Rizwan Ali Ansari · Irshad Mahmood
Editors

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Volume 2: Microbial Interactions

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Preface

In order to understand the plant fitness entirely, it is high time for researchers to relinquish the obsolete theories and must unravel unexplored aspects pertaining to plant health. The book "Plant Health Under Biotic Stress" is being published in two volumes to provide the articulated, justified and updated information which are either directly or indirectly related to soil and plant health. Plant Health Under Biotic Stress – Volume 2 (Microbial Interactions) accounts for the application of plant strengtheners, biofertilizers, bio-inoculants, phytostimulators, biopesticides, biocontrol agents, etc in the amelioration of plant fitness. There is a wide spectrum of bio-inoculants which are used in various plant protection strategies. Literature on microbial root colonization, plant growth enhancement, and also on rescue of plants from attack of various soil-borne pathogens have been presented in a well manner. Potentiality of biocontrol endophytic fungi, bacteria, and actinomycetes enhancing the crop resistance ability against pathogens attack leading to improved plant health has also been underpinned. It is anticipated that the book will be useful to advisers, extension officers, educators, and advanced researchers who are concerned about the protection of plant health as well as environment.

A sincere acknowledgment is extended to Prof. Tariq Mansoor, Hon'ble Vice Chancellor, Aligarh Muslim University, Aligarh, India, for being a constant source of inspiration for the researchers.

Professor Akhtar Haseeb, Ex-Vice Chancellor, Narendra Deva University of Agriculture & Technology, Kumarganj, Faizabad, India; Prof. Saghir A. Ansari, Dean, Faculty of Agricultural Sciences; Prof. M. Yunus Khalil Ansari, former Chairperson, Department of Botany; Prof. Nafees A. Khan, Chairperson, Department of Botany; Prof. Mujeebur Rahman Khan, Chairperson, Department of Plant Protection; Prof. Zaki A. Siddiqui; Prof. Iqbal Ahmad; Prof. A. Malik; Prof. P. Q. Rizvi, Prof. M. S. Ansari; Prof. M. Haseeb; Prof. S. Ashraf; and Dr. R.U. Khan of Aligarh Muslim University, Aligarh, India, deserve special thanks for providing us critical suggestion during the write-up of this book.

This book would have remained just a dream if Dr. Rose Rizvi has not come and taken up each hurdle translating it into an enjoyable moment. She assisted us from onset of this journey and therefore indeed deserves to be acknowledged with great appreciation. In addition, Dr. Sartaj A. Tiyagi, Dr. Safiuddin, Dr. Aisha Sumbul, Mr. Hari Raghu Kumar, and Ms. Aiman Zafar were constantly surrounded with us whenever we felt like giving up – sincere thanks to all of them.

Editors would have not completed this task without endless support, prayers, and encouragements of their elders during light and dark situations.

We can never forget our "little doctor," Mr. Ayan Mahmood, who used to practically look up and smile at us with two lovely and twinkling eyeballs, each time muttering words of comfort and encouragement.

We hope that our efforts to forward the readers toward the better state of plant science shall be fruitful.

Aligarh, India

Rizwan Ali Ansari
Irshad Mahmood

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About the Editors

Dr. Rizwan Ali Ansari is a young and active faculty member of Faculty of Agricultural Sciences, Aligarh Muslim University, Aligarh, India. He obtained his Ph.D. from the same university and has been involved in the research and development strategies of plant pathology/nematology. He has been engaged in the formulation of management modules involving various microorganisms, antagonists and organic additives active against a wide range of soil-borne plant pathogens infesting several agricultural crops. He has also attended several national and international conferences so far and received prestigious awards by various scientific societies like Society of Plant Protection Sciences (SPSS) and Nematological Society of India (NSI) for his outstanding contribution in the field of plant pathology/nematology. He has published several book chapters, research and review articles pertaining to the utility of organic additives, mycorrhizal fungi as well as plant growth-promoting bacteria in the sustainable management of plant pathogens in various journals/books of great repute. Judicious application of organic additives and biological agents in the management of plant diseases, amelioration of soil and crop health and survey on disease prevalence caused by soil-borne pathogens on various economically important crops are the current research domain of Dr. Ansari.

Dr. Irshad Mahmood is working as a professor of plant pathology and nematology in the Department of Botany, Aligarh Muslim University, Aligarh. He obtained his PhD from Aligarh Muslim University in. the field of plant pathology and nematology. Promotion of organic farming across the world by utilizing organic additives and potent microorganisms for the sustainable management of phytoparasitic nematodes and plant pathogenic fungi resulting to augment soil and plant health is the domain of his research. He has been engaged with teaching programme of undergraduate and postgraduate-level students for the last 30 years and has many overseas visits including the United States, France and the United Kingdom. He has attended a significant number of national and international conferences pertaining to wide area of agricultural sciences and published around 150 original research papers, review articles and book chapters in various refereed national and international publication media, most of them in very high impact factors. He has successfully completed many training courses in various ICAR-sponsored research institutes in India and also in North Carolina State University, Raleigh, USA. He is also an active member of national and international scientific organizations; an expert for selection committee; a reviewer of journals, doctoral theses and funding agencies; and a recipient of Scientist of the Year award in the field of plant pathology and nematology. He has guided ten PhDs, several MPhil and a large number of MSc dissertations. He has also been engaged in the establishment of a joint government project with Aligarh Muslim University for improvement of infrastructural facilities in botanical garden to facilitate ex situ conservation and propagation of rare, endangered and threatened plants and the plants endemic to the region.

Chapter 1
Endophytic Bacteria: Prospects and Applications for the Plant Disease Management

P. Latha, M. Karthikeyan, and E. Rajeswari

Abstract Biological control of plant diseases has metamorphosed into a unique field of science and development, and this field is fast happening in recent years. Bacterial endophytes are a group of microorganism which can colonise in any part of a plant devoid of symptoms or harmful effects in the plant in which they inhabit for their survival. The endophytic bacterial species have been identified by numerous researchers, and they have increasingly been reported to reduce the growth and activity of a plethora of plant pathogens. The interest of the researchers in this field is ever expanding given the potential it possesses to serve as an alternative to synthetic fungicides. The primary aim of this review is to trace the development in endophytic bacterial research and to communicate the researchers with updated information which will serve as a catalyst for their research endeavours. The review started with a prologue about endophytes, their diversity and existence. A systematic review on the colonisation of endophytic bacteria has been given which unravels the processes involved in their entry into the rhizosphere, then cortex and xylem and further their movement to the vegetative and reproductive organs of plants. This has followed the review on the control of various plant diseases through endophytic bacteria, viz. wilt, damping off and rot, foliar fungal diseases and bacterial diseases. The control of postharvest diseases and nematodes by endophytic bacteria has also been discussed. The major processes involved in the mode of action or mechanism of control of diseases have been discussed in different heads, namely, competitive root colonisation, competition for ferric iron ions, antibiosis and antibiotics suppressing pathogens, induced systemic resistance (ISR), signal interference, food and space competition, and minimization of the factors responsible for virulence of pathogens. Quite a few literatures have been discussed on the application of bacterial endophytes through different modes of applications. The review ends with future thrust which will go long way in indicating the future niche research areas on endophytic bacteria.

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1.1 Introduction

Plant diseases pose humongous biotic stress to plants which results in huge economic loss for farmers besides spoiling the food through toxin production during storage also. The deliberate urge of farmers to combat the diseases resulted in the invention of several fungicides and a bactericidal molecule, the application of which culminates in environmental degradation ultimately endangering the health of human kind. Several plant pathogens developed resistance to these chemicals and render plant health management difficult. In order to get rid of these problems, biocontrol of plant diseases assumed greater significance.

The biocontrol interventions have been concentrated in the rhizosphere for a very long time, and plant growth promoting rhizobacteria (PGPR) have intensively been researched by various researchers. The microbes colonising internal tissues have recently been given laser beam focus by the researchers due to the ever-increasing scope of them being exploited for enhancing the growth of the plants and reduction of disease causing pathogens. Among these microbes the role of bacterial endophytes in suppression and control of plant diseases has been intensively reported by researchers in the recent past. Though enough review has been attempted, still there existed scope for updating the reviews in order to enlighten the researchers working in this area. Hence, this review is an attempt to comprehensively cover the research work which has been carried out in bacterial endophytes and to link what has been done and what is to be done in the future.

It would be appropriate to define 'endophytic bacteria' from previous literature before discussing the mode of action. Holliday (1989), Schultz and Boyle (2006) were of the view that endophytic bacteria are colonisers of internal tissue of crop plants which do not exhibit any sort of external symptoms or inimical effect on the plants in which they live and colonise. Almost all plant species that exist on earth harbour one or more than one endophyte in their system (Strobel et al. 2004). Wilson (1995) defined endophytic bacteria as prokaryotes that tried to colonise the xylem and phloem vessels of disease free plants which do not cause any harm to the plant in which they reside. In recent past, researchers defined endophytes as 'endosymbionts' which inhabit the inner parts of plant tissues and do not damage or inflict diseases which could be isolated through adherence of aseptic methods (Arnold and Lutzoni 2007; Khan et al. 2015).

The earlier works of researchers indicated the mutual benefits among plants and microorganisms, and they were of the view that the fungi which were not known for inflicting diseases in crop plants possessed the forte of the traits of microbial endophytes (Carroll 1988; Clay 1988). Despite the fact that Hollis (1951) identified bacteria in disease-free potato tissues seven decades back, the bacterial endophytes were less researched than fungal endophytes. Bacterial species could be isolated from seeds and fruits of agricultural and horticultural crops (Mundt and Hinkle 1976; Kirchhof et al. 1997). Sturz et al. (1997) examined crop plants with big bacterial population of 10^7 colony forming units (cfu) g^{-1} of plant matter in wet weight, whereas Hallmann et al. (1997) reported that population sizes of 10^2 and 10^6 cfu g^{-1} were predominantly observed in most parts of the plants.

The dwelling of endophytic bacteria inside the plant parts has been well documented by researchers. Andrews (1992) while commenting on the dwelling place of endophytes did report that endophytes survive in a totally secluded milieu, when compared to microorganisms living in the root zone and above root zone, whereas the researchers like Schulz et al. (2002) and Arnold and Lutzoni (2007) reported that endophytic bacteria could survive in roots, stem, leaves, flowers, seeds and fruits of the crop plants.

A growing body of literature indicated an array of advantages of endophytes. Kang et al. (2007) detailed the growth-promoting characteristics of endophytes, while Kloepper et al. (2004) and Senthilkumar et al. (2007) demonstrated the disease-inhibiting traits of endophytes. The nature of endophytes in strengthening the defence mechanism of crops to various plant diseases was researched upon by Bargabus et al. (2002), Mishra et al. (2006) and Bakker et al. (2007). Anti-herbivory products were found to be instigated by endophytes (Sullivan et al. 2007) besides catalysing biological nitrogen fixation in plants (Martinez et al. 2003; Jha and Kumar 2007) and enhancing the upward movement of plant mineral (Malinowski et al. 2000). Backman et al. (1997) discussed various factors influencing endophytes as biocontrol agents against various plant diseases like specific bacterial species colonising in a particular crop species, the changing population in different seasons, the pattern with which they have been colonising and their capacity to mobilise inside the tissues and to stimulate systemic resistance.

1.2 Diversity of Endophytic Bacteria and Their Existence in Plant Parts

The dwelling of endophytic bacteria and the diversity of their genera have been a research issue taken up by many researchers, and maiden credible findings came out about the separation of endophytic bacteria from parts of plants which were sterilised using sodium hypochlorite or similar agents as reported by Samish and Dimant (1959) which was endorsed by Mundt and Hinkle (1976) and Miche and Balandreau (2001). Since then almost 200 bacterial genera from 16 phyla were reported as endophytic bacteria (Malfanova 2013). Sun et al. (2017) and Sessitsch et al. (2012) meticulously grouped them into cultural and uncultural bacteria, and majority of them were found to be associated with the species, namely, *Acidobacteria*, *Actinobacteria*, *Aquificae*, *Bacteroidetes*, *Cholorobi*, *Chloroflexi*, *Cyanobacteria*, *Deinococcus-Thermus*, *Firmicutes*, *Fusobacteria*, *Gemmatimonadetes*, *Nitrospira*, *Planctomycetes*, *Proteobacteria*, *Spirochaetes* and *Verrucomicrobiae*.

Malfanova (2013) reviewed in depth the diversity of entophytic bacteria and reported that three major phyla were studied predominantly by the researchers, namely, *Actinobacteria*, *Proteobacteria* and *Firmicutes*. Taghavi et al. (2010), Deng et al. (2011), Weilharter et al. (2011) and Pedrosa et al. (2011) analysed the bacterial species in different parts of plants and observed that *Azoarcus*, *Acetobacter* (renamed as *Gluconobacter*), *Bacillus*, *Enterobacter*, *Burkholderia*, *Herbaspirillum*, *Pseudomonas*, *Serratia*, *Stenotrophomonas* and *Streptomyces* were the predominant bacterial endophytes colonised in plant tissues.

Hallmann and Berg (2006) were of the opinion that the species of the above genera are found to colonise in most of the soil and rhizosphere of the plants, whereas Compant et al. (2010) in their study confirmed the presence of endophytes above the root zone, flowers and also seeds. Hallmann et al. (1997) reviewed the diversified host plants of endophytic bacteria which was updated by Rosenblueth and Martinez-Romero (2006) and Berg and Hallmann (2006) who presented a rather comprehensive list of bacterial endophytes which were reported to be isolated from a wide range of plants.

Jesus and Lugtenberg (2014) reported that bacterial endophytes are omnipresent and can be identified from many sites in the plant, such as the root, stem, leaf, berry, seed and xylem sap, which was endorsed by a score of researchers like Rosenblueth and Romero (2006), Mercado-Blanco and Bakker (2007), Malfanova et al. (2013), Berg and Hallmann (2006) and Weyens et al. (2009). Endophytes population are always greater in the roots than any other organs of plants. In the root the average density is 10^5 cfu per g fresh weight, whereas average values of 10^4 and 10^3 are reported for stem and for leaf, respectively (Jesus and Lugtenberg 2014). Vendan et al. (2010) analysed the presence of endophytic bacteria in ginseng and reported that *Staphylococcus* spp. and *Bacillus* spp. were predominant in the stems of 1- and 4-year-old plants, respectively. The dominant endophytic groups of *Sphagnum* mosses were associated with the bacterial endophytes, namely, *Burkholderia*, *Pseudomonas*, *Flavobacterium*, *Serratia* and *Collimonas* (Shcherbakov et al. 2013). The upper part of poplar tree (*Populus* spp.) harbours abundant *Pseudomonas* and *Curtobacterium* spp. of bacterial endophytes (Ulrich et al. 2008).

Ryan et al. (2008) indicated that endophytic bacteria can be isolated from all kinds of plants in the plant kingdom irrespective of the nature of plants like trees, herbs, shrubs, etc. Lodewyckx et al. (2002) elaborated the main methods used for the isolation and characterisation of bacteria and reported at least 81 bacterial species which were found to be associated with crop plants. The presence of a variety of endophytic bacteria in a toluene-contaminated field was reported by Porteous-Moore et al. (2006) isolated endophytic bacteria from poplar tree and tried to find out the effectiveness of endophytic bacteria in phytoremediation which was endorsed by the findings of Loy et al. (2007).

1.3 Colonisation of Endophytic Bacteria in Rhizosphere and Rhizoplane

Colonisation of endophytic bacteria in plants started with the rhizosphere and moves on to the other parts of plants. The rhizosphere and rhizoplane colonisation of endophytic bacteria has been extensively reviewed. A variety of plant growth-promoting bacteria were said to be colonised in the rhizosphere, and they gained entry into other plant parts which was first reported by Galippe (1887) and proved again by di Vesta (1888). Smith (1991) reported that before this, it was thought that the healthy plants did not harbour microorganisms. In the previous decade many researchers demonstrating a wide range of endophytic bacteria possessed growth promotion and characters of suppression of pathogens. Many researchers including James et al. (2002), Compant et al. (2005b) and Hardoim et al. (2008) were concomitant with the opinion that endophytic bacteria tended to colonise the roots first followed by other parts of the plants. Notwithstanding, the researchers like Sessitsch et al. (2002) and Berg et al. (2005) argued that prominent and unique endophytic bacterial strains were found in all parts of plants starting from roots to flowers, fruits and seeds indicating differential capacities of bacterial strains to grow in various parts of plants. Population densities of bacterial species in the rhizoplane were in the range of 10^5 to 10^7 cfu g^1 of fresh weight (Bais et al. 2006). Gamalero et al. (2004) indicated that root zones of different crop species were reported to colonise endophytic bacteria in varied density of population.

Gamalero et al. (2003) reported that the cells of the bacterium first find a niche in the root zone which could be seen as a unitary cell clinging onto the root surfaces consequently observed as doublets in the rhizodermis. Benizri et al. (2001) pointed out that endophytic bacteria could stabilise themselves as microcolonies or microfilms once they colonise the entire rhizoderm. Root exudation in the form of amino acids, organic acids and other components which nourish bacterial species in the rhizosphere and rhizoplane helped colonisation. Lugtenberg and Kamilova (2009) argued that the endophytic bacterial strains were observed to be chemoattracted and migrated towards the exudates which catalyse the colonisation and multiplication. Further research on the root exudates revealed that variation in crop variety, differential stage of crop and varied amount of biotic and abiotic stresses amounted to varied nature of release of root exudates which were found to facilitate the growth of differential endophytic bacteria in the root zone. Besides, the research on root exudates indicated that some of the exudates were inimical for bacterial strains which may spoil colonisation (Bais et al. 2006; Haichar et al. 2008). The infection of phytopathogen also influenced the secretion of exudates from roots, which was proved by a study of Rudrappa et al. (2008) who found that the secretion of malic acid attracted *Bacillus subtilis* and catalysed the colonisation of the endophytic bacteria in the root zone of the plant resulting in the formation of a biofilm which guarded the roots from the virulent pathogens causing diseases. Bacterial colonisation was also affected by root mucilages, and it was found in a study conducted by Mandimba et al. (1986) that *Azospirillum* spp. strains were reported to be attracted by the root mucilage produced in the root zone of maize, whereas another study conducted later on by Humphris et al. (2005), in maize crop, reported the negative effect of root mucilage which averted colonisation of the strain SBW25 of *P. fluorescens* strain and their interaction in the root zone of maize.

Various mutational studies proved that the prerequisite for endophytic establishment depends on the attachment of bacterial cells to the root. A huge number of components which are found in the exterior of bacterial strains are involved in the process of attachment of bacterial cells to the roots. These views were supported by the findings of Dorr et al. (1998) who reported that BH72, an endophytic diazotroph of rice, and type IV pili which could be encoded by *pil*AB are needed for the connection of *Azoarcus* sp. in the root zone of rice. The dependence on liposaccharide for the attachment of *Herbaspirillum seropedicae*, to root surfaces of maize, was reported by Balsanelli et al. (2010). In their study they found that juxtaposing a wild type of maize, a mutated strain of maize with varied starch composition, exhibited lesser root sticking and endophytic spreading. An analogous study carried out by Meneses et al. (2011) reported the importance of exopolysaccharide for the adhesion of endophytic bacteria *Gluconacetobacter diazotrophicus* to the root zone of rice plants.

1.4 Entry Mechanism of Endophytic Bacteria

The review on penetration process suggested active and passive mechanisms. Hardoim et al. (2008) were of the view that the endophytic bacteria can also follow passive mechanism and it need not be always active mechanism for the penetration into plant tissues and hence at one or other stages of their life all bacteria that colonise the rhizosphere can be expected to be an endophytic bacteria. According to Reinhold-Hurek and Hurek (1998), cracks which are formed at the tips of the roots or the infection inflicted by harmful microbes could serve as a passive entry for endophytic bacteria. Combined with active penetration, this mode of entry has been reported by Reinhold-Hurek and Hurek (1998) for *Azoarcus* sp. BH72, and the entry of *Burkholderia vietnamiensis* in rice was reported by Govindarajan et al. (2008). In grapes the entry of *B. phytofirmans* PsJN was reported by Compant et al. (2005). In mulberry the access of *B. subtilis* Lu144 and *B. cepacia* Lu10–1 to the root zone was reported by Ji et al. (2010). James et al. (1994) found *Gluconacetobacter diazotrophicus* Pal5 gained entry through cracks in sugarcane. Hardoim et al. (2008) reviewed specific adaptations nodulating bacteria possessed for active penetration of the root system, an example of which was elucidated by Goormachtig et al. (2004) wherein *Azorhizobium caulinodans* entered the root of semiaquatic *Sesbania* *rostrata* via splits likely to happen in the lateral root and gained entry through cortical and intercellular cracks.

Garg and Geetanjali (2007) while discussing the colonisation process in legumes known for nodulation, indicated that the preferred entry is through hairy roots. They also reported that prior to the formation of infection thread, they used to penetrate the tissues in the rhizosphere and consequently penetrate the nodules which are specialised organs developed by legumes.

Numerous works done by researchers like Compant et al. (2005a), Haas and Défago (2005), Raaijmakers et al. (2008) and Lugtenberg and Kamilova (2009) revealed a common finding that secondary metabolites produced by bacterial strains did provide a competitive advantage for those bacterial strains against other microorganisms and could catalyse the colonisation in roots. Van Loon and Bakker (2005) indicated that the antibiotics produced by certain bacterial strains were very much helpful for rhizosphere colonisation. The research papers of Nakayama et al. (1999), Nielsen et al. (2002), Raaijmakers et al. (2002) and de Souza et al. (2003) supported this view and quoted several antibiotics like 2,4-diacetylphloroglucinol (DAPG), hydrogen cyanide, phenazine, etc., which were found to be helpful in colonisation of bacterial strains in the rhizosphere. Duijff et al. (1997) and Bohm et al. (2007) reported in their work that lipopolysaccharides, flagella, pili and twitching motility were found to affect endophytic colonisation and bacterial mobility within host plants. A review of Lodewyckx et al. (2002) elaborated the enzymes responsible for degradation of cell wall which aid in the penetration of bacterial strains and spreading within the plant which has been confirmed by the work of Krause et al. (2006) wherein genome analysis of the non-nodulating endophyte *Azoarcus* sp. BH72 was carried out which revealed that the these endophytes carried genes possessing cell wall-degrading enzymes such as cellulases and polygalacturonases.

1.4.1 Colonisation of Endophytic Bacteria in the Cortex and Xylem Vessels of Plants

In order to move from the rhizoplane to the cortex or the root system, the endophytic bacteria have been reported to involve in translocation processes through active or passive mechanisms. Gregory (2006) reported in his study that the endodermis in the root zone hinders the further colonisation of endophytic bacteria and very few bacterial species could find an entry through and proved the report of the previous workers in this area. James et al. (2002) reported that either some endophytic bacteria entered through the endodermis through secretion of cell wall dissolving enzymes or some of them took a passive way during the disruption created in the root phase for the formation of secondary roots (Gregory 2006).

James et al. (2002) explained that the species of endophytic bacteria, namely, *Herbaspirillum seropedicae* Z67, need to pierce the pericycle after the endodermis in the root zone to reach the xylem vessel in rice. Compant et al. (2005b,

2008) confirmed this process of penetration of *B. phytofirmans* strain PsJN in grapes. This phenomenon holds good for most of the endophytic bacteria colonising internal tissues of the root. Further James et al. (2002), Compant et al. (2005) and Gasser et al. (2011) opined that the piercing of endodermis in the root zone of crop plants to gain an entry into xylem vessels could be possible for only a small number of species of endophytic bacteria. Reviews revealed that, despite the endophytic bacteria reaching the root xylem vessels passing all hurdles, the inducement of defence mechanism in the host plants by the bacteria is significant for colonisation in internal tissues (Rosenblueth and Martínez-Romero 2006). James et al. (2002), Compant et al. (2005b) and Miché et al. (2006) reported that the defence mechanism could result in cell walls of plants getting strengthened and the materials encircling the xylem vessel got established besides the development of gum inside the tissues of xylem.

Sattelmacher (2001) and Bacon and Hinton (2006) argued that the nutrient availability is enough to facilitate the growth of endophytic bacteria though its availability is minimal in xylem which has been evidenced from several radioactive labelling experiments in potato plants with $13CO_2$ which detected the isotope in photosynthetic metabolites and in varied bacterial endophytes (Rasche et al. 2009). Malfanova et al. (2013) found that the endophytic bacteria available in the root zone of cucumber was able to make use of Larabinose, a predominantly available sugar found in xylem fluid of an array of plants which is very much differing with *Pseudomonas* spp. found in other crops. Bartz (2005) contemplated the movement of beneficial endophytic bacteria and reported that these bacteria could move from one to another xylem element through perforated plates. This mechanism does not involve the enzymes catalysing the dissolvement of cell walls as the sizes of the holes in the plates were large enough to push the bacteria inside xylem vessels. Further work of James et al. (2002) and Compant et al. (2005b) who tracked the movement of endophytic bacteria reported the involvement of bacterial flagella to further aid their migration into the tissues of plants.

1.4.2 Colonisation of Endophytic Bacteria in Vegetative and Reproductive Parts of Plants

The inflorescence and fruits of some plants were reported to harbour endophytic bacterial species according to the studies of Mundt and Hinkle (1976) as well as Misaghi and Donndelinger (1990). Endophytic bacterial species could be found in seeds of rice according to Okunishi et al. (2005). Cankar et al. (2005) and Barac et al. (2004) were able to isolate the species of endophytic bacteria, namely, *Pseudomonas* and *Rahnella*, from seeds of Norway spruce and yellow lupine.

Compant et al. (2008) in their experiment in cv. Chardonnay grapevine variety, after application of *B. phytofirmans* strain PsJN in soil, observed that the endophytic bacterial species was found to move from roots to flowers and tried to colonise in aerial parts of the grapevine. Graner et al. (2003), Okunishi et al. (2005), Furnkranz et al. (2012) and Compant et al. (2011) offered credible evidence of presence of endophytic bacterial species in reproductive organs of plants including inflorescence, seeds and fruits which were confirmed through isolation and microscopic observation.

1.5 Biocontrol Mechanisms Exhibited by Endophytic Bacterial Strains

The mode of action of endophytic bacterial strains has been enunciated by various researchers, and voluminous literature is available on this aspect. An attempt has been made to classify those mechanisms and detailed in the following section.

1.5.1 Competitive Root Colonisation

The applications of biocontrol agents resulted in the competition of the microbes present in biocontrol agents and the microflora already existing in the soil. The potential of the endophytic bacteria depends on, over a period of time, how efficient the colonisation happens in the root zone, the ability of them to survive the competition and their multiplication all through the tissues of roots (Whipps 1997). There are certain traits which facilitate competitive root colonisation, namely, differential phase of growth, ability to stick onto the roots, ability to move, effective use of the organic acids present in root exudates and the synthesis of various components including amino acids, type III secretion system (TTSS), lipopolysaccharides, nucleotides, etc. (Lugtenberg and Kamilova 2009).

The efforts of scientists to untangle the mechanism with which the endophytic bacteria safeguard plants from various diseases resulted in significant findings. Especially plant growth-promoting bacteria (PGPB) dwelling in the rhizosphere have been identified by many researchers as protectors of plants from various diseases. It has been observed by researchers that the epidermis of the root harbours lot of nutrients which pull a large variety of microorganism including the ones which cause diseases also. The hectic competition which persists among beneficial and harmful microorganisms for food resulted in the inhibition of disease-producing microorganism to inflict diseases in plants. There were reports which indicated the role of flagella in the migration of PGPB towards the nutrient-rich root surfaces, and these PGPB were adept in making use of the nutrients which are primarily the root exudates oozing from root surfaces (Duffy 2001; Turnbull et al. 2001).

1.5.2 Competition for Ferric Iron Ions

Iron is an important element of survival of microorganisms which is in high demand as mostly the iron exists in unavailable form in root zone. Studies of Loper and Henkels (1997), Whipps (2001) reported the emitting of siderophores by plant growth-promoting bacteria, a compound with lesser molecular weight, which facilitated the PGPB to effectively attain the iron in the ferric ion which will be easily available to them. He further elaborated that notwithstanding the effectiveness of siderophores produced by bacterial species varied in gaining iron, their presence will check the fungal pathogens to make use of siderophores which endanger the disease-producing pathogen by making them starve for iron which is an important element for survival. This mechanism has been very much observed in the suppression of *Erwinia carotovora* through application of *P. fluorescens*, an endophytic bacterium which actively competes with the pathogen for bioavailable iron.

1.5.3 Competition for Nutrients and Niches (CNN)

There were several benefits for those endophytic bacteria controlling disease causing pathogens through the mechanism of competition for nutrients and niches. The foremost benefit is that this mechanism is being liked by researchers as the bacterial strains which possess these mechanisms can easily be selected for experiments. Secondly, the endophytic bacteria classified under CNN are not known for production of antibiotics, which facilitates their registration by regulatory authorities, as usually the antibiotic-producing microbes are not preferred to be allowed into soil environment. Thirdly, supposing a situation has arisen wherein the merger of the two mechanisms, namely, CNN and production of antibiotics, is preferred, the bacterial strains which are known for exhibiting both the mechanisms can be isolated and utilised for experiments (Malfanova 2013). This combination of mechanism was demonstrated by Pliego et al. (2008) who recorded the suppression of root rot disease in avocado through the combination of these mechanisms.

1.5.4 Antibiosis and Antibiotics Suppressing Pathogens

Antibiosis is an important mechanism which was reported to curtail the growth of pathogens in crop plants, and several researchers worked on this mechanism and tried to demystify the processes involved in it. Antibiosis is the process of the release of secondary metabolites like antibiotics and other volatile compounds by the beneficial microorganism to check the pathogenesis of disease producing microorganisms (Fravel 1988).

Haas and Défago (2005) highlighted the antibiotics like volatile HCN, phenazines and pyoluteorin which are responsible for antibiosis. Later, Dandurishvili et al. (2011) have identified newer antibiotics, namely, D-gluconic acid, 2-hexyl-5-propyl resorcinol and the volatiles 2,3-butanediol, 6-pentyl-α-pyrone and DMDS which are produced by endophytic microbes facilitating faster antibiosis.

Tabbene et al. (2009) reported that *Bacillus* species could produce peptide antibiotics in abundance, whereas Zhang et al. (2013) found out that *Bacillus* species could synthesise volatile compounds with lesser molecular weight and several lipopeptides with specific activities against phytopathogenic fungi. Among these lipopeptides, surfactin, fengycin, polymyxin, bacitracin and the group of iturin can elicit relevant properties (Ongena and Jacques 2008). The lipopeptides' structural differences are strongly related to their antifungal and antibacterial activities (Ramkumar et al. 2013). Thus, fengycin and iturin are known for having antifungal activities (Savadogo et al. 2011).

The effectiveness of iturins to suppress the bacterial pathogens causing diseases was studied by Zeriouh et al. (2011) who recorded the reduced incidence of *Pectobacterium carotovorum* and *Xanthomonas campestris* by the antibiosis of iturins. Fengycin, yet another antibiotic produced by bacterial endophytes, could be observed in apple plant and found to be useful in checking the population of *Botrycis cinerea* (Toure et al. 2004). The role of fengycin in reducing the incidence of brown rot in peach was reported by Yanez-Mendizábal et al. (2011).

Bais et al. (2004) found that surfactin, an antibiotic known for the control of plant pathogens, was found to be effective against *Pseudomonas syringae* on *Arabidopsis*. Ongena et al. (2007) and Henry et al. (2011) were the researchers who tried to find the combination of fengycin and surfactin in suppressing plant pathogens and reported that in bean and tomato plants, these two antibiotics could be able to prompt the various pathways responsible for resistance to diseases. Consortia of antibiotics including surfactin, iturin and fengycinin were observed to be produced by endophytic bacterial species *Bacillus* species PGPBacCA1 in soybean to suppress the growth of pathogen producing charcoal rot (Torres et al. 2016).

Dwivedi and Johri (2003) identified another group of antibiotics, phloroglucinols, which could strengthen the defence mechanism of plants by way of serving as elicitor of phytoalexins. Plenty of literature supported the ability of phenazines, a heterocylic secondary metabolite, as antibiotic which can lessen the virulence of pathogens in plants (Pierson and Pierson 2010). Phenazine-1-carboxamide, phenanazine-1-carboxylic acid and phenanzine-1-carboxamide are some of the phenazine compounds released as antibiotics in plant system and reported by researchers to control *R. solani*, *X. oryzae* in rice and *P. myriotylum* in cocoyam and *P. splendens* in beans (Pierson and Thomashow 1992; Perneel et al. 2008; Shanmugaiah et al. 2010). The scientists have observed endophytic bacterial species *P. fluorescens*, *P. chlororaphis* and *P. aeruginosa* PNA1 in the plants which were reported to produce the various phenazine compounds.

Pyrrolnitrin, cyclic lipopeptides and massetolides are the antibiotic substances produced by a wide range of endophytic bacterial species. Pyrrolnitrin could suppress a wide range of fungal pathogens belonging to three fungal families, namely, deuteromycete, ascomycete and basidiomycete. Massetolide could facilitate biofilm formation which is an important defence mechanism towards plant pathogens. *P. fluorescens* BL915, *P. fluorescens* SS101 and various *Pseudomonas* strains were found to be responsible for the production of these antibiotics (Ligon et al. 2000; Katz and Demain 1977; de Bruijn et al. 2008).

Phenols are another group of antibiotics involved in antibiosis in crops and reduced the incidence of plant diseases. Saidul et al. (2001) reported about the formation of 2-acetamidophenol catalysed by *Pseudomonas fluorescens* strain 2–79 (NRRL B-15132) which could lessen the virulence of most of the disease-causing pathogens in wheat. Salicylic acid, yet another phenolic derivative, was reported to inhibit plant pathogens by serving as a messenger (Wildermuth et al. 2001). The research work of Liechti and Farmer (2002) and Diaz et al. (2003) brought to light another phenolic compound, jasmonic acid, which can suppress pathogens by way of regulating and mediating the response of plants to pathogens.

Gao Zhenbeng et al. (2017) reported that volatile organic compounds pyrazine (2,5-dimethyl), benzothiazole, phenol (4-chloro-3-methyl) and phenol-2,4-bis (1,1-dimethylethyl) from *Bacillus velezensis* ZSY-1 exhibited significant antifungal activity against *Alternaria solani*, *Botrytis cinerea*, *Valsa mali*, *Monilinia fructicola*, *Fusarium oxysporum* f. sp. *capsicum* and *Colletotrichum lindemuthianum* and the inhibition rates were found to be 81.1%, 93.8%, 83.2%, 80.9%, 76.7% and 70.6%, respectively.

1.6 Plant Growth Promotion

Endophytes were found to accelerate plant growth through a plethora of mechanisms. It includes primarily phytostimulation (e.g. by hormone production) followed by biofertilisation (e.g. by fixation of atmospheric nitrogen, solubilisation of minerals such as phosphorus and formation of siderophores to scavenge Fe3+ ions under Fe3 + −limiting conditions). The third mechanism is the induction of stress tolerance (e.g. by regulation of the release of quantity of stress hormone by the enzyme 1-aminocyclopropane-1-carboxylate deaminase), and the fourth mechanism is the rhizoremediation (i.e. protection of plants by rhizobacteria against environmental pollutants).

Lugtenberg et al. (2013) reported the production of hormones by bacteria like ethylene, cytokinins, gibberellins, auxins, etc. Majority of rhizosphere bacteria are found to produce auxins which are very much important for lateral root formation (Pliego et al. 2011). Spaepen et al. (2009) in their paper published in *Annals of Botanical Research* explained about different pathways of synthesis of plant growth-promoting hormones. They reported the secretion of tryptophan, a constituent of exudates of roots, as the antecedent for the initiation of synthesis of indole acetic acid pathway which is being utilised by the bacteria present in the root zone. This view of Spaepen et al. (2009) was confirmed by the study of Kamilova et al. (2006) who found that the growth of radish got enhanced through tryptophan-induced IAA secretion from a bacterial strain WCS365 of *P. fluorescens* which has increasingly been recommended for biological control of diseases. Further, it was recorded by Spaepen et al. (2009) that IAA production was enhanced due to the presence of *Azospirillum brasilense* which spiked the formation of lateral roots and root hair formation ultimately resulting in increased production of exudates from roots.

Numerous rhizosphere bacteria are reported to produce gibberellins (Pliego et al. 2011) which are responsible for cell division, cell elongation and seed germination. The studies carried out by researchers to analyse the growth promoting ability of bacteria living in the root indicated the secretion of growth promoting substances, namely, cytokinin, GA, acetoin and 2,3-butanediol, by *Acinetobacter calcoaceticus*, *Bacillus* spp. and other rhizosphere-dwelling bacterial species in various crops including cucumber, Chinese cabbage, etc. (García de Salome et al. 2001; Kang et al. 2009; Ryu et al. 2003).

Hardoim et al. (2008) documented an array of bacteria in the root zone which were found to produce an enzyme called 1-aminocyclopropane-1-carboxylate deaminase which was responsible for removing stress induced in crop plants due to the production of ethylene as a result of various biotic and abiotic stresses in crop plants. According to Ryu et al. (2003) endophytic bacteria secrete some volatile compounds, namely, acetoin and 2,3-butanediol, to enhance the growth of plants in general. Genomic sequencing of *Enterobacter* sp. 638 indicated the production of such components in poplar, a biofuel feedstock plant, which was helpful in the availability of sucrose facilitating the production of phytohormones which could enhance growth of plants (Taghavi et al. 2010).

Many of the endophytic bacterial strains were found to facilitate the availability of nutrients like nitrogen and phosphorus to the plants via soil. Vendan et al. (2010) and Shcherbakov et al. (2013) reported the ability of endophytic bacteria to fix atmospheric nitrogen in plants. Phosphorus is an important growth-promoting nutrient for various crops whose availability is a biggest problem, and whatever phosphorus applied to soil in organic or inorganic form could not be readily taken by the plants. Researchers have been able to isolate the endophytic bacterial species which are useful in converting the unavailable nutrients into available form. Studies indicated that phosphate-solubilising *Pseudomonas* spp., *Bacillus megaterium* and *Bacillus* spp. were found to provide phosphorus in available form and increased the growth and yield of maize, sugarcane and canola, respectively (De

Freitas et al. 1997; Sundara et al. 2002; Rodriguez et al. 2006; Vyas and Gulatti 2009; Smyth 2011).

Reinhold-Hurek and Hurek (1998) in their research paper in *Trends in Microbiology* detailed the role of siderophores as a response to overcome iron-limiting conditions in plants which was reported in many studies. It was found that endophytic bacteria could synthesise siderophores to cope with microenvironments such as the root interior which is highly depleted of bioavailable iron. Several reports indicated production of siderophores by bacterial species may affect iron plant nutrition. For example, Becker et al. (1985) reported that iron uptake in pea (*Pisum sativum* L.) and maize (*Zea mays* L.) is inhibited when purified pseudobactin is applied to plants. In peanuts (*Arachis hypogaea* L.) amendment with Fe^{3+} pseudobactin resulted in lime-induced chlorosis amelioration (Jurkevitch et al. 1998).

Iron availability to plants grown in hydroponics and pot culture was also facilitated by endophytic bacterial strains. Duijff et al. (1994) observed that the plants could make use of Fe^{3+} –pseudobactin-358 which also enhanced the synthesis of chlorophyll in plants. Sharma et al. (2003) conducted a pot experiment in mung bean (*Vigna radiata* L. Wilczek) inoculated with *Pseudomonas* sp. strain. The bacterial strain was able to synthesise siderophore which was reported to enhance the iron available to the plant system which could increase the level of chlorophyll and reduction of chlorosis in bean plants.

Pirttila et al. (2004) reported the ability of endophytic bacterial species to provide necessary vitamins to crops which can enhance the growth of crops. Compant et al. (2005) identified several physiological processes which were catalysed by endophytic bacteria, thus improving the growth and yield potential of crops. In the leaves of plants, the endophytic bacterial species could facilitate adjustment of osmotic pressure and regulation of stomatal openings. In roots the bacteria could alter the biochemical processes of availability of nutrients to the plants. Besides, the role of endophytic bacteria for the remediation of polluted soils with heavy metals and regeneration of forest has been increased in the recent past, and there were several instances that endophytes are being used for such purposes.

1.7 Induced Systemic Resistance (ISR)

Resistance in crop plants for phytopathogens has been debated widely, and numerous research findings were evolved to decipher the mechanism. There was a consensus among researchers that induced systemic resistance (ISR) could be offered by microorganisms to combat pathogens. ISR is the immunity response mechanism inherent in crop plants which is triggered by the beneficial bacteria present in the rhizosphere such as *P. fluorescens* strains WCS417R and WCS365 (van Loon and Bakker 2003; Kamilova et al. 2005; Van Wees et al. 2008).

Stadnik (2000) defined ISR as the external agents mediating enhanced resistance and altering the genome of the plant. ISR is different from systemic acquired resistance (SAR) in several physiological and biochemical phenotypes (Van and Elsas 2008) and can be induced by many different bacterial surface molecules, secreted metabolites and volatiles (Lugtenberg et al. 2013). Examples of bacterial endophytes which have been suggested or claimed to induce ISR are *Bacillus amyloliquefaciens*, *Bacillus pumilus*, *Bacillus subtilis*, *Pseudomonas fluorescens*, *Pseudomonas syringae* and *Serratia marcescens* (Kloepper and Ryu 2006).

The plants which got immunised through ISR can guard the plants against a score of disease causing pathogens of different origins. In plants which possess stronger ISR, the response for defending the pathogens entering the plants used to be swifter which offers high level of resistance to the plant for diseases. Numerous studies portrayed the event of ISR in different crops inoculated with varied bacterial species dwelling in root zone (Van Peer et al. 1991; Liu et al. 1995; Raj et al. 2003; Halfeld-Vieira et al. 2006; Van Loon 2007).

Bonaldo et al. (2005) listed the advantages of ISR wherein they pointed out the efficiency against an array of pathogens, exhibition of varied resistance methods, efficient utilisation of energy and exploitation of genetic ability to induce resistance in the plants which are vulnerable for diseases. Several studies demonstrated that the different crop plants exhibit differential ISR and the efficiency also varied from plant to plant which was reported to be regulated by jasmonic acid and ethylene in most of the plants (van Wees et al. 2000; Van Loon and Bakker 2003). De Weert et al. (2007) reported that toll-like receptors were utilised by the ISR mechanism which was analogous to inherent immunity. Studies indicated that complete colonisation of bacteria in root zone is not necessary for initiation of ISR which indicated even partial colonisation can bring out ISR. Further, apart from living endophytic bacterial species, even dead microorganism can activate ISR (Dekkers et al. 2000). A long list of literature indicated that ISR can be activated through several compounds produced by endophytic bacteria like salicylic acid, c-LPs, pyocyanins, siderophores, etc. (Audenaert et al. 2002; Ryu et al. 2003; Schuhegger et al. 2006; Pérez-García et al. 2011).

Hallmann et al. (1995) reported that ISR mechanism was enhanced in plants treated with endophytic bacteria which resulted in enhanced protection against parasitic nematodes responsible for extensive damage to crops. They further stressed that a huge potential is there for researchers to venture into research linking ISR and plant parasitic nematode control in several crops.

Endophytic bacteria treated with chitosan, which is available in the cell wall of fungi, could accelerate the ISR which effectively check the growth of pathogens, and research studies involving such chemical elicitors for enhanced ISR in crops would pave way for designing disease management protocol with a combination of methods (Benhamou et al. 1998).

Induction of resistance promoted by plant growth-promoting rhizobacteria (PGPR) is active according to the researchers, Hoffland et al. (1995) and Pieterse et al. (1998) and Romeiro (2000); the ISR is facilitated via production of salicylic acid with induction of PR proteins via the production of the jasmonic acid and ethylene. They further explained the process that during the colonisation of endophytic bacteria in the rhizosphere region, the elicitors produce certain bacterial molecules which served as biochemical signal which culminates in the encoding of genes responsible for these processes and the ISR is initiated in the plant. Wei et al. (1991) who worked on the plants exhibiting ISR reported that cucumber is the best example of exhibitor of ISR mechanism and demonstrated the suppression of anthracnose caused by *Colletotrichum orbiculare* through the activation of ISR.

Chen et al. (2000a, b) and Saikia et al. (2004) contemplated that the formation of enzymes like peroxidases, lipoxygenases, chitinases and glucanases which are responsible for the inhibition of the growth of pathogens is the forte of the qualities of endophytic bacterial species. The scientists recorded the production of the enzymes like peroxidases in cucumber plant effectively reduced the incidence of *Pythium aphanidermatum*, and similar mechanism was observed by Young et al. (1995) in rice and wheat. Yet another mechanism indicated by Li et al. (1991) was the induction of phytoalexins enhanced by the formation of the enzyme called lipoxynase which was inhibitory to the incidence of diseases. Daniel and Purkayastha (1995), Nakkeeran et al. (2006) and Saikia et al. (2006) in their research papers emphasised that the more production and involvement of enzymes, the more would be the ISR, ultimately resulting in pathogenesis which differed based on the nature of host and disease-inflicting pathogens.

1.7.1 Signal Interference

Dong et al. (2004) identified a mechanism wherein the production of exoenzymes could be controlled by inactivating the N-acyl homoserine lactone molecule which is essential for exo-enzyme production. Dandurishvili et al. (2011) reported the control of crown gall disease in tomato inflicted by the pathogen *Agrobacterium* through reduction of transcription of N-acyl homoserine lactone synthase genes *phzI* and *csaI* activated by root zone bacterial strains *P. fluorescens* B-4117 and *S. plymuthica* IC1270.

1.7.2 Detoxification and Degradation of Virulence Factors

Detoxification of toxins secreted by pathogens would serve as a way to suppress the activity of pathogens which has been displayed by several endophytic bacteria (Compant et al. 2005). Toyoda and Utsumi (1991) reported that fusaric acid, a toxin secreted by *Fusarium* species, a major wilt-causing pathogen, could be suppressed by the endophytic bacterial strains of *B. cepacia* and *Ralstonia solanacearum.*

Compant et al. (2005) reported that the virulence factor of pathogens could be deprived by some of the endophytic bacteria. Uroz et al. (2003) discussed about the quorum-sensing capacity of bacterial endophytes through inhibiting the expression of genes responsible for virulence of pathogens. Von et al. (2003) remarked that autoinducer-mediated quorum- sensing is an important mechanism that has been relied upon by the pathogens as this mechanism could bring down the virulence of pathogen to inflict diseases. This mechanism has been considered to be of paramount importance since the pathogen could be taken cared of by the mechanism of quorum-sensing after the pathogen gets established in the plant system.

A summary of the literature pertaining to the mode of action of endophytic bacteria is provided in Table 1.1 for better understanding of readers.

Table 1.1 Summary of mode of action of endophytic bacteria

Broad mode of action	Mechanism involved	References
Competitive root colonisation	Differential phase of growth, ability to stick onto the roots, ability to move, effective use of the organic acids present in root exudates and the synthesis of various components including amino acids, type III secretion system	Whipps (1997), Lugtenberg and Kamilova (2009), Duffy (2001) and Turnbull et al. (2001)
Antibiosis and antibiotics suppressing pathogens	Production of antibiotics like phenazines, pyoluteorin, pyrrolnitrin and the volatile HCN	Gupta et al. (2001), Fravel (1988), Haas and Défago (2005), Dandurishvili et al. (2011), Tabbene et al. (2009), Zhang et al. (2013), Ongena and Jacques (2008), Ramkumar et al. (2013), Caldeira et al. (2011), Savadogo et al. (2011), Zeriouh et al. (2011), Touré et al. (2004), Yánez- Mendizábal et al. (2011), Ongena et al. (2007); Henry et al. (2011), Torres et al. (2016), Dwivedi and Johri (2003), Pierson and Pierson (2010), Shanmugaiah et al. (2010), Pierson and Thomashow (1992), Perneel et al. (2008), Ligon et al. (2000), Katz and Demain (1977), Wildermuth et al. (2001), Liechti and Farmer (2002), Diaz et al. (2003) and Gao Zhenbeng et al. (2017)
	Production of antibiotics, namely, D-gluconic acid, 2-hexyl-5-propyl resorcinol and the volatiles 2,3-butanediol, 6-pentyl-α-pyrone and DMDS	
	Among lipopeptides, surfactin, fengycin, polymyxin, bacitracin and the group of iturin can elicit relevant properties of disease control	
	Production of phloroglucinol, pyrrolnitrin, phenols and volatile organic compounds like pyrazine (2,5-dimethyl), benzothiazole, phenolic derivatives	
Signal interference	Inactivation of AHL molecule required for exo-enzyme production	Dong et al. (2004) and Dandurishvili et al. (2011)

(continued)