

Khalid Rehman Hakeem
Mohd Sayeed Akhtar *Editors*

Plant, Soil and Microbes

Volume 2: Mechanisms and Molecular
Interactions

 Springer

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Khalid Rehman Hakeem • Mohd Sayeed Akhtar
Editors

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Interactions

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This Book is Dedicated to



Sir Syed Ahmad Khan
(1817-1898)

*A great visionary, statesman, Muslim reformer of the 19th century
and founder of Aligarh Muslim University, India*

Foreword

Worldwide considerable research in the area of belowground plant-microbe interaction is quite important to enrich soil fertility and in the enhancement of crop productivity. It seems imperative to understand the modifications of belowground interactions under specific plant and microbe communication system accomplished by molecular dialogues. It is, therefore, essential to decode and explore this molecular language so as to establish a successful tripartite relationship among plant, soil and microbes. The soils are the product of rocks, minerals and organic matters with a pivotal role in ecology. Most of the plants depend on soil, but plants and their associated microorganisms are also important component together in the formation and sustainability of rhizospheric ecology. The understanding about plant, soil and microbe interaction is limited; molecular mechanisms and other several consequences may reveal with other process yet to be explored. This book entitled *Plant, Soil and Microbe, Volume 2: Mechanisms and Molecular Interactions* deals with how plant-microbe interactions occur using molecular pattern and applied in environment scavenging such as pesticide degradation and polycyclic aromatic hydrocarbons (PAHs) remediation. The importance of fungal symbiosis, tripartite interactions among plant-*Trichoderma*-pathogen with special reference to proteomic tools in biocontrol, has been described. The mechanism of plant growth promoting rhizobacteria-soil-root interaction, their ability towards growth, secondary metabolite production and nutrient uptake in medicinal and aromatic plants has been suitably mentioned. The bacterial determinants and plant defence induction in sustainable agriculture have an added advantage to strengthen the concept of biocontrol of deleterious phytopathogens. The elaborative description on the molecular identification of phytoplasma diseases in ornamental plants is itself appealing. The introductory account on allelochemicals from ascocarp of *Tuber* species is a point of difference. Besides, mycorrhizal associations, the biocontrol potential of *Bacillus thuringiensis*, genomics of plant-soil microbial diversity and the importance of root exudates in rhizosphere ecosystem and phytohormones in abiotic stress tolerance of plants have been elaborated. It is oceanic to gain update in the quest for knowledge of plant-soil-microbial interactions and their applications in a befitting manner. The editors *Khalid Rehman Hakeem* and *Mohd. Sayeed Akhtar* have put some

outstanding efforts to compile subject experts' contribution in a very attractive manner with an understanding of sequences of the chapters. *Plant, Soil and Microbe, Volume 2: Mechanisms and Molecular Interactions* includes broad contributions from all dimensions of agronomy. Specifically, this volume describes a holistic view of plant-microbe interactions, and its recent molecular mechanism emerged from studying multi-tropic interaction. The editors have immensely provided a solid foundation of the subject interesting for the researchers involved in soil microbiology, plant pathology, ecology and agronomy.

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D.K. Maheshwari

Preface

Plants are exposed to a huge diversity of microbes in the environment. Owing to the broad range of microbes, a complex set of molecular mechanisms mediates the plant-microbe interactions. These interactions have been seen to possess both negative and positive effects on either or both the members. Considering the importance of these ground rhizospheric microorganisms in the plant disease protection, it came into highlight from research that the combined application of these microorganisms is more beneficial than the use of a single agent and provides a better management against the soil-borne plant pathogens. The interaction of these microorganisms also provides an overview about the biological functions of soil and its interaction with the plant-microbe system, nutrient management, biogeochemical cycling, water various environmental condition in response to biotic and abiotic stresses, signalling of molecules during host-pathogen interaction, role of phytohormones against the environmental stresses and the major challenges in the formulation of microorganisms for the biocontrol products. The molecular approach of these microorganisms is also the basis for understanding the mechanism involved in disease suppression by these hidden underground beneficial microbes.

This volume with 18 chapters from experts on the subject describes a holistic view of plant-microbe interactions and its recent molecular mechanism emerged from studying multi-tropic interaction. It is imperative to understand the modifications of belowground interactions under specific plant and microbe communication system accomplished by molecular dialogues. We hope that the book will be helpful for the graduate students, teachers, researchers and industry persons, who are interested in soil microbiology, plant pathology, ecology, environmental sciences and agronomy.

We are highly grateful to all our contributors for readily accepting our invitation for not only sharing their knowledge and research but for venerably integrating their expertise in dispersed information from diverse fields in composing the chapters and enduring editorial suggestions to finally produce this venture. We greatly

appreciate their dedication. We are also thankful to Prof. (Dr.) D. K. Maheshwari for his suggestions and writing the foreword for this volume. We also thank Springer-International team for their generous cooperation at every stage of the book production.

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nanobiotechnology. He is author and coauthor of about 50 research articles in peer-reviewed journals, contributed 12 book chapters in the books published by Springer-Verlag and also edited 4 books with international publishers. He is serving the scientific community as editorial board member and reviewer of several high-impact international journals. His current research is focused on the rhizospheric plant-microbe interactions and their molecular biotechnology, bioremediation, biomineralization, nano-fertilizers and nanobiotechnology.

Plant-Microbe Interactions: A Molecular Approach

Mustafeez Mujtaba Babar, Sumayyah Fareed Khan,
Muhammad Kazim Zargaham, Najam-us-Sahar Sadaf Zaidi, and Alvina Gul

Abstract Plants thrive in a complex environment comprising of various biotic and abiotic agents. Like all biological systems, these agents tend to interact with the plant body. Microorganisms form a major portion of the ecosystem and have been found to inoculate or infect members of all the kingdoms. Plants and microbes have developed molecular mechanisms to interact with one another and attain the maximum benefit from the interactions. This mutualistic relationship provides benefit not only to the microbes but also to the plants. Based upon this complex molecular interplay, a number of mechanisms have been studied and are currently being employed for the agricultural, environmental, and health benefits. The principles of biofertilization and bioremediation utilize the plant-microbe interactions for the survival of the two players along with contributing to the food chain and the ecosystem. Similarly, the secondary metabolites obtained from these organisms contribute to human medical and agricultural welfare. These processes are regulated by a variety of biological, physical, chemical, and environmental factors, the study of which can be helpful in exploiting better outcomes from the interaction. The advent of modern techniques has helped in deciphering the role of various molecular players of the plant-microbe interactions. Moreover, they can be employed for regulating the plant-microbe interaction for improved efficiency. The current chapter discusses the molecular mechanisms involved in the plant-microbe interactions exhibited in biofertilization, bioremediation, biocontrol, and induced systemic resistance. Afterwards, the factors affecting the molecular machinery involved in these pathways have been discussed. Toward the end, a brief introduction of the genetic

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manipulative techniques and their applications in the plant-microbe interactions has been presented.

Keywords Molecular interaction • Rhizosphere • Biofertilization • Bioremediation • Genetic engineering

1 Introduction

Plants and microbes are the two most abundant organisms in the biosphere. They exist even in the geographical regions that are otherwise not inhabited by humans and other larger animals. The interaction between these organisms has, hence, long been established. This relationship has been seen to possess both negative and positive effects on either or both the members. Infection of plants with bacterial, viral, or fungal pathogens often leads to disease and death of the plant. Similarly, in response to the microbial infections, plants have developed ways and means to protect themselves by producing products that kill these microbes. Contrarily, a number of microbial and bacterial species interact with one another in a positive manner for the benefit of both the organisms. Plants, being larger in size with a well-developed nutrient processing mechanism, can offer both support and nutrition to the microbes. On the other hand, bacterial species in close contact with plants can offer exogenous metabolites and supplements that would, otherwise, not be available to the plant. Moreover, many beneficial microbes defend the host plants against the infection from pathogenic bacteria by releasing agents that specifically kill the invading microbes (Thomashow and Bakker 2015). Such a strong interaction requires a highly efficient communication pathway involving multiple molecular players. A continuous trans-cellular and inter-organismal control of molecules ensures the systematic coordination of signals to “detect, regulate, and affect” in response to particular stimuli (Trapet et al. 2015). The response is, hence, observed in the form of a defensive, regulatory, or conducive outcome. The developments in the field of molecular sciences have exhibited the involvement of a complex interplay of physical, chemical, biological, and environmental signals to regulate the plant-microbe interactions including biofertilization, bioremediation, antibiosis, and biocontrol. The recent understanding in the rapidly developing field of plant-microbe molecular interactions has been presented here.

2 Biofertilization

An important application of the microbe-plant interaction is the biofertilization process in which the symbiotic relationship between the two partners is exploited for promoting the growth of the plants. In the process, the bacteria utilize the nitrogen from the environment to produce nitrogen-containing compounds that are useful for the plants.

In turn, plants provide harbor and carbon source to the bacteria. This natural process accounts for nearly 65 % of the nitrogen fixation for the agricultural crops worldwide (Prasad et al. 2015). Many legumes are used as fertilizers as they tend to promote the nitrogen fixation process by harboring the bacteria necessary for nitrogen fixation. The most common strains of bacteria utilized for the process belong to the *Rhizobium*, *Azorhizobium*, and *Sinorhizobium* genera and are collectively referred to as plant growth-promoting rhizobacteria, or PGPR (Berrada and Fikri-Benbrahim 2014).

The interaction initiates when the bacteria secrete the signaling molecules, mainly lipooligosaccharides, that result in an increase in the growth of stem and root nodules (Mabood et al. 2014). Thereafter, the bacteria penetrate the cortical tissue, divide there, and differentiate into nitrogen-fixing bacteroids. The plant develops a low oxygen status, resulting in the activation of nitrogenase—an enzyme that converts atmospheric nitrogen to ammonia. The genes mainly involved in the process are nitrogen fixation (*nif*) and nodule formation (*nod*) (Gomes et al. 2015). Though the pathway of bacterial strains involved in the signaling process is well known, efforts are underway to decipher the genomic and proteomic machinery of the plants involved in nitrogen fixation. Understanding these mechanisms can potentially help in introducing similar pathways in nonleguminous plants in order to induce a greater capability to fix atmospheric nitrogen. This can, hence, be helpful in increasing the yield of widely cultivated food and cash crops like cotton and rice.

Much similar to the bacterial strains that reside on various plant parts, a number of free-living bacterial species are also involved in the nitrogen fixation process. These rhizobacteria include *Acetobacter*, *Azotobacter*, *Azospirillum*, and *Azoarcus*. They function in a manner much similar to the endophytic bacteria present on the roots and shoots of the plants. At a low oxygen concentration, the nitrogenase complex present in the bacterial proteome converts the atmospheric nitrogen to plant-usable ammonia (Ipata and Pesi 2015). The genetic machinery employed by the free-living microbes is much similar to that utilized for nitrogen fixation, utilization, and regulation by the endophytic bacteria. For agricultural purposes, both the endophytic and free-living bacteria are coated on the seeds and then introduced in the soil. For an efficient biofertilization process, the bacteria are expected to achieve a cell count that is capable enough to survive and establish their presence for an extended time period. A high number does not only help in developing a better source for plant nourishment but also aids in warding off the microbes that might adversely affect the plants (Rogers and Oldroyd 2014). In response, the healthy plant provides nutrients and helps the bacteria to colonize the root and shoot systems of the plant.

Recent findings of the molecular players involved in the biofertilization process have provided a new avenue for exploiting this symbiosis for increasing the agricultural yield. Many bacteria in the rhizosphere have been found to contain certain genes on the chromosome, within the symbiotic island or the symbiosis plasmid (*sym*), that mimic the rhizobial type III secretion system (Ji and Dong 2015; Almario et al. 2014). This genetic machinery is involved in the secretion of certain “symbiosis-forming proteins” which have been isolated from a number of plant-beneficial bacterial strains including *Pseudomonas fluorescens*. Similarly, *nif* genes

have also been isolated in a number of free-living nitrogen-fixing bacteria including *Azoarcus* species (Devi and Momota 2015).

An understanding of the genes and gene products involved in various steps of this process can potentially be helpful in replicating the same mechanisms in plants that, otherwise, do not establish a symbiotic relationship with nitrogen-fixing bacteria. Attachment of the bacteria to the seeds is generally the first step of the inoculation process. In a recent study on *Pseudomonas putida* strains, gene products homologous to calcium-binding protein and multidrug efflux have been found to be actively involved in the interaction with seeds (Molina-Santiago et al. 2014). Similarly, molecular dissection of *Pseudomonas fluorescens* has shown the presence of a number of *rhi* genes (rhizosphere genes) that are involved in the process of nutrient absorption from the plants, bacterial metabolism, and secretion of active agents (Moreno and Rojo 2014; Pizarro-Tobías et al. 2015). A number of genes involved in root colonization have also been identified in other species of *Pseudomonas* and *Bacillus* and other bacterial genera including the ones taking part in biofilm formation and lipopeptide and polyketide metabolite production. Similar studies have shown the plant-induced activation of ABC transporters and porins in various PGPRs (Wisniewski-Dyé and Vial 2015). One additional advantage of introducing PGPRs is their ability to retard the growth of other microbes. Insertion of gene segments (operons), genes, and genetic cassettes has yielded the expression of secondary metabolites that help in protecting the PGPRs and, ultimately, the host plants from unwanted microbial infections. PCA (phenazine-1-carboxylic acid), PCN (phenazine-1-carboxamide), and ACC (1-aminocyclopropane-1-carboxylic acid) are some of the metabolites that aid the colonization of beneficial bacterial strains on the root surface (LeTourneau et al. 2015; Shahverdi et al. 2014; Kim et al. 2014). Microbe-plant interactions are dependent upon a number of abiotic factors as well. Of chief importance in this respect are the soil pH, presence of organic acids, stress factors, and the availability and nature of carbon source.

Biofertilizers, hence, provide a highly efficient and environment-friendly means for providing the plants with the required nutrition to supplement their growth requirements. Many bioinoculants, including *Rhizobium* and *Bradyrhizobium*, are available in the market for the purpose. Alternate bacterial strains including *Bacillus*, *Pseudomonas*, and *Streptomyces* are now being promoted commercially as well. Though significant progress has been made in deciphering the underlying mechanisms, further investigation in this regard can help in improving the overall efficiency of the naturally as well as the artificially induced biofertilization process.

3 Rhizoremediation by Plant-Microbe Cleaning Team

The application of microbe-plant interaction is not only limited to the use of microorganisms for the development and production of useful metabolites for agricultural purposes. A relatively newer, yet highly established, technique is the exploitation of this interaction for the bioremediation process. Pollutants, from

both organic and nonorganic sources, deteriorate the ecological and biogeographical status of various areas. They are generally deposited in certain areas of the ecosystem which, thereafter, act as nuclei for environmental distress. As per recent estimates, the cost to restore the polluted sites in the USA alone would cost nearly two trillion dollars (Knight et al. 2015). The methods generally adopted for the removal of waste matter include incineration and landfilling which further contribute to increasing the air, land, and water pollution. In contrast to these techniques, bioremediation offers a cheaper, safer, and smarter environmentally friendly alternate for treating the waste material. The underlying principle of bioremediation is the use of biological system, generally microbes or plants, for converting the highly toxic agents to safer products. The genoproteomic machinery of the biological organisms is highly adaptive in nature and, hence, when exposed to the new environmental and/or nutritional conditions, tend to utilize these pollutants and convert them into less toxic products. This process is referred to as natural attenuation and has been employed on large scale for the treatment of polycyclic aromatic hydrocarbons (PAH) polluted sites (Srivastava 2015; Juhasz 2014). Moreover, many industrial solvents including toluene, benzene, and ethylene have also been rendered nontoxic by the same phenomenon (El-Naas et al. 2014). Another similar term, phytoremediation, defines the process, whereby the pollutants are detoxified by plants (Bisht et al. 2015). Plants carry out the process by absorbing the pollutants from the soil, transporting them to the shoot, and/or converting them into relatively safer products. Mustard, sunflower, tobacco, and maize have been found to attain these goals in a number of studies (Prasad 2015).

A combination of natural attenuation and phytoremediation is observed in the case of rhizoremediation in which the interaction of microbes and plants is exploited for detoxifying the pollutants. Rhizosphere—comprising the symbiotic bacteria in the roots of plants—has been related to the degradation of many pesticides, herbicides, and PAH-containing pollutants (Hou et al. 2015; Fulekar 2014). The effectiveness of rhizoremediation process depends upon a number of factors including the plant species, microbial strains, and type of pollutant among other pedological and botanical factors. Legumes and grasses are considered to be the most suitable species that can contribute to the process (Brígido and Glick 2015). They have an extensive branching in their roots which usually homes a large number of bacteria. This mechanism provides an efficient means to detoxify the pollutants. At the molecular level, the pollutants are generally subjected to metabolism by the microbial or botanical enzymatic systems. In certain cases, however, they are mineralized, thereby resulting in the immobilization of these agents (Helbling 2015). The resulting products formed by either one of the symbionts can also be utilized by the other partner for its benefit.

A number of methods have been employed for utilizing the rhizoremediation process for achieving maximum efficiency. Some researchers have reported the introduction of a bacterial strain along with the plant seed. This strategy can help in the propagation of the bacterial strain along with the growing root system of the plant. Such interaction has been exploited for the degradation of naphthalene—a toxic organic compound (Agarry and Oghenejoboh 2015). Introducing a consortium

of diverse bacterial strains has been found to degrade a number of pollutants as each strain tends to employ a different catabolic pathway to detoxify the respective pollutant (Fuentes et al. 2014). In addition to these strategies, genetically engineering the microbes and plants to produce transgenic varieties with greater or diverse ability to detoxify the environmental pollutants can be even more useful (Peng et al. 2014; Mouhamad et al. 2014; Jagtap and Bapat 2015). Transgenically produced tobacco plants, expressing the mammalian cytochrome P450 system, have been found to metabolize a number of pollutants including chloroform and trichloroethylene (Renault et al. 2014). The molecular tools can, hence, be employed for improving the activity of this efficient microbe-plant interaction to attain maximum ecological and biological benefits.

4 Biocontrol and Antibiosis

Microbe-plant interactions may be presented in a number of ways. In the case of a symbiosis, both the members benefit. However, in the case of parasitism, the host organism has to bear the adverse consequences of the interaction. Most microorganisms tend to possess a number of mechanisms to defend themselves and their symbiotic partners from pathogenic microbes. The use of microbes or microbe-derived products for inhibiting the growth of pathogenic agents is covered under the scope of biocontrol and has been investigated in a number of recent studies. The environmental and health concerns associated with the conventional tools have shifted the focus toward the use of these environmentally friendly, efficient, and reproducible biocontrol methods.

A number of mechanisms are employed by the microbes to defend themselves and their symbiotic partners, the plants, from pathogenic microorganisms. The chief technique among these biocontrol strategies is the upregulation of antibiosis process by the production of secondary metabolites that either kill the pathogenic bacteria or retard their growth (Clay 2014). *Pseudomonas*, for instance, produces DAPG for attaining effective biocontrol (Weller 2015). Similarly, nonpathogenic strains of *Agrobacterium* produce a highly effective antibiotic agrocin that specifically kills the pathogenic species of bacteria (Hooykaas 2015). Apart from producing secondary metabolites, a number of beneficial microbes compete with other organisms for nutrients and space, thereby inhibiting the secondary infections. Moreover, in certain stress conditions, the microbes produce entities that absorb nutrients and trace elements from the environment protecting the growth of pathogenic organisms. In this respect, siderophores and pyoverdines are released by microbes to sequester the essential elements. A number of antibiotics have been reported that play a significant role in the biocontrol process. Table 1 represents a few examples of the agents generally involved in antibiosis and, therefore, biocontrol process.

The application of the antibiotics in the biocontrol process has been characterized by employing various techniques of genetic engineering. Using these techniques, a detailed insight of microbe-plant interactions has been attained. Mutants

Table 1 Secondary metabolites produced by plant-microbe interactions for attaining effective antibiosis

Metabolite	Activity
Ammonia	Bactericidal, fungicidal
Butyrolactones	Fungicidal
Kanosamine	Fungicidal
HCN	Bactericidal, fungicidal
Oligomycin	Fungicidal
2,4-diacetylphloroglucinol	Fungicidal
Viscosinamide	Bactericidal, fungicidal
Zwittermicin	Bactericidal, fungicidal

lacking the production of antibiotics and those overexpressing their production are employed for studying the effects of antibiotics on the biocontrol process. Conversely, probes or reporter genes have also been utilized for the identification and characterization process. These molecular techniques have provided a thorough understanding of the operons, genes, and gene clusters that are involved in protecting the plants from the adverse effects of pathogenic bacteria (Singh and Singh 2014). Many of these techniques have established an increased presence of the bacterial strains to the improved biocontrol process.

Among the organisms that are generally employed for achieving biocontrol, *Pseudomonas* strains are considered to be one of the most important candidates. This bacterial species is relatively fast growing with ideal lab handling properties. Moreover, its genome can be easily manipulated. *Pseudomonas* is competitive with a number of nutritional sources and can easily thrive in new nutritional and environmental conditions (Mercado-Blanco 2015). In nature, pseudomonads have been found to carry a strictly regulated antibiosis controlling system. It is found to be composed of two main parts: the sensor and the cytoplasmic unit. The environmental sensor system is generally a membrane protein that is activated or triggered by certain environmental factors. Though these factors have not been fully characterized at the molecular level, yet they are considered to be either the part of the chemical exudates from the host plants, chemicals from the pathogenic bacteria, or the products produced in the soil as a result of the presence of pathogenic bacteria (Carvalhais et al. 2015). The second component, the cytoplasmic response factor, initiates the signaling process that results in the production and release of the antibiotic agent thereafter. An imbalance in either of the components results in the inactivation or discrepancy in the antibiosis. For instance, a mutation in membrane or the cytoplasmic genes lead to the incapability of the cells to produce *Phl*, *Plt*, HCN, protease, and phospholipase, the agents generally used for inhibiting the propagation of pathogenic bacteria (Almario et al. 2014; Sharma et al. 2014; Llamas et al. 2014). Moreover, among the fungal species that have been exploited for attaining biocontrol, *Trichoderma* species is the established choice (Srivastava et al. 2014). The fungus can be easily grown and has a wide host range. Similarly, nonpathogenic species of *Pythium* and *Fusarium* are also being used for biocontrol (Gerbore et al. 2014; Zarafi et al. 2015). Unlike bacterial biocontrol agents which

have been effective in controlling both bacterial and fungal infections, fungi are effective in controlling the infection by other fungal species only. The molecular mechanisms of fungus-based biocontrol are not very well understood and, hence, are under investigation by a number of research groups worldwide.

The mechanisms adapted by the microbes are effective in preventing the growth of bacterial and fungal pathogens. One such example is the biocontrol of a few varieties of *Gaeumannomyces graminis* which are involved in the take-all disease of wheat by *Pseudomonas aureofaciens* (Panwar et al. 2014). The bacteria produce a toxin PCA that specifically acts as a fungicidal agent (Borriss 2015). Much similar to the molecular mechanism mentioned earlier, the infection of the roots by the fungus causes the exudation from the roots. This exudate causes an increase in bacterial propagation of both pseudomonads and other beneficial bacteria. Within the bacterial cells, there is an upregulation of the expression of *phzI* gene, resulting in an increased activity of *N*-acyl-L-homoserine lactone or generally referred to as HSL (Khabbaz et al. 2015; Schenk et al. 2014). This ultimately leads to an increase in the production of PCA which inhibits the further colonization and propagation of the fungus on roots. Similarly, the other bacteria in and near the infection region also cause an increase in the production of PCA aiding the biocontrol against pathogenic fungi. Apart from the *phzI* gene, two sigma factors *rpoS* and *rpoD* have also been found to control the transcription and, thereafter, expression of the PCA (Duca et al. 2014). In certain cases as in *Pythium debaryanum* infections, there is an upregulation of trehalose signaling (Smeekens 2015). This ultimately signals the activation of bacterial systems in pseudomonads to provide an effective biocontrol cover to plants including sugar beet. Therefore, a multicomponent system is involved, directly or indirectly, in activating the antibiosis process in bacterial population (Fig. 1).

Another mechanism adopted by the beneficial microbes to inhibit the growth of pathogenic organisms on the host plant is the direct interaction of the bacteria with the parasite followed by the release of cell-degrading enzymes. Actinomycetes, a gram positive group of soil bacteria, tend to parasitize the fungal pathogen and degrade the spores of the fungi. The bacteria interrupts the transport of nutrients from plant to the fungus and an increase in bacterial colonization that leads to an increased biotic stress on the fungus or a complete degradation of the fungus, owing to the release of extracellular enzymes. Cellulases and glucanases are the enzymes that have been established to cause the degradation of cellulose and chitin component of the fungal pathogens (Kubicek et al. 2014; Turrà et al. 2014). Similarly, molecular intervention studies have also identified the involvement of endochitinase and other proteases in the prevention of fungal infections in cotton, wheat, and berries (Nagpure et al. 2014).

The competition for nutrition and space within the rhizosphere also plays a major part in the biocontrol process. An increase in the number of “beneficial” microbes causes the pathogenic bacterial and fungal species to compete for space, carbon source, nitrogen source, micronutrients, and the infection/inoculation sites on the host plant. The growth of pathogenic strains of *Fusarium oxysporum*, generally associated with *Fusarium* wilt in tomato, legumes, tobacco, and banana, is suppressed by the presence of nonpathogenic strains of the same fungal species (Jiménez-Díaz et al. 2015). Apart from the competition for space, certain microbial

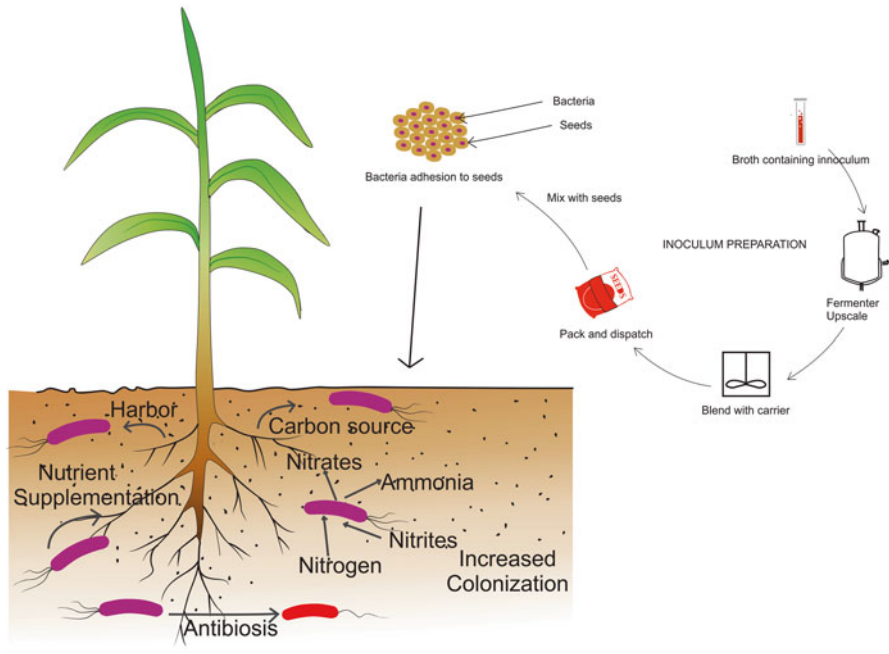


Fig. 1 Inoculation of microbes for biofertilization and biocontrol process

species require a specific nutrient for their survival. Unavailability of the appropriate amounts of the nutrient causes the ultimate death of the pathogenic microbes. An interesting example of this phenomenon is the biocontrol achieved in the wheat rhizosphere against the pathogenic varieties of *Gaeumannomyces* species due to the limited availability of thiamine (Kemen 2014). The microorganisms involved in the biocontrol process have developed a number of means to increase their survival. Modification of the transport proteins to cause an enhanced absorption of the nutrients, faster growth cycles, and rapid induction of inoculation at the preferred sites of infection provides them with a major edge over the pathogenic forms. One such example is the interaction of *Idriella bolleyi* fungi with the cortical cells, leading to the prevention of infection from pathogenic fungi. The fungus occupies the upper region of the root system and travels down in growing nodules to establish its role as an effective biocontrol agent. Though the competition provides adequate defense to the plant from the pathogenic bacteria, further research in the molecular mechanisms involved in the process is still needed.

An interesting example of the biocontrol process that employs the production of secondary metabolites along with the principle of nutrition competition is the production of siderophores or iron-chelating agents (Xia et al. 2014). Under iron-stress conditions, microbial species produce the molecules which sequester the limited

amount of iron available in the plant rhizosphere, making it unavailable to the pathogenic microbes. The siderophores tend to chemically interact with the oxidized form of iron, ferric ions, and aid in their mobilization into the cell. Pseudomonads, for instance, produce pyoverdine and pyochelin, which transport the iron intracellularly preventing the attack of bacterial and fungal organisms on the roots of various crops (Cézard et al. 2015; Cunrath et al. 2015). Siderophores may be used only by the bacteria that produces them, or once released, they may also be utilized by other bacterial species. Apart from the nonspecificity of the bacteria, siderophores also cause the chelation of other metals like aluminum, copper, zinc, manganese, lead, and cadmium (Braud et al. 2015). Additionally, these molecules might also cause the induction of resistance within the plants to a number of pathogens.

Though most of the biocontrol mechanisms involve the use of a single microbe, the involvement of multiple organisms for protecting the plants from infection can be very effective. These microbes can act in harmony and provide synergistic benefits. Addition of multiple microbial species including different species of bacteria or fungi or a bacterial-fungal consortium can be highly effective in inhibiting the growth of pathogenic microbes. A variety of mechanisms can, hence, be exploited for the purpose. Various combinations of *Bacillus* species have been found to protect cucumber and tomato plants from different pathogens (Xu et al. 2014; Hao et al. 2014; Singh and Siddiqui 2015). Similarly, *Trichoderma* and *Pseudomonas* strains have been used in combination for protecting the plants from *Pythium* infection (Kumar et al. 2014). Employing microbial consortia not only helps in providing effective biocontrol, but reports have also suggested an improvement in plant health owing to the induction by PGPRs. The interaction between the indigenous microbial population and the inoculated biocontrol agents has to be considered while devising an effective biocontrol strategy.

In general, the beneficial microbes are introduced in the plant rhizosphere by coating the seeds or the roots of plant saplings with the microbial inoculum. In addition to exogenously introducing the microbes, certain agricultural practices also tend to promote the growth of beneficial bacteria within the rhizosphere. Of prime importance among these are the crop rotations, introduction of soil amendments, soil fumigation, and solarization (Chandel 2015; Sun et al. 2015). These methods are considered safe by the farmers as no genetic or microbial manipulation is involved. A deeper understanding of the plant-microbe interaction is necessary to integrate the molecular techniques with the current agricultural practices. Currently, enhanced efforts are being made to produce transgenic microbes that can provide effective biocontrol. Moreover, the role of environmental conditions, local fauna, and cropping systems is also being studied to help in improving the overall effectiveness of the process.

5 Systemic Resistance

Microbial infection of plants generally causes either of the two presentations: an infection exhibited in the form of plant disease or the development of resistance to the pathogenic agent. In case of an infection, the pathogen or the pathogenic metabolites target various parts of the plant and are then spread throughout the

plant body, ultimately, resulting in the phenotypic changes and finally death. Conversely, for inducing the systemic resistance, following a microbial infection, there is an oxidative stress condition at the local site, resulting in the apoptosis of these cells (Baxter et al. 2014). The rapidly dividing pathogens are entrapped within the cells and, hence, do not mobilize to other parts of the plant body. At the same time, a number of secondary metabolites, including phytoalexins, pathogenesis-related proteins (PR proteins), and proteases, are produced that help in the prevention of the pathogenic attack at any secondary site (De Coninck et al. 2015). The release of these metabolites, especially PR proteins, has been related to the phenomenon known as “induced systemic resistance”—*the vaccination of the plants* (Pieterse et al. 2014a). Moreover, the cell morphology at the local site is also changed in order to prevent the colonization and exaggerated infection at various secondary sites.

The main molecular players involved in ISR are the PR proteins which are generally classified into two main classes: the acidic PR proteins and the basic PR proteins (Golshani et al. 2015). The first category includes the proteins that are generally found in the intercellular spaces, while the basic PR proteins are mainly concentrated in the intracellular regions, for instance, within the vacuole of the plant. Both the classes are functionally similar but vary mainly in the amino acid sequences and, therefore, the molecular weights as well. A number of PR proteins possess chitinase or glucanase activity which helps the plant to defend themselves against the pathogenic fungal species (Ng and Wong 2013). These proteins hydrolyze the cell wall of the fungus, thereby preventing the plant from fungal infection. The role of a large number of PR proteins is, however, still unknown. Generally, they have been isolated in biotic stress conditions from a number of plants and, therefore, serve as excellent markers for correlating the microbial infection. On similar grounds, phytoalexins, in particular camalexin, have been related to ISR and hence help in promoting plant defense against the microbes (An and Mou 2014). Both PR proteins and phytoalexins induce the nonspecific protection of the plants, i.e., the induction of systemic resistance by any one type of the microbe can help in the prevention of attacks by other microbial species.

The mechanism of ISR initially involves the priming or sensitization process in which the microbial pathogen is “sampled” by the plant (Fu and Dong 2013). This results in a complex molecular interplay, causing the activation of the signaling and effector functions, thereafter. The chief among the chemical molecules acting as the inducers for ISR is β -aminobutyric acid (Justyna and Ewa 2013). The activation is followed by the secondary changes including the morphological adaptations like lignification or regulation of other functions including the overexpression of PR proteins and phytoalexins. The exact molecular mechanisms of the priming pathways are, however, still under investigation. After the priming has occurred, the signaling pathways are activated in a manner to prepare the whole plant for protection against the pathogen attack. Salicylic acid (SA)-mediated pathways are considered the most active way to effectively establish the ISR (An and Mou 2014). Infection at the primary site leads to an increase in the endogenous production of SA adding the metabolite into the vascular system of the plant. SA is produced and released from

sites other than that of primary infection as well, causing thereby a “SA storm” within the plant body. The role of SA has been established in a number of plants including wheat, rice, potato, and certain legumes mediated by salicylate synthase (SAS) as well as naphthalene hydroxylase G (*nahG*) gene systems (Kobayashi 2015; Puntus et al. 2015). However, genetic engineering experiments have also lead to the identification of other non-SA systems in the activation and maintenance of ISR. The exact nature of molecules, however, still remains to be established.

As discussed, the effects of the molecules produced during ISR may be in the form of morphological, physiological, or metabolic changes. A diverse set of signaling pathways and chemical reactions are generally involved in the process. These pathways might synergize or antagonize the effects of one another. An in-depth understanding of the molecular players involved in inducing ISR is necessary to devise means to protect the host plants. A number of research groups have investigated the role of various plant metabolites in the ISR regulation. The production of jasmonic acid (JA) is one such pathway adopted by many plants to defend themselves from the microbial and even animal attacks (Carvalhais et al. 2015). In response to the wounding at the primary site of infection/ingestion, the membrane lipids are converted to linolenic acid ultimately transforming to JA. Systemin is another molecule that has been indicated to play a role in the activation of these pathways (Huffaker 2015). The release of JA, hence, results in the overexpression of genes encoding proteinase inhibitors and other enzymes involved in the production of volatile oils, phenolics, and alkaloids, all of which play an important role in the biodefense process. These mechanisms have been well characterized in the case of legumes in response to fungal infection by *Trichoderma viride* (Ruocco et al. 2015). In this case, cellulysin released by the fungus induces the production and release of JA and downstream volatile compounds (Pushpalatha et al. 2013) (Fig. 2).

Whether mediated by SA or JA, ISR has been effective in protecting the plants from subsequent microbial and herbivore attacks. In certain cases, it has been observed that the metabolites produced by one pathway can confer resistance against the pathogens that, otherwise, induce the metabolite production by other pathways. In the case of watermelon, for instance, the attack of the crop by thrips and other insects leads to the protection against fungal attack by *Colletotrichum* species (Lima et al. 2014). Similarly, beetle attacks can help in preventing attacks from *Rumex* species of fungal pathogens (Hejcman et al. 2014). A number of research groups have also reported the antagonistic responses when the plants are attacked by different organisms or have been induced to produce ISR against pathogens. In the case of tomato, for example, chemically induced ISR causes a decrease in the ability of the plant to respond to wound-induced proteinase inhibitors. Moreover, treating the plants with salicylic acid, acetyl salicylic acid, or other chemical inducers also leads to a partial reduction in the systemic resistance. These compounds interact with the octadecanoid-signaling cascade, upstream pathway for the production of JA, and inhibit it in a competitive, dose response manner (Vidhyasekaran 2015). In general, the pattern of ISR involves either of the three mechanisms: the induction by a biological agents against a biological agent, a chemical agent against a biological agent, or a biological agent against a chemical agent. A detailed investigation of these methods needs to be

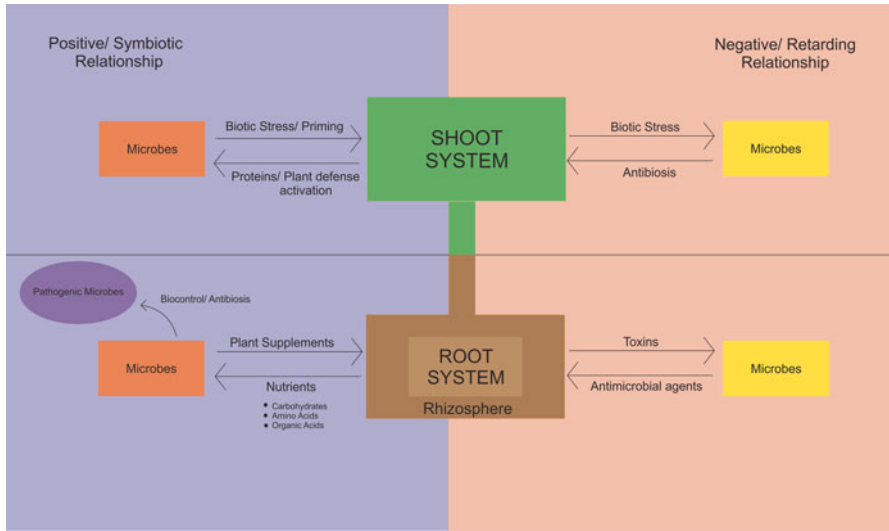


Fig. 2 Biodefense mechanisms in plants based upon plant-microbe molecular interactions

done in order to establish an appropriate means to induce systemic resistance against various pathogenic organisms.

One of the major disadvantages of the ISR mechanism, however, is that the plants are not protected until they have not been exposed to the pathogen at least once. Therefore, in case the primary microbial attack is quite significant, there would be a total failure of resistance mechanisms. Moreover, predictive information needs to be attained in order to prevent the plants from subsequent attacks from the microbes. Concurrent, biotic, and abiotic stress factors should also be considered as either of these can also cause an increase in the propensity of the microbes to cause infection. Therefore, a complex molecular interplay is involved in the induction and sustenance of ISR.

6 Factors Affecting Plant-Microbe Interactions

6.1 Mechanical Signals

Plants respond to a number of physical stimuli. Certain plants possess highly sensitive mechanosensory cells that respond to the external stimuli very rapidly. This can be observed in the case of *Mimosa* and *Dionaea* species of plants (Johnson et al. 2014). In a large variety of plants, however, the response is not as fast, yet there is always a change in the morphological, cellular, or molecular machinery owing to the mechanical simulation. Jasmonic acid, for instance, is

known to be involved in inducing plant resistance against various microbial pathogens (Pieterse et al. 2014b). An increase in the jasmonic acid generally mimics the mechanical stimulation and vice versa. This phenomenon coordinates an exaggerated response to bacterial and fungal organisms. Similarly, calcium levels are also changed in response to any mechanical stimuli, causing the activation of a variety of downstream defense response players (Stael et al. 2015). These stimuli are known to upregulate the touch-inducible genes encoding the calmodulin protein that is associated with the development of immunity against the pathogens. It is, therefore, evident that on exposure to these mechanical stimuli, specific molecules are activated within the plant body that mimic the microbial infection aiding the development of resistance, thereafter.

Microbes exploit mechanical stimulation to interact with the plants. Many fungi produce a penetration peg to aid its entry into the cell as well as for providing the support to the pathogen (Wang and Qi 2015). After gaining a strong support, the hyphae utilize shear mechanical force to breach further into the underlying tissue. This phenomenon has been observed in the case of *Colletotrichum* and *Magnaporthe grisea* species. After this initial physical interaction, the fungus causes an imbalance in the molecular and chemical homeostasis leading to various presentations within the cells including the nuclear repositioning as observed in the case of an abiotic stress response in plants as well. The response has been well characterized in *Gigaspora* and *Phoma medicaginis* species infection in plants. In case of plant-microbe infection, the nuclear repositioning is supported by the development of a penetration apparatus that facilitates the entry of the fungus in to the plant body. Membrane reorganization, cytoplasmic streaming, microtubule reaggregation, and other mechanical responses are also observed in combination with the molecular reactions in response to a microbial infection (Ueda et al. 2015). Extracellular ATP or eATP acts as a signaling molecule to cause the activation of a number of effector molecules including lectin nucleotide phosphohydrolase (LNP) and other kinases through G-protein complexes (Fliegmann and Bono 2015).

Elicitins are another group of molecules that are produced as a result of microbial infection. Following an increase in calcium concentration and oxidative stress, certain kinases are activated. These kinases, for instance, in *Phytophthora* species, cause the activation of nucleotide-binding-site Leucine-rich repeats, or NBS-LRR proteins (Reddy et al. 2015). These proteins cause a hypersensitive reaction that further warrants the activity of self-defense mechanisms. Among other instances of use of mechanical forces for establishing the microbial infection in plants is the development of infection thread. The rhizobacterium is located on the root nodules. The presence of a small colony of microbes induces the production of root hair curl (Fournier et al. 2015). The structure tends to curl onto itself resulting in an increased force and, hence, plant response to both biotic and abiotic stress factors. Based on the induction of host responses to both biotic and abiotic stress factors, it is imperative that the physical and mechanical stimuli act in a similar way as other induction molecules.

6.2 Chemical Signals

The exposure of a plant to the microbial attack leads to a variety of chemical modifications. These changes are observed in response to certain enzyme-activated reactions or release of certain metabolites that ultimately lead to the generation of new chemical entities. The chief among the chemical modifications are the redox reactions and the generation of oxygen moieties. Pathogen-triggered immunity (PTI), for instance, is the resistance developed as a result of microbial recognition and involves multiple players for the generation of ultimate response (Pieterse et al. 2014a). The microbes are identified by means of representative pathogen-associated molecular patterns, or PAMPs (Macho and Zipfel 2014). This is followed by the induction of PR genes and an outburst of reactive oxygen species, or ROS (Corpas et al. 2015). These mechanisms lead to the ability of plants to effectively defend themselves against a microbial attack. Microbes have, in response, developed mechanisms to establish their pathogenicity by the release of effector molecules that interfere with the intracellular PTI responses. Plants have developed another mechanism, referred to as effector-triggered immunity or ETI, which can detect the effector molecules or the accompanying alterations within the plant cell, leading to the generation of a secondary immune response against the pathogen (Cui et al. 2015). Both ETI and PTI are mediated by the generation of large amounts of ROS that are involved in the direct killing of the microbes, retardation of their growth, or generation of mechanism to induce apoptosis in order to reduce the microbial spread within the plant body. Microbes, with their high genetic adaptability, have developed means to prevent the effects of ROS and establish their infection in the host plants.

The chemical interplay between microbes and host plants should, therefore, be deciphered in order to develop effective means to utilize the genetic engineering technologies for the benefit of plants. The nature of the stress molecules helps in determining the pathways involved in the interactions. Plant-derived ROS, for instance, not only lead to the development of resistance against the microbe but also act as a trigger for the generation of microbial responses against the ROS release. In *Magnaporthe* species, glutathione peroxidase, catalases, transcription factors, and serine-rich proteins are all involved in mounting a successful response against the host ROS. The genes including *HYR*, *API*, *DES1*, *CATB*, *NOX1*, and *NOX2* are upregulated for the generation of an effective response (Demidchik 2015). In other pathogenic fungi like *Podospora* and *Epichloe*, these changes have been related to the modifications in their growth patterns represented by alterations in hyphae growth, spore-forming ability, and establishment of infection. Based upon similar studies, it is established that the ROS are not solely effective in inducing or neutralizing the pathogen infection on plants. Contrarily, in certain microbial species, these chemical signals act as triggers for enhancing the microbial attack. The exaggerated response involving catalases, ROS, and, the ultimate generation of, hydrogen peroxide might be effective in inhibiting a localized attack (Lindermayr and Durner 2015). However, to effectively control the infection, other molecular and biological players are also required, for instance, the upregulation of proteins and certain mechanical changes.