratia*, and (*Brady*)*Rhizobium* are mainly involved in establishing symbiotic and associative-symbiotic interactions with plant roots where ultimately both partners are benefited (Egamberdiyeva 2005; Tilak et al. 2005). There are two main types of BNF:

1. Symbiotic nitrogen fixation, e.g., (*Brady*)*Rhizobium* and *Frankia* in leguminous and nonleguminous actinorhizal plants, respectively
2. Non-symbiotic nitrogen fixation, e.g., *Cyanobacteria*, *Azotobacter*, *Azospirillum*, etc.

6.2.1.1 Symbiotic Nitrogen Fixation

Rhizobia are classically defined as symbiotic bacteria that invade the roots and stems of leguminous plants to fix nitrogen (van Rhijn and Vanderleyden 1995). It is a synthesis of NH_4^+ (a plant usable form of N) using atmospheric N_2 (plant non-usable form of N) by *rhizobia* in nodules of leguminous plants. The important nitrogen-fixing *rhizobial* genera in legumes are *Rhizobium*, *Bradyrhizobium*, *Allorhizobium*, *Mesorhizobium*, *Azorhizobium*, and *Sinorhizobium*, each of which belongs to a distinct and well-established phylogenetic group (Hungria and Vargas 2000; Sy et al. 2001). Besides rhizobia, many *Frankia* species has also been reported to form nodules in nonleguminous actinorhizal plants for N_2 fixation (Zhang et al. 2012). Moreover, non-rhizobial strains may also occupy nodule cells and benefit the plants. Hameed et al. (2004) reported the occupation of a phosphate solubilizing *Agrobacterium* strain Ca-18 with the nodule cells. Many other studies have also described the existence of non-rhizobial bacteria in root nodules of leguminous crops (Rajendran et al. 2012; Tariq et al. 2012).

6.2.1.2 Non-symbiotic Nitrogen Fixation

The atmospheric dinitrogen fixation without the formation of nodules is termed as non-symbiotic nitrogen fixation. The non-symbiotic diazotrophic genera include *Azotobacter*, *Azospirillum*, *Acetobacter*, *Azoarcus*, *Bacillus*, and *Pseudomonas* (Saharan and Nehra 2011). Many cyanobacterial genera have been identified as free-living diazotrophic bacteria (Fiore et al. 2005). In a recent study, conducted in China, the non-symbiotic nitrogen-fixing bacterial diversity was categorized as *Proteobacteria* (63.9%), *Actinobacteria* (32.2%), *Firmicutes* (1.9%), and *Bacteriodetes* (1.9%), and many bacterial genera were found as free-living nitrogen fixers such as *Arthrobacter*, *Mitsuaria*, *Burkholderia*, *Sinorhizobium*, *Pseudomonas*, and *Rhizobium* at lower taxonomic level (Xu et al. 2012).

6.2.1.3 Biochemistry and Genetics of Biological Nitrogen Fixation

The process of BNF is complex and involves many functional and regulatory genes (Dixon and Kahn 2004). The reduction of atmospheric nitrogen is performed by a nitrogenase enzyme, a dimer of two metalloproteins: nitrogenase iron protein (Fe protein) and nitrogenase molybdenum-iron protein (Mo-Fe protein) (Einsle et al. 2002; Strop et al. 2001). Nitrogen, as a substrate, is bound to molybdenum-iron-sulfur homocitrate clusters of Mo-Fe protein, and the same phenomenon is utilized by other substrates such as acetylene, protons, etc. (Postgate 1982). The second protein (Fe-protein) shuttles electrons to Mo-Fe-protein, and this process consumes two Mg-ATP for each electron (Halbleib and Ludden 2000). The complete process of BNF can be expressed as follows:

$N_2 + 10H^+ + 8e^- + nMgATP \rightarrow 2\,NH_4^+ + H_2 + nMgADP + nPi\,, n \geq 16$ (Dean and Jacobson 1992)

Thus, the process is energy demanding and consumes 8 mol of ATP to produce 1 mol of NH_4^+. This ratio may be much higher under natural conditions (Hill 1992). The diazotrophic ability of soil bacteria can be measured in vitro through acetylene reduction assay (Dilworth 1966).

6.2.1.4 Genes Involved in Biological Nitrogen Fixation

Different species have different number and arrangement of genes engaged in the process of BNF. The Mo-Fe is a tetrameric ($\alpha_2\beta_2$) protein, encoded by *nifDK*, and Fe-protein is a homodimer (α_2), encoded by *nifH* (Halbleib and Ludden 2000). So these structural genes along with many regulatory and accessory genes are responsible synthesis of *nif* regulon (Dean and Jacobson 1992). The *nifD* and *nifK* genes are part of same operon, while *nifH* is also considered, in some studies, a part of the same operon. Nitrogenase metal clusters, synthesized by *nifE* and *nifN*, are found together on the operon *nifEN*, which may have arisen from the duplication of two operons *nifDK* and *nifEN*, considered as the core operons (Fani et al. 2000). A number of other genes are also present to supplement these operons which are responsible for coding proteins responsible for electron transport (*nifF*, *nifJ* in *Klebsiella pneumoniae*), regulation (*nifA*) or Fe-Mo cofactor (*nif*B, *nif*V in *Klebsiella pneumoniae*) synthesis (Triplett et al. 1989). In rhizobial species, *fix* and *nod* genes are present which control nitrogen fixation and nodule formation, respectively. While in free-living diazotrophs like *Klebsiella pneumonia*, many of these genes are absent (Dean and Jacobson 1992). Apart from the standard nitrogenase nitrogen-fixing system (*nifDK* and *nifH*), two alternative nitrogen-fixing systems have also been well characterized (Bishop and Premakumar 1992). These systems do not carry molybdenum; instead one carry vanadium (*vnfDK* and *vnfH*) while the other contain only iron and no unusual metal (*anfDK* and *anfH*). All these systems share significant sequence homology but still enough difference for identification. The two alternative systems are regulated under Mo-deficient conditions (Bishop and Premakumar 1992).

6.2.2 Phosphate Solubilization and Mobilization

Plant phosphate availability is improved by arbuscular mycorrhizae through the increase in root surface area, thus forming channels of phosphate nutrition (Osorio and Habte 2015). Plant growth-promoting rhizobacteria (PGPR) facilitate plants to obtain nutrition from inorganic and organic pools of soil through mineralization and solubilization processes (Hilda and Fraga 1999). If all the microbial population of soil is considered, phosphate solubilizing bacteria (PSB) constitute 1–50% (Chen et al. 2006).

Thus, they stimulate phosphorus uptake and significantly modulate plant growth, physiology, and yield (Arcand and Schneider 2006; Chen et al. 2006; Perez et al. 2007). Various strains of *Bacillus*, *Pseudomonas*, *Enterobacter*, and *Rhizobium*

along with *Aspergillus* and *Penicillium* fungi were found to be the most influential P solubilizers (Whitelaw 1999). The mechanism of P-solubilization is associated with organic acids released by P-solubilizing bacteria, lowering the pH of rhizosphere. Thus, the organic acid production causes the chelation of H^+ ions in the root microenvironment, and insoluble phosphates are transformed into soluble form (Mullen 2005; Trivedi and Sa 2008). Two major mechanisms of bacterial phosphate solubilization are:

1. Mineral phosphate solubilization
2. Organic phosphate solubilization

6.2.2.1 Mineral Phosphate Solubilization

Mostly, microbial mineral phosphate solubilizing ability corresponds to production of organic acids (Rodriguez et al. 1999). Phosphate solubilizing bacteria are known to produce many organic acids like malic acid, oxalic acid, gluconic acid, 2-keto gluconic acid, citric acid, lactic acid, propionic acid, succinic acid, and formic acid, and most of these organic acids especially 2-ketogluconic acid, malic acid, oxalic acid, and citric acid are found in rhizosphere of various crops and vegetables (Jaeger III et al. 1999; Chen et al. 2006; Gulati et al. 2010; Shahid et al. 2015). In Gram-negative bacteria, glucose is oxidized to gluconic acid (GA), and biosynthesis of GA is catalyzed by glucose dehydrogenase (GDH) enzyme. Pyrroloquinoline quinone (PQQ) acts as cofactor of GDH (Goldstein 1994). A gene cluster consisted of six open reading frames (pqqA, B, C, D, E, and F) leads to the formation of PQQ (Kim et al. 1998a; Meulenberg et al. 1992). The *pqqE* coding sequence is the most conserved and is considered to be responsible in mineral phosphate solubilization (Perez et al. 2007; Shahid et al. 2012).

Goldstein and Liu (1987) cloned mineral phosphate solubilizing (MPS) gene from Gram-negative bacteria *Erwinia herbicola* for the first time. Expression of this gene in *E. coli* HB101 resulted in the production of GA and solubilization of hydroxyapatite. *E. coli* has the capability of synthesizing GDH but is unable to synthesize PQQ and GA. The protein encoded by cloned 1.8 kb fragment is similar to the gene III product encoded by PQQ synthesis gene complex from *Acinetobacter calcoaceticus* and to *pqqE* of *Klebsiella pneumonie* (Liu et al. 1992). Moreover, a 7 kb fragment from genomic DNA of *Rahnella aquatilis*, responsible of inducing hydroxyapatite solubilization in *E. coli*, was analyzed, and two complete and one partial ORFs were found. One of the complete ORFs was cloned and was found analogous to *pqqE* of *E. herbicola, K. pneumoniae*, and *A. calcoaceticus* (Kim et al. 1998a), and the partial ORF was found similar to *pqqC* of *K. pneumoniae.* Another gene (*gabY*) of *Pseudomonas cepacia*, carrying GA production capacity and MPS ability, has been characterized (Babu-Khan et al. 1995), and the recombinant protein sequence showed no similarity with the previously cloned gene carrying GA production ability but was identical to histidine permease protein. Containing this gene, *E. coli* was capable of producing the GA only when functional glucose dehydrogenase gene (*gcd*) was expressed. Thus, it was speculated that the synthesis of

PQQ was accomplished through an alternative pathway, or the production of *gcd* cofactor was different from PQQ (Babu-Khan et al. 1995).

Other genes related to MPS do not relate to *pqq* DNA or *gcd* biosynthesis mechanism. According to another report, a DNA segment isolated from *Enterobacter agglomerans* demonstrated MPS in *E. coli* JM109 without changing the pH of medium (Kim et al. 1997). Thus, acid production is not the only choice for MPS by bacteria (Illmer and Schinner 1995). Mineral phosphate solubilization capability of PGPB was attempted to be improved by the cloning technique using PQQ synthetase gene of *Erwinia herbicola* (Rodríguez et al. 2000). The gene was isolated by Goldstein and Liu (1987) and was subcloned in a broad host range vector (*p*KT230). Thus, the expression of recombinant molecule was obtained in *E. coli* and then transformed to PGPB strains (*Burkholderia cepacia* and *Pseudomonas aeruginosa*) by tri-parental conjugation. Many exconjugants selected on the specific medium produced larger halo zones on medium with tricalcium phosphate as a sole P source. So, heterologous expression of PQQ synthetase gene resulted in increased MPS ability in PGPB.

6.2.2.2 Organic Phosphate Solubilization

Organic form of soil phosphorus can be released by three groups of enzymes:

1. Nonspecific acid phosphatases: by dephosphorylation of phospho-ester and/or phosphor-anhydride bonds in organic matter
2. Phytases: involved in the release of P from phytic acid
3. Phosphonatases and C-P lyases: by cleavage of C-P bond in organo-phosphonates

Currently, the main focus of research is on acid phosphatases and phytases as their substrates are present in huge amounts in soil.

6.2.2.2.1 Nonspecific Acid Phosphatases (NSAPs)

Bacterial nonspecific acid phosphatases consist of three molecular families designated as A, B, and C (Thaller et al. 1995). During the last decade, these enzymes were studied for their biotechnological applications, and class A NSAPs were successfully used for environmental bioremediation of uranium-contaminated wastewater (Macaskie et al. 1997). NSAPs may also be used for gene expression in PGPB by recombinant DNA technology for improved phosphate solubilization. Several phosphate solubilizing genes from Gram-negative bacteria have been isolated and characterized (Rossolini et al. 1998). These genes, when expressed in PGPB, can enhance phosphate solubilizing ability of bacteria. Some of these genes code for the acid phosphatases which perform the same function in soil. For instance, the *acpA* gene of *Francisella tularensis* encodes for a substrate-specific acid phosphatase with maximum efficiency at pH 6 (Reilly et al. 1996). In addition, *PhoC* gene, coding for NSAP class A and *napA* gene for class B, was very promising and isolated from *Morganella morganii* (Maria et al. 1995; Thaller et al. 1994). In rhizobacteria,

a gene was isolated from *Burkholderia cepacia* which codes for two acid phosphatases *napD* and *napE* along with an outer membrane protein responsible for P transport to the cell (Deng et al. 2001, 1998).

6.2.2.2.2 Phytases

Phytases are not yet potentially exploited for organic phosphate solubilization of soil. A significant portion of soil organic phosphorus is comprised of phytate (Richardson 1994). Plants are not directly dependent on phytate for their P requirements. A significant improvement in growth and P uptake in *Arabidopsis* plants was observed when phytase gene (*phyA*) from *Aspergillus niger* was genetically engineered (Richardson et al. 2001a). It has also been reported that microbial inoculation increases the inositol phosphate utilization by plants (Richardson et al. 2001b). Therefore, development of high phytase producing inoculants would be of great importance for enhancing plant growth and phosphorus contents (Hanif et al. 2015). Phytases are also produced by roots of several plant species (Li et al. 1997; Lung et al. 2008). *E. coli* phytase genes (*appA* and $appA_2$) have been isolated and characterized (Golovan et al. 1999; Rodriguez and Fraga 1999). Similarly, phytase genes have been cloned from *B. subtilis* and *B. licheniformis* (Tye et al. 2002). A *phyA* gene of *B. amyloliquefaciens* FZB45 stimulated the maize growth in the presence of phytate and under limited phosphate conditions (Idriss et al. 2002). In addition, thermally tolerant phytase gene (*phy*) has been reported and characterized from *Bacillus* sp. DS11 (Kim et al. 1998b) and *B. subtilis* VTT E-68013 (Kerovuo et al. 1998).

6.2.3 Plant Growth Hormone Production

Plant growth hormones are organic compounds that act as messengers and help plants to respond to their environment. They are very effective even if synthesized in a very small quantity and may inhibit plant growth if present in large amounts (Arshad and Frankenberger 1991). They are synthesized in one plant part and then transported to the other, where they may cause the physiological response and effect on growth and fruit ripening. In this way, they are also referred to as plant growth regulators (Davies 2010). There are five main groups of plant growth regulators:

1. Auxins
2. Gibberellins
3. Cytokinins
4. Ethylene
5. Abscisic acid

Among these, indole-3-acitic acid (IAA) is considered to be the most important phytohormone which plays a major role in cell growth and division and known to increase the lateral root development in plants (Seo and Park 2009). Many bacterial genera, including *Azospirillum*, *Azotobacter*, *Bacillus*, *Enterobacter*, and

Pseudomonas, have been reported to produce a considerable amount of IAA in vitro and in vivo (Chen et al. 2006; Nahas 1996; Venieraki et al. 2011). The bacterial genus *Azospirillum* is known to produce a good concentration of IAA for plant growth (Saharan and Nehra 2011). IAA acts as signal molecule for plant development including organogenesis and has a potential role in cell division, expansion, elongation, and gene regulation (Ryu and Patten 2008). Phytohormones has been reported to be synthesized by phosphate solubilizing bacteria (Chen et al. 2006; Vassilev et al. 2006). Diverse bacterial species are known to produce IAA in pure culture and soil, and their interactions with plant roots have been widely studied (Akram et al. 2016; Leveau and Lindow 2005; Rodriguez et al. 2004; Venieraki et al. 2011). IAA is responsible for the phyto-stimulation, and many microorganisms use it as a tool for interacting with plants. Thus, IAA is also involved in bacterial colonization with plant roots. It also acts as a signaling molecule in bacteria and directly affect bacterial physiology (Barazani and Friedman 1999; Spaepen et al. 2007). On the basis of potential for auxin production by rhizosphere microorganisms, effective plant growth-promoting bacteria from plant rhizosphere can be screened and reinoculated on plants for growth and yield improvement (Khalid et al. 2004). Some microorganisms like *Azospirillum* produce IAA in the presence of L-tryptophan. Tryptophan acts as a precursor for the production of IAA (Tien et al. 1979). Inoculation of crop plants with IAA-producing bacterial isolates augments plant growth. A significant increase in root proliferation and root dry matter was observed in eucalyptus cuttings when grown on a substrate inoculated with IAA-producing rhizobacteria (Teixeira et al. 2007). Other phytohormones like gibberellins, cytokinins, ethylene, and abscisic acid are also reported to be produced by plant-associated bacteria and stimulate plant growth and development. The most important microbially produced gibberellin is gibberellic acid. Similarly, cytokinins are adenine derivatives, and microbial synthesis of cytokinins in the rhizosphere and its effect on plant physiological pathways are being investigated (Baca and Elmerich 2007).

6.2.4 Biocontrol

Microorganism, being indigenous to soil and rhizosphere, play a vital role in the biocontrol of phytopathogens. They can suppress a broad range of bacterial, fungal, and nematode diseases and are also effective against viral diseases. PGPR are being used as biocontrol agents all over the world. They have produced significant results against plant pathogens in vitro and in greenhouse, but their performance in the field are still inconsistent. They have also been successfully used in integrated pest management programs (Siddiqui 2006). They also have natural ability to restrain soilborne pathogens (Weller et al. 2002). Shoda (2000) reviewed that bacterial genera *Pseudomonas*, *Bacillus*, *Alcaligenes*, and *Agrobacterium* have been successfully identified as biocontrol agents. In addition, many other bacteria such as *Micromonospora*, *Streptomyces*, *Streptosporangium*, and *Thermobifida* are reported to act as biocontrol agents (Franco-Correa et al. 2010). Genus *Pseudomonas* is the

largest group considered to have biocontrol activity, and *P. fluorescens* strain WCS374 increased the reddish yield up to 40% by suppressing the *Fusarium* wilt disease (Bakker et al. 2007; Kremer and Kennedy 1996). *Pseudomonas* has many traits which are involved in plant growth promotion and biocontrol (Weller 1988). Bhattacharyya and Jha (2012) reviewed the following characteristics of *Pseudomonas* making them as potential biocontrol agents:

1. Rapid in vitro production to construct a mass growth
2. Ability to utilize metabolites and exudates of seed and roots
3. Ability to colonize the rhizosphere and spermatosphere
4. Capability of producing a wide range of bioactive metabolites (antibiotics, siderophores, volatiles, and other growth promoting substances)
5. A strong competitive ability with other microorganisms in environment
6. Ability to adapt environmental stresses
7. Development of induced systemic resistance in plants
8. Production of hydrogen cyanide (HCN)

6.2.5 Production of ACC Deaminase

An appropriate amount of ethylene is essential for plant growth and development, but its high concentration may affect plant cellular processes and retard plant growth. PGPR were able to regulate the ethylene level in root zone of *Arabidopsis thaliana* using their 1-amino-cyclopropane-1-carboxylic acid (ACC) deaminase, which actually prevents ACC to take part in ethylene biosynthesis pathway (Desbrosses et al. 2009). Using this mechanism, plants were able to tolerate environmental stresses by keeping a normal amount of ethylene in their root zone. A number of PGPR strains like *Achromobacter*, *Azospirillum*, *Pseudomonas*, *Enterobacter*, *Bacillus*, and *Rhizobium* have been found to show this mechanism (Duan et al. 2009; Ghosh et al. 2003; Govindasamy et al. 2008).

Ghosh et al. (2003) reported the enhanced root length in *Brassica campestris* by three *Bacillus* spp. (*Bacillus circulans* DUC1, *Bacillus firmus* DUC2, and *Bacillus globisporus* DUC3), carrying ACC deaminase activity. Similarly, root and shoot dry matter was increased in *Brassica napus* after the inoculation with *Pseudomonas asplenii* which contain ACC deaminase gene (Reed and Glick 2005). Thus, PGPR possessing ACC deaminase activity increase plant biomass in a stressed environment like salinity, temperature, drought, waterlogging, pathogenicity, and contaminants (Saleem et al. 2007). PGPR can also be genetically modified to perform this function. The efforts to express ACC deaminase gene to plant genome have been made to modify the plant species, but these efforts have yet not come up with complete success due to certain constraints like international trade agreements and proprietary rights on genetically modified crops and also due to some limitations in recombinant DNA technology.

6.3 Mechanisms Behind Plant-Pathogen Interactions

Plants constantly remain under threat of array of pathogens that have the capability of provoking disease. Pathogens include diverse organisms (bacteria, fungi, oomycetes, and viruses) which usually share common infection strategies but may also have pathogenicity determinants unique to each. Plants, in turn, defend themselves from possible damages of infection. However, plants do not possess a mobile defense system, and they largely depend on the inherited immunity patterns and systemic signals originating in response of pathogens (Ausubel 2005; Jones and Dangl 2006). The pathogen-plant interaction is a two-way process. Pathogen attempts to manipulate the biology and physiology of the host cell for generating an environment favoring pathogen growth. The plant cell responds by recognizing and targeting potential pathogen landing on its surface. Both plant and pathogen genes evolve together over a course of time, with emergence of new elicitors/effectors and corresponding plant resistance analogs, enabling this two-way communication to continue.

The following sections will highlight our current understanding about the plant-pathogen interaction, both at physiological and molecular levels.

6.3.1 General Classification of Plant Pathogens

Plant pathogens can be divided into three groups, i.e., biotrophs, necrotrophs, and hemi-biotrophs (Li et al. 2013):

1. Biotrophs tend to keep plant tissues alive as they majorly feed on living cells. Their penetration and infection strategy are such that they induce minimum damage to cell. PAMP-triggered immunity (PTI) is mainly involved in responses to biotrophs. (Lazniewska et al., 2012).
2. Necrotrophs release cell wall-degrading enzymes (CWDE) making host cells vulnerable which mostly lead to cell death. They feed on the materials released from the infected tissue. DAMP-triggered immunity (DTI) is primarily involved in providing resistance against necrotrophs (Wen, 2013).
3. Hemi-biotrophs are given the name because of the presence of an initial biotrophic phase pursued by a necrotrophic stage where they can live as saprophytes. Both PTI and DTI may get activated in response to the attack of a hemi-biotroph (Fawke et al. 2015).

6.3.2 Pathogen Infection to Host Cell

A successful infection requires entry of a pathogen into host cell. Stomata, hydathodes, and wounded tissues are the main cell entry points for pathogenic bacteria, and majority of the invaded bacteria proliferate in apoplast regions, only. Oomycetes and pathogenic fungi develop specialized feeding structures called haustoria which

invaginate into the host plasma membrane. The plasma membrane of host cell as well as of haustoria and contiguous extracellular matrix together constitute an intimate interface that determines the outcome of host-pathogen communication. In addition, pathogens also release compounds like cell wall-degrading enzymes (CWDE) and extracellular polysaccharides (EPS) which make tissue soft, enhance maceration, prevent desiccation, provide defense against host resistance factors, and, hence, facilitate pathogen invasion.

6.3.3 Plant Defense Responses

Plants respond to a potential pathogen at two levels (Jones and Dangl 2006). The first level include inherited basal responses (known as PAMP-triggered immunity, PTI) immediately after a pathogen invades host surface and attempts to penetrate inside. The second defense level (called effector-triggered immunity, ETI) is represented by host resistance against the pathogen-released effectors. Both these levels are crucial to minimize the pathogenicity but at different phases of infection (Li et al. 2013).

6.3.3.1 Basal Resistance or PAMP-Triggered Immunity (PTI)

It is the first line of active plant defense and is activated by the recognition of a virulent pathogen itself or released elicitors called pathogen-associated molecular patterns or microbe-associated molecular patterns (PAMPs or MAMPs), hence named as PAMP-triggered immunity (PTI). PAMPs are generated by microbial molecules, i.e., activators of XA21-mediated immunity, methylated DNA, double-stranded DNA, elongation factor peptides, flagellar proteins, lipopolysaccharides, and peptidoglycans (Li et al. 2013; Zeng et al. 2010).

PAMP triggers are perceived by plant pattern-recognition receptors (PRRs) localized at host cell surface (Dodds and Rathjen 2010). PRRs are receptor-like transmembrane proteins with most having a ligand-binding ectodomain (for PAMPs recognition) and a cytoplasmic kinase signaling domain (catalytic domain). Certain plant-generated signal molecules such as ethylene, jasmonic acid, and salicylic acid regulate the role of PRRs against a particular infection. Failure of proper perception of PAMPs results in high disease incidence, signifying the importance of PRR-based perception and PTI patterns. Plant and animals PRRs possess analogous structural domains, indicating their convergent evolution in two different domains of life.

Being a first line of defense, PTI is often phenotypically reflected by callose deposition, cell wall thickening, and stomata closure, as well as physiologically by production of antimicrobial compounds and reactive oxygen species (ROS). Moreover, PTI activates the mitogen-activated protein kinases and calcium signaling and induces changes in expression of pathogen-responsive genes (Nürnberger et al. 2004). This basal resistance strategy minimizes spread of further infection to nearby tissues (Chisholm et al. 2006). However, pathogens are equipped with mechanisms to counter plant-produced antimicrobial compounds and ROS. *Xanthomonas*

campestris pv. campestris showed enhanced synthesis of catalase and peroxidases while, *X. campestris* pv. phaseoli synthesizes alkyl hydroperoxidase reductases for neutralization of plant produced anti-pathogen compounds/ROS.

Besides this, PTI may get activated by damage-associated molecular patterns (DAMPS). DAMPs serve as signals to trigger the PTI response in infected host plants, in a similar way as for PAMPs. DAMPs are triggered by synthesis of endogenous small peptides and/or cell wall fragments that are released from damaged or stressed cells (Li et al. 2013).

6.3.3.2 Pathogen-Induced Resistance or Effector-Triggered Immunity (ETI)

After successful penetration, a pathogen tries to suppress the components of PTI by release of certain effectors. A large set of effectors have been characterized (Mesarich et al. 2016; Stergiopoulos and de Wit 2009). Effectors manipulate host metabolism and defense mechanisms to facilitate further spread and virulence by various ways.

6.3.3.2.1 Effectors

To overcome plant defense mechanisms, pathogens produce a wide range of virulence factors like cell wall-degrading enzymes, effector proteins, plant hormones, and certain toxins. Among all of these, effector proteins [avirulence (Avr) proteins] play pivotal role. These are expressed by avirulence (Avr) genes which are associated with genomic islands and/or transposable elements. In addition, lateral gene transfer through bacteriophages, integrative or conjugative elements, and bacterial plasmids helped in acquisition of Avr genes.

The bacterial effectors are released into plant cells via type 3 secretion system (T3SS) to suppress plant defense mechanisms. In order to weaken the host defense programs, effectors must target host components involved in immune responses. These may alter the physiology of host plant for enhanced pathogen infestation and/or disturb the host plant defense mechanisms. Virulence mechanism of a variety of effectors has been explored at the molecular level. The AvrPto effector of Pseudomonas syringae targets plant FLS2, and AvrPto/FLS2 interaction modulates flagellin induced PTI responses and, in turn, enhances pathogen virulence in tomato and *Arabidopsis* (Xiang et al. 2008). The C-terminal E3 ligase domain of *P. syringae* AvrPtoB effector ubiquitinates plant produced FLS2 and suppresses PTI by degrading FLS2 (Göhre et al. 2008). In addition, AvrPtoB also targets CERK1 for degradation by ubiquitination of CERK1 kinase domain (Gimenez-Ibanez et al. 2009).

Similarly, *Arabidopsis* MAP kinases (MPK3 and MPK6) are inactivated by HopAI1 through removal of phosphate group from phosphor-threonine leading to suppression of PTI responses. In *Arabidopsis*, the AvrB effector of *P. syringae* mimics coronatine leading to activation of jasmonate signaling cascade, and resultantly flg22-induced deposition of callose reduced and cells become more susceptible (Gimenez-Ibanez et al. 2009; He et al. 2004; Shang et al. 2006). The effector AvrAC of *Xanthomonas campestris* pv. campestris (Xcc) is delivered into host cell as an

uridylyl transferase that catalyzes addition of uridine monophosphate onto BIK1 and RIPK (receptor like cytoplasmic kinases involved in PTI). The conserved phosphorylation sites present in the activation loop of BIK1 and RIPK are modulated and, therefore, reduce their kinase activity and capability of downstream signaling (Deslandes and Rivas 2012).

Effectors from filamentous fungal pathogens and their host targets are comparatively less characterized. The results of the study reveal that fungal pathogens use almost the same strategies as used by bacterial pathogens. A strong virulence effect by leaf mold fungus *Cladosporium fulvum* and rice blast fungus *Magnaporthe oryzae* is found to be dependent on synthesis of Ecp6 and Slp1 effectors, respectively. Both of the effectors (Ecp6 and Slp1) compete with receptors CEBiP and CERK1, for chitin binding, to block host PTI responses (de Jonge et al. 2010). The effector AvrPiz-t of *M. oryzae* enhances virulence by suppressing PTI through targeting host RING E3 ubiquitin ligase APIP6. *Ustilago maydis* (corn smut fungal pathogen) synthesizes and releases an apoplastic effector "Pep1" to suppress ROS burst, a typical PTI response, by directly targeting the apoplastic peroxidase "POX12."

6.3.3.2.2 Resistance Proteins

Plants possess corresponding R proteins, the product of resistance (R) genes, to recognize the pathogen-produced Avr protein. There are eight major variants of R genes (and hence R proteins) as reviewed by (Gururani et al. 2012). The R protein variants have major differences in their organization of amino acid motif as well as their membrane spanning domains (Fig. 6.1). It has been observed that leucine-rich repeats (LRRs) are common in majority of the R proteins indicating their importance in recognition of a specific pathogen.

The first class of resistance proteins is a group of cytoplasmic proteins which possess LRR and nucleotide-binding site (NBS) motifs along with an N-terminal domain with homology to the toll-interleukin-1-receptor (TIR) domain present in mammalian proteins. The flax L6, tobacco N, and RPP5 R proteins are grouped in the first class of R proteins. The second major class of R genes includes the genes encoding for cytoplasmic proteins with a C-terminal LRR, a supposed N-terminus coiled coil domain (CC) and a NBS. These have been identified in *Arabidopsis* (RPS2 and RPM1 resistance proteins against *P. syringae*) and tomato (resistance protein I2 against *Fusarium oxysporum*). The third class of R gene family consists of extra cytoplasmic leucine-rich repeats (eLRR), associated to a transmembrane domain (TrD). The proteins are devoid of NBS motif. eLRRs are not directly engaged in pathogen recognition and/or activation of host defense genes. However, eLRRs play a significant role in certain defense proteins like polygalacturonase inhibiting proteins (PGIPs). The representative genes of this class include *C. fulvum* R genes (Cf-2, Cf-4, and Cf-9) that possess an eLRR, a membrane-spanning domain and a short cytoplasmic C-terminus region. The fourth class of resistance genes is characterized by Xa21, a rice R gene against Xanthomonas. The Xa21 consists of eLRR, TrD, and an intracellular serine-threonine kinase (KIN) domain as shown in Fig. 6.1. The group of proteins having a TrD fused to a putative CC domain (e.g., The *Arabidopsis* RPW8) constitutes the fifth class of R proteins. The sixth class of

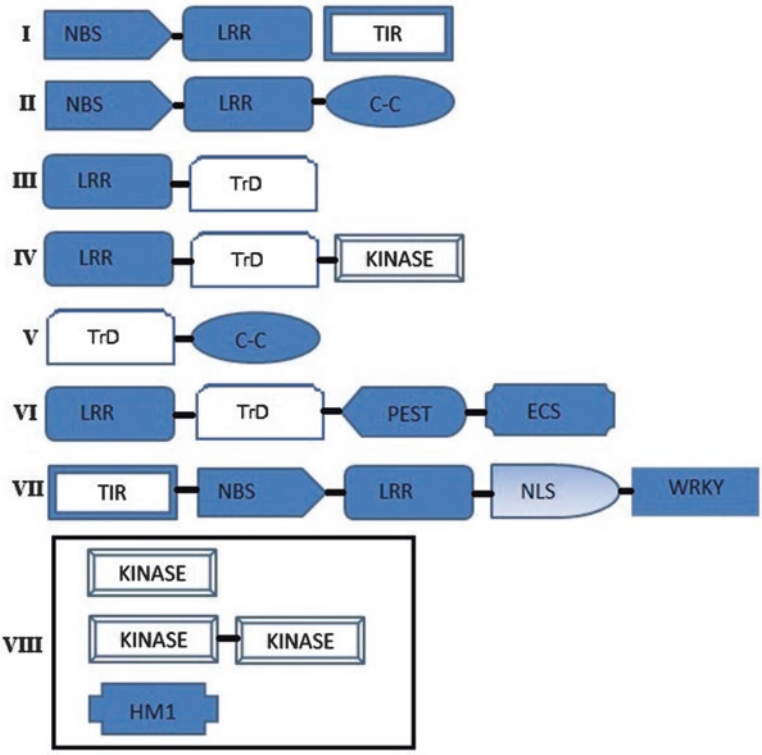

Fig. 6.1 Plant resistance proteins (R proteins): types and position of important domains. Nucleotide-binding site (*NBS*), leucine-rich repeats (*LRR*), coiled coil (*C-C*), transmembrane domain (*TrD*), interleukin-1-receptors (*TIRToll*), protein degradation domain (proline-glycine-serine-threonine, *PEST*), endocytosis cell signaling domain (*ECS*), nuclear localization signal (*NLS*), amino acid domain (*WRKY*), helminthosporium carbonum toxin reductase enzyme (*HM1*)

R proteins contains putative eLRRs associated to a PEST (Pro-Glu-Ser-Thr) domain for protein degradation and short protein motifs (ECS) that can target the protein for receptor mediated endocytosis. The examples of this group include tomato Ve1 and Ve2 R proteins. However, in few studies, Ve1 and Ve2 proteins have been classified as PAMP receptors. The *Arabidopsis* RRS1-R that confers resistance against phytopathogen *Ralstonia solanacearum* is a good representative of the seventh class of R proteins. These proteins have a C-terminal extension together with a WRKY domain as well as a presumed nuclear localization signal (NLS) sequence. The WRKY domain is the given name because of the presence of a conserved N-terminal amino acid (WRKYGQK) sequence along with a zinc finger-like motif.

Few enzymatic proteins have been categorized in the eighth class of plant R proteins. These are devoid of LRR or NBS domains. The enzyme HC toxin reductase, encoded by the maize Hm1 gene, detoxifies a specific cyclic tetrapeptide toxin, essentially required for pathogenicity, of the fungus (HC toxin). Hence, HC toxin reductase provides protection against southern corn leaf blight caused by

Cochliobolus carbonum (a fungal pathogen). Similarly, the Rpg1 gene from barley encodes a receptor kinase-like protein having two tandem protein kinase (kinase-kinase) domains. The protein does not have any membrane-spanning domain and other known sequences present in classical R proteins. However, the protein provides barley resistance against stem rust, hence considered a potential R protein (Jones et al. 1994).

6.3.3.2.3 Avr/R Protein Interaction

The Avr/R protein interaction determines the host specificity, pathogenicity level, degree of damage, and subsequent pathogen spread to nearby tissues. In addition, differentiation of pathogen as biotroph or necrotroph is also achieved by Avr/R protein interaction by initiating a crosstalk between response pathways and regulating balance of salicylic acid (a signal for resistance against biotrophs) and level of jasmonic acid along with ethylene (both promote defense against necrotrophs). However, it has been found that NB-LRR protein-mediated disease resistance is much more effective against biotrophs or hemi-biotrophs but not against necrotrophs (Glazebrook 2005).

In response to effectors, plants exhibit a second line of defense initiated by the recognition of a specific effector followed by triggering a stronger resistance response named as effector-triggered immunity (ETI). ETI is a quicker and robust version of PTI (Tao et al. 2003; Thilmony et al. 2006; Truman et al. 2006) that usually culminates in hypersensitive response (HR) characterized as death of infected cells. It generally does not extend beyond the infected area and help in restriction of pathogen growth. However, it is not always observed and not a requirement for triggering ETI. This Avr/R gene recognition pattern has been historically termed as "gene-for-gene resistance" (Gururani et al. 2012). Under pathogen favorable circumstances, the effector modulates the effector-mediated signal cascade and suppresses ETI (instead of activating it) which leads to effector-triggered susceptibility (ETS).

6.3.3.3 Mechanism of R Protein-Effector Interaction

6.3.3.3.1 Direct Interaction

The R protein may directly recognize pathogen-released effector, in a similar way like ligand binds its receptor (Fig. 6.2). This was elucidated by studying the interaction between rice Pita CC-NB-LRR immune receptor and *Magnaporthe grisea* (a fungus) AVR-Pita effector (Jia et al. 2000). A single amino acid substitution in the LRR abolished this interaction and resulted in loss of resistance. Similarly, RRS1-R immune receptor of *Arabidopsis* recognizes directly PopP2 (a bacterial effector) (Deslandes et al. 2003). Yeast two-hybrid analysis revealed a significant direct interaction between flax rust fungus AvrL effectors with corresponding plant immune receptors (encoded from L locus) leading to activation of resistance (Dodds et al. 2006).

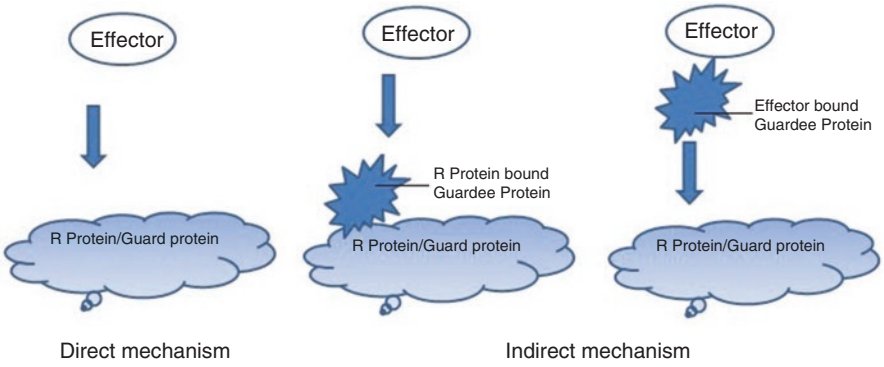

Fig. 6.2 Effector(s) and plant R (resistance) proteins: elucidation of direct and indirect mechanisms

6.3.3.3.2 Indirect Interaction: Guard Hypothesis

The R proteins may also interact with effectors indirectly in a more complex way. The guard hypothesis suggests that effectors induce modulations in certain host proteins (called guardee proteins) which are assessed by R proteins (guard protein). A guard-guardee protein interaction then activates a signal cascade for initiation of protective measures (Jones and Dangl 2006). Two variations exist in this hypothesis:

1. The guardee protein remains bound, constitutively, to guard protein even before an effector come and modulate the guardee.
2. The guard protein receptor interacts with its guardee, only after the later come in contact with an effector.

6.3.3.4 Evolution of Effector and Resistance Specificities

Interaction and two-way communications between pathogen and host plant cells led to the evolution and emergence of new groups of effectors and corresponding R proteins generating an arms race termed as gene-for-gene concept. The plant-microbe coevolution and plant immune responses can be described in a "zigzag" model consisted of four phases, initially proposed by (Jones and Dangl 2006):

Phase I: Plant recognition receptors (PRRs), located at cell surface, recognize PAMPs (or MAMPs) released from invading microbe(s) to trigger first line of defense, i.e., PTI that attempts to limit the invasion of a potential pathogen.

Phase II: Within a host cell, a successfully invaded pathogen synthesizes and releases effectors to initiate virulence by suppressing PTI. The interaction determines the plant-microbe relationship leading to effector-triggered susceptibility (ETS).

Phase III: Plants deploy intracellular immune proteins (i.e. R proteins/ NB-LRR proteins) to detect pathogen-initiated effectors. These proteins detect effectors either directly or indirectly. This triggers ETI, a stronger immune response that

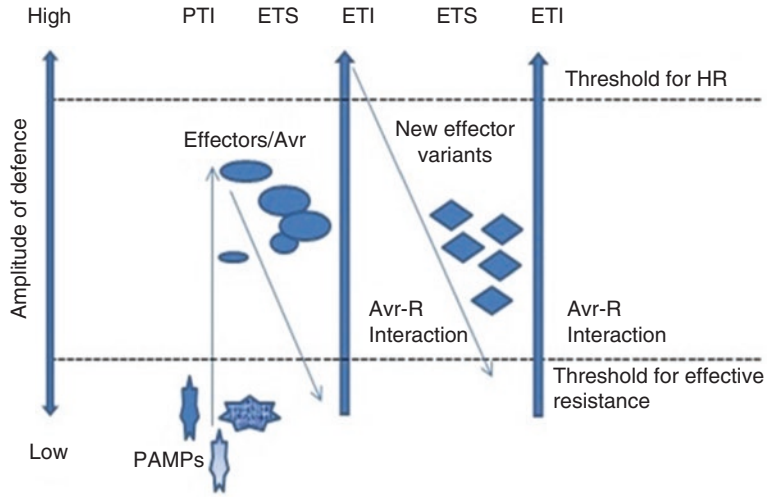

Fig. 6.3 Zigzag model: a depiction of coevolution of pathogen effectors and plant R (resistance) proteins as proposed by Jones and Dangl (2006)

provides resistance against a pathogen and often climaxes in tissue hypersensitive response (HR), i.e., a programmed cell death at the infection site.

Phase IV: In response to plant-induced pressure, the effectors undergo modifications to escape ETI. New variants of effectors evolve suppressing host ETI and triggering ETS again. The process of natural selection plays a vital role in the development of new effector and corresponding R specificities.

Hence, at population level, the coevolutionary arms race between a plant species and a pathogen determines the consequences of a pathogen attack with ETI and ETS occurring alternately as represented in Fig. 6.3.

6.3.3.5 Non-host Resistance

Majority of the pathogens fail to infect plants as these can resist an invaded pathogen and, hence, are supposed to be non-hosts. This non-host resistance is distinctly different from pathogen-mediated resistance, complex, durable, and a multigenic trait. There are two possible ways that lead to two types of non-host resistance mechanisms, i.e., type I and type II (Mysore and Ryu 2004).

6.3.3.5.1 Type I

A pathogen fails to suppress PTI and grow on a new evolutionarily divergent host due to its ineffective effectors. The host displays a strong PTI response but no ETI or HR. The attack of nonadapted barley pathogen, *B. graminis* f. sp. *hordei* (Bgh) on *Arabidopsis* (a non-host plant), results in enhanced synthesis of cell wall appositions (act as physical barriers) and antimicrobial metabolites to limit pathogen entry. But *Arabidopsis* did not display HR response in this non-host resistance mechanism (Thordal-Christensen 2003).

6.3.3.5.2 Type II

This non-host resistance involves recognition of pathogen effectors; its mechanism resembles ETI and often culminates at HR. It was observed that soybean, a non-host for *P. syringae* pv. tomato, recognized AvrA and AvrD effectors through Rpg2 and Rpg4 proteins when infected with *P. syringae* pv. tomato. Similarly, *AvrRxo1* produced by *Xanthomonas oryzae* pv. oryzae was recognized by maize (a non-host for the said pathogen) *Rxo1*. In addition, *Arabidopsis* displayed resistance to a fungal pathogen of Brassica (*Leptosphaeria maculans*) which was achieved by unlinked R proteins. Hence, poorly explored R protein-mediated responses also play significant role in broadening the resistance mechanisms and may minimize pathogen host specificity (Senthil-Kumar and Mysore 2013).

6.4 Conclusion

It can be concluded that a variety of mechanisms are utilized by microbes to interact with plants. These mechanisms are broadly classified into two categories, viz., symbiotic interactions and pathogenic interactions. Symbiotic interactions between plants and microbes involve a variety of activities of mutual benefits like nitrogen fixation, P solubilization, growth hormone production, and biocontrol with a variety of genetic and metabolic pathways involved. Plant defense responses against a pathogen can be categorized into two levels, i.e., basal resistance and pathogen-induced resistance. The former are early level responses initiated upon a pathogen recognition by host cell surface localized receptors, while the latter are induced by

Table 6.1 Some mechanisms of plant growth promotion by microorganisms

Type	Definition	Mechanism	References
Biofertilizer	A biological substance which improves the plant growth through increased nutrient acquisition	Biological nitrogen fixation, nutrient solubilization, and mobilization	Hanif et al. (2015), Kapoor et al. (2008), Rinaldi et al. (2008), Shahid et al. (2012), Somers et al. (2004), and Vessey (2003)
Phytostimulator	The substances with the ability to produce plant growth hormones like IAA, gibberillic acid, Cytokinins and ethylene	Production of phytohormones	Akram et al. (2016), Hanif et al. (2015), Lugtenberg et al. (2002),and Somers et al. (2004)
Biopesticide	The biological substances that indirectly promote plant growth by suppressing the plant diseases	Production of lytic enzymes, siderophores, antibiotics, HCN, and induced systemic resistance	Chandler et al. (2008), Somers et al. (2004), Vessey (2003), Ali et al. (2016), Somers et al. (2004), and Yasmeen et al. (2012)

Table 6.2 List of Avr genes (with plant pathogens) and corresponding R genes (with host plants)

Avr gene(s) (plant pathogen species)	R gene(s) (host plant species	References
Bacteria		
Avr-Bs2 (Xanthomonas campestris)	*Bs2 (Capsicum annuum)*	Minsavage et al. (1990)
Avr-Xa1 (X. oryzae)	*Xa1 (Oryza sativa)*	Yoshimura et al. (1998)
Avr-Pto, Avr-PtoB (Pseudomonas syringae pv. *tomato)*	*Pto (Lycopersicum esculentum)*	Abramovitch et al. (2003)
AvrRpm1 (P. syringae)	*RPM1 (Arabidopsis thaliana)*	Hubert et al. (2003)
AvrRpt2 (P. syringae)	*RPS2 (A. thaliana)*	Bent et al. (1994) and Whalen et al. (1991)
AvrRps4 (P. syringae)	*RPS4 (A. thaliana)*	Gassmann et al. (1999) and Hinsch and Staskawicz (1996)
AvrPphB (P. syringae)	*RPS5 (A. thaliana)*	Jenner et al. (2003) and Swiderski and Innes (2001)
Fungi		
AvrMla (Blumeria graminis)	*Mla (Hordeum vulgare)*	Zhou et al. (2001)
Avr2 (Cladosporium fulvum)	Cf-*2 (Lycopersicum esculentum)*	Rooney et al. (2005) and van Esse et al. (2008)
Avr4 (C. fulvum)	Cf-*4 (L. esculentum)*	Thomas et al. (1997)
Avr5 (C. fulvum)	Cf-*5 (L. esculentum)*	(Dixon et al. 1998)
Avr9 (C. fulvum)	Cf-*9d (L. esculentum)*	Jones et al. (1994)
Avr1 (Fusarium oxysporum)	*I2 (L. esculentum)*	Ori et al. (1997) and Simons et al. (1998)
AyrL AvrN, AvrL567 genes (Melampsora lini)	*L N, L5, L6, and L7 (Linum usitatissimum)*	Dodds et al. (2006) and Lawrence et al. (1995)
Avr-Pita (Magnaporthe grisea)	*Pi-ta (Oryza sativa)*	Jia et al. (2000) and Kang et al. (2005)
AvrRP-I-D (Puccinia sorghi)	*Rp1 (Zea mays)*	Collins et al. (1999)
Avr-Rpg1 (Puccinia graminis f sp. *tritici)*	*Rpg1 (Hordeum vulgare)*	Brueggeman et al. (2002) and Horvath et al. (2003)
Oomycetes		
Avr3 (Bremia lactucae)	*Dm3 (Lactuca sativa)*	Meyers et al. (1998) and Michelmore and Wong (2008)
ATR1 (Hyaloperonospora arabidopsis)	*RPP1-Nd/WsB (Arabidopsis thaliana)*	Rehmany et al. (2005)
ATR13 (H. arabidopsis)	*RPP13-Nd (A. thaliana)*	Alfano and Collmer (1996) and Bittner-Eddy et al. (2000)
AvrB, AvrRPP1A, AvrRPP1B, AvrRPP1C, AvrRPP2	*RPP1, RPP2, RPP4, RPP5, RPP8 (A. thaliana)*	Botella et al. (1998), McDowell et al. (1998), Parker et al. (1997), Van Der Biezen et al. (2002)
AvrRPP4, AvrRPP5, AvrRPP8 (Prenospora parasitica)		
Avr1 (Phytophthora infestans)	*R1 (Solanum tuberosum)*	Ballvora et al. (2002)

(continued)

Table 6.2 (continued)

Avr gene(s) (plant pathogen species)	R gene(s) (host plant species	References
Avr-blb1 (P. infestans)	*Rpi-blb1 (S. tuberosum)*	Vleeshouwers et al. (2008)
PiAvr2 (P. infestans)	*Rpi (S. tuberosum)*	Lokossou et al. (2009) and Vossen et al. (2005)
Avr3a (P. infestans)	*R3a (S. demissum)*	(Armstrong et al. 2005)
Ipio, Ipib, Ipi-o4 (P. infestans)	*RB (S. bulbocastanum)*	Champouret et al. (2009) and van West et al. (1998)
Avr3b-Avr10-Avr11 locus (P. infestans)	*R3b, R10, R11 (S. tuberosum)*	Jiang et al. (2006)
Avr1a, Avr3a and Avr3c (P. sojae)	*Rps1a, Rps3a, Rps3c (Glycine max)*	Dong et al. (2009), Mao and Tyler (1996), and Qutob et al. (2009)
Viruses		
Bean dwarf mosaic virus (Bdm)	*BV1 protein (Phaseolus vulgaris)*	Garrido-Ramirez et al. (2000)
Coat protein (cucumber mosaic virus)	*RCY1 (Arabidopsis thaliana)*	Takahashi et al. (2001)
Vpg (cucumber mosaic virus)	*At-eIF4E1 (cum1)/ At-eIF4G (cum2) (A. thaliana)*	Gallois et al. (2010) and Yoshii et al. (2004)
3'half of genome (lettuce mosaic virus)	*mo1, mol2 (Lactuca sativa)*	Gao et al. (2004) and Nicaise et al. (2003)
Vpg (pea seed borne mosaic virus)	*sbm1 (Pisum sativum)*	Keller et al. (1998)
Nla protease (potato virus X)	*Ry (S. tuberosum)*	Mestre et al. (2000)
Vpg (tobacco etch virus)	*Pot-1 (*Lycopersicon spp.	Moury et al. (2004)
Vpg (rice yellow mottle virus)	*eIF(iso)4G1 (Oryza sativa)*	Hébrard et al. (2010)
Hc-pro and P3 cistron (soybean mosaic virus)	*Rsv1 (Glycine max)*	Eggenberger and Hill (1997)
VPg (turnip mosaic virus)	*At-eIF(iso)4E (A. thaliana)*	Wittmann et al. (1997)
TuRBO1, TuRBO3, TuRBO4, TuRBO5, TuMV P3 (*Turnip mosaic virus)*	P3, CI *(Brassica napus)*	Jenner et al. (2000) and Jenner et al. (2003)

pathogen produced effectors and are largely controlled by plant resistance (R) proteins. There are both direct and indirect mechanisms by which pathogen effects interact with host resistance proteins. Moreover, the pathogen (or its effectors) and host resistance specificities continuously evolve together making an arms race named as "gene-for-gene concept" (Tables 6.1 and 6.2).

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