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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R. A. Ansari, I. Mahmood (eds.), *Plant Health Under Biotic Stress*,
https://doi.org/10.1007/978-981-13-6040-4_1

Keywords Endophytic bacterial diversity · Colonisation · Mode of action · Plant disease control

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)

Table 1.1 (continued)

Broad mode of action	Mechanism involved	References
Competition for ferric iron ions	Production of siderophores to catch hold of ferric ion and to deprive the pathogens for iron	Loper and Henkels (1997) and Whipps (2001)
Competition for nutrients and niches (CNN)	The mechanism involved in competitive root colonisation applies for CNN also	Pliego et al. (2008) and Malfanova (2013)
Detoxification and degradation of virulence factors	Fusaric acid detoxifies the toxins produced by pathogens.	Toyoda and Utsumi (1991), Uroz et al. (2003), Von et al. (2003) and Compant et al. (2005)
	Quorum-sensing ability by degrading autoinducer signals, thereby inhibiting expression of numerous virulence genes	
Induced systemic resistance (ISR)	Resistance induced by the production of salicylic acid, c-LPs, pyocyanins, siderophores, etc.	Li et al. (1991), Wei et al. (1991), Van Peer et al. (1991), Daniel and Purkayastha (1995), Young et al. (1995), Hoffland et al. (1995), Hallmann et al. (1995), Liu et al. (1995), Van Wees et al. (1997), Benhamou et al. (1998), Pieterse et al. (1998), Romeiro (2000), Chen et al. (2000a, b), van Wees et al. (2000), Dekkers et al. (2000), Audenaert et al. (2002), Stadnik (2000), Iavicoli et al. (2003), Ryu et al. (2003), Van Loon and Bakker (2003), Raj et al. (2003), Silva et al. (2004), Kloepper et al. (2004), Saikia et al. (2004), Campos et al. (2004), Kamilova et al. (2005), Halfeld-Vieira et al. (2006), Saikia et al. (2006), Kloepper and Ryu (2006), Schuhegger et al. (2006), Nakkeeran et al. (2006), de Weert et al. (2007), Ongena et al. (2007), van Loon (2007), Van Wees et al. (2008), Van and Elsas (2008), Pliego et al. (2011) and Pérez-García et al. (2011)
	Combined application of endophytic bacteria and chemical elicitors such as chitosan, a chitin derivative, will enhance ISR	
	Increased production of peroxidases, PPO and PAL enhances ISR	
	The action of lipoxygenase products which contributes to induction of phytoalexins	

1.8 Endophytic Bacteria Suppressing Wilt-Causing Pathogen in Plants

Among the diseases, wilt is a prominent disease caused by pathogens of fungal and bacterial origin which could bring huge economic loss to the farmers. The prominent fungal pathogens causing wilt are *Fusarium* and *Verticillium* species, the control of which is onerous since these pathogens are soilborne. Often, the chemical measures to control wilt do not bear fruit as the pathogen has a wide range of host and sustained in soil for a very long time. Hence, the biological control of wilt assumed greater importance which resulted in many scientists venturing into the research on finding suitable endophytic bacteria to control wilt diseases.

A number of studies showed endophytic bacteria were reported to suppress the growth of wilt-producing pathogen in cotton. Lin et al. (2013) conducted a pot experiment with 60 strains of endophytic bacteria isolated from *Sophora alopecuroide* to control *Verticillium* wilt (*Verticillium dahliae*), and the mean control effect of two strains, namely, *Bacillus subtilis* KDRE01 and *Bacillus megaterium* KDRE25, was worked out. The results indicated that the mean control effect of the two endophytic bacteria was 84.91% and 78.82%, respectively, and the strains differed significantly at 5% level of significance.

Chen et al. (1995) reviewed earlier studies on cotton involving endophytic bacterial strains, *Aureobacterium saperdae*, *B. pumilus*, *Burkholderia solanacearum*, *Phyllobacterium rubiacearum* and *Pseudomonas putida*, which were isolated from internal tissues of cotton and were found to suppress vascular wilt in cotton caused by *F. oxysporum* f. sp. *vasinfectum*.

Xia et al. (1996) observed that the endophytic bacteria had more potent antagonistic activity against *V. dahliae* than the rhizosphere bacteria and elicited induced response in cotton against wilt pathogen, and the findings were endorsed by Fu et al. (1999a, b), and reported the toxin produced by *V. dahliae* was effectively suppressed by antagonistic activity of endophytic bacteria.

Sturz et al. (1999) reported that the disease causing wilt pathogens, namely, *F. avenaciarum, F. sambucinum* and *F. oxysporum*, were found to be controlled by endophytic bacteria isolated from potato tubers. Further in vitro antagonism was exhibited by endophytic bacteria isolated from live oak stems which could lessen the virulence of *C. fagacearum* (Brooks et al. 1994).

Amaresan et al. (2014) in their study in chillies pertaining to the isolation and characterisation of endophytic bacteria on chilli diseases found that the antagonistic activity against *Fusarium oxysporum* was to the tune of 37.8%. In the study the authors could identify the ability of bacterial isolates BECS7, BECS4 and BECL5 in terms of catalysing the growth, suppressing the pathogenesis and promoting enhanced yield. Further the authors argued that the bacterial strains that produced different hydrolytic enzymes, such as protease, had inhibited the growth of pathogenic fungi *F. oxysporum*. Besides reducing the pathogenesis of *Fusarium oxysporum*, the proportion of endophytes was found to enhance the germination potential of seed and crop growth. These findings were in line with the results reported by Nielson and Sorensen (1999) in their study on barley and sugar beet and Nejad and Johnson (2000) in oilseed rape and tomato.

Literature on application of endophytic bacteria in isolation was found to arrest the growth of *Fusarium* minimally, and it was suggested by several researchers to use a combination of endophytic bacteria which yielded desired results. Smith et al. (2003) in their study on management of *Fusarium* wilt in banana using bacterial endophytes reported that de-flasking stage was optimal for allowing the bacterial strains. In their study, they found that under greenhouse conditions, the incidence of

Fusarium oxysporum f. sp. *cubense* was found to be reduced through the application of two strains of *Pseudomonas* 84 and 4B into the rhizosphere of banana.

Similarly, studies conducted by Ayyadurai et al. (2006) and Getha et al. (2005) using singular soil antagonistic bacteria *Pseudomonas fluorescens*, *P. aeruginosa*, *Burkholderia cepacia* and *Streptomyces* sp. to investigate the efficiency of bacterial species for the suppression of the *Fusarium oxysporum* f. sp. *cubense* did not result in complete control of the disease. Earlier Guetsky et al. (2001) also advocated through their studies that combination of biocontrol agents with multiple traits could be very useful to combat the biotic and abiotic stress in the field.

Taking a cue from these studies recommending the use of combination of bacterial isolates, Thangavelu and Gopi (2015) conducted a study to evaluate the effectiveness of bacterial isolates in suppressing of *Fusarium* wilt in cv. Grand Naine banana. The authors of the study took 24 different combinations of both rhizospheric and endophytic bacterial isolates, and they conducted experimental trials in pot culture. Results of the study indicated that five combinations involving four endophytic bacterial isolates, namely, *Pseudomonas putida*, *Acromobacter* spp., *Rhizobium* spp. and *Bacillu*s *flexus*, and two bacterial isolates live in the root zone of plants, namely, *Bacillus cereus* and *Pseudomonas putida*, were reported to control the *Fusarium* wilt fully. The study was conducted in the field with the same set of treatment wherein the bacterial isolates were applied in the soil and the data were recorded. The field study results indicated that the same five combinations which were found to be effective in controlling *Fusarium* wilt in pot culture experiments were also effective in field conditions. Bunch weight and number of banana hands were the yield parameters estimated in the study. The data pertaining to these two parameters indicated that the average number of banana hands increased up to 155% and average bunch weight increased up to 214% when compared to control.

Sundaramoorthy et al. (2012) conducted a similar study in chilli pepper using the combinations of rhizospheric and endophytic bacterial strains for the control of *Fusarium* wilt incidence. They found that endophytic bacterial strain *P. fluorescens* (Pf1) and rhizospheric bacterial strains *B. subtilis* (EPCO16 and EPC5) were found to reduce the incidence of wilt in the range of 17% to 30% when compared to control. The reports of Ganeshmoorthi et al. (2008) and Latha et al. (2009) were in conformity with their previous researchers who reported that combination of biocontrol agents would be more effective in controlling plant diseases rather than a single biocontrol agent.

Nagarajkumar et al. (2004) indicated that the wilt pathogens, *F. oxysporum* and *R. solani*, could be effectively controlled by the application of *Pseudomonas* strains through the formation of secondary metabolites, enzymes and siderophores which were produced in abundance.

Wang et al. (2013) investigated the antagonistic ability of *Bacillus amyloliquefaciens* W19 on *Fusarium* wilt of banana and reported that W19 strain was found to observably suppress *Fusarium* wilt and enhance the development of banana plants when combined with the organic fertiliser (OF). Two kinds of antifungal lipopeptides (iturin and bacillomycin D) produced by W19 strain were detected and identified using HPLC-ESI-MS. Another lipopeptide, called surfactin, was also produced by the thick biological film forming W19 strain. In addition to lipopeptide, 18 volatile antifungal compounds with significant antagonistic effect against *F. oxysporum* were detected and identified.

Many research studies conducted in tomato revealed that different endophytic bacterial isolates were found to control the *Fusarium* and *Verticillium* wilt of tomato. Endophytic bacteria *Bacillus* sp. could be able to control *V. dahliae* and *F. oxysporum* f. sp. *lycopersici* in rape and tomato plants, respectively. They found that *Bacillus* sp. could inhibit mycelial growth and reported 75% reduction in infection. Further, they reported production of volatile metabolites other than hydrogen cyanide. *Pseudomonas* sp. strain PsJN was reported to enhance resistance against *Verticillium* wilt in tomato up to 5 weeks (Hall et al. 1986; Sharma and Nowak 1998; Nejad and Johnson 2000).

M'Piga et al. (1997) studied the suppression of *F. oxysporum* f. sp. *radicis-lycopersici* by *P. fluorescens* in tomato. While explaining the mode of action, they reported the combined effect of structural and biochemical barriers to the growth of plant pathogens suppressing the incidence.

Duijff et al. (1997) confirmed the control of *Fusarium* wilt in tomato by *P. fluorescens* WCS417r and found that colonisation of epidermal or hypodermal cells or cortical intercellular spaces by WCS417r led to the thickening of cortical cell walls in tomato plants which checks the entry of pathogen producing *Fusarium* wilt. Another study which used *B. pumilus* SE-34 for the reduction of pathogenesis of *F. oxysporum* f. sp. *radicis-lycopersici* in tomato provided evidence of suppression of the wilt-producing pathogen through induction of resistance either alone or in combination with chitosan (Benhamou et al. 1998).

Endophytic bacteria from *Datura stramonium* could be used as an effective suppressor of *Fusarium* wilt in tomato as reported by Abdallah et al. (2016). The authors of the study screened ten bacterial isolates from *D. stramonium* for the containment of *Fusarium* wilt in tomato which is inflicted by the pathogen *Fusarium oxysporum* f. sp. *lycopersici* (FOL) and to accelerate the growth. The study revealed that the bacterial isolates S37 and S40 were found to reduce the leaf yellowing symptom within the range of 88% to 94%. There was 95–96% reduction in vascular browning due to the effect of these bacterial isolates juxtaposing the data from untreated control.

Vitullo et al. (2012) studied the mechanisms of BO7, a strain of *Bacillus amyloliquefaciens* taken from orchard soil, to reduce the incidence of vascular wilt fungus *Fusarium oxysporum* f. sp. *lycopersici* (FOL) and reported that three of the surfactin lipopeptides which are similar in structure were involved in the antibiosis. Further the study results revealed that one of the three compounds was found to possess huge antifungal properties to control FOL.

Realising the scope of *B. amyloliquefaciens* claimed to possess extensive antagonistic potential against pathogens which has been documented by several researchers (Zouari et al. 2016; Chen et al. 2016), Shahzad et al. (2017) did experiment the antagonistic potential of *B. amyloliquefaciens* RWL-1 on the *Fusarium* wilt of tomato (*Fusarium oxysporum* f. sp. *lycopersici*). The in vitro experimental study involving the dipping of tomato roots in bacterial culture revealed that *B. amyloliq-*

uefaciens RWL-1 could not only suppress the pathogenic fungal growth significantly but also reduced the incidence of disease symptoms in the field.

The authors of this study found that the introduced RWL-1 could produce bioactive constituents, siderophores and organic acids, which could assist plants to counteract disease-induced stress. The study results also found that RWL-1 inoculation increased the production of plant defence hormones like salicylic acid, which was not observed in control. Further amino acids like glutamic acid and aspartic acid were produced in abundance in RWL-1-inoculated plants in comparison to the control. The study results were in line with the findings of Pratelli and Pilot (2014), Khan et al. (2015), Waqas et al. (2015) and Shahzad et al. (2016).

A summary of the literature pertaining to the endophytic bacteria controlling wilt-producing pathogens is provided in Table 1.2 for better understanding of readers.

1.8.1 The Endophytic Bacterial Cultures Suppressing the Pathogens of Damping Off and Rot

Damping off and rot are the important soilborne diseases caused by fungal pathogens, and their inhibition by endophytic bacteria through various mechanisms has been studied by researchers. A nutshell of literature is given in the following section.

1.8.2 Endophytic Bacteria Controlling Damping Off

Melnick et al. (2008) tested four *Bacillus* spp. to assess their efficacy in restricting the pathogen *Phytophthora capsici* which caused damping off in cacao seedlings. The study results revealed that two species, namely, *B. cereus* BT8 and BP24, applied with a surfactant were found to significantly reduce the incidence of the disease.

Muthukumar et al. (2010) to assessed the efficacy of ten endophytic isolates of *Pseudomonas fluorescens* to control damping-off disease in chillies caused by *Pythium aphanidermatum.* Among the ten isolates tested, *P. fluorescens* EBS 20 was found to produce bigger inhibition zone, and the mycelial growth in petridish was minimal. Further, the authors found that the inhibition of damping-off disease could be mainly attributed to the secretion of salicylic acid, siderophore and hydrogen cyanide in abundance by *P. fluorescens* EBS 20 which are known for blocking the incidence of diseases and progression of symptoms. These findings were cor-

Table 1.2 Endophytic bacteria and wilt disease control

S. No	Crop	Pathogens causing wilt	Endophytic bacteria reported to control/reduce wilt incidence	Mode of action	References
1.	Tomato	*Verticillium dahliae* *F. oxysporum* f. Sp. *lycopersici* *F. oxysporum* f. Sp. *radicis-lycopersici*	*Pseudomonas* sp. strain PsJN *P. fluorescens* WCS417r *B. pumilus* SE-34 *Bacillus amyloliquefaciens* BO7 *B. amyloliquefaciens* RWL-1	Production of volatile metabolites. Combined effect of structural and biochemical barriers to reduce the pathogenesis. Effective colonisation and thickening of cortical cell walls in tomato plants. Induction of resistance either alone or in combination with chitosan. Antifungal action of surfactin lipopeptides. Combating effects of siderophores and organic acids. Production of plant defence hormones, jasmonic acid and salicylic acid which enhance ISR.	Hall et al. (1986), Nejad and Johnson (2000), Sharma and Nowak (1998), M'Piga et al. (1997), Duijff et al. (1997), Benhamou et al. (1998), Vitullo et al. (2012) and Shahzad et al. (2017)
2.	Cotton	*F. oxysporum* f. Sp. *vasinfectum* *Verticillium dahliae*	*Aureobacterium saperdae* *Bacillus pumilus* *Burkholderia solanacearum* *Phyllobacterium rubiacearum* *Pseudomonas putida* *Bacillus subtilis* KDRE01 *Bacillus megaterium* KDRE25	Antibiosis through production of antibiotic components. Inhibition of mycelial growth and toxin production causing wilt in cotton.	Chen et al. (1995), Lin et al. (2013), Xia et al. (1996) and Fu et al. (1999a, b)

(continued)

Table 1.2 (continued)

S. No	Crop	Pathogens causing wilt	Endophytic bacteria reported to control/ reduce wilt incidence	Mode of action	References
3.	Banana	*F. oxysporum* f. Sp. *cubense* race 4 *Fusarium oxysporum* f. Sp. *cubense*	*Burkholderia cepacia* *Pseudomonas* strains 84 and 4B *Pseudomonas putida strains* *Bacillus cereus* strains *Acromobacter* spp. *Bacillus cereus* *Bacillus flexus* strains *Rhizobium* spp. *Bacillus amyloliquefaciens* W19	Colonise hyphae of the fungus and its macrospores. Mycelial deformation with terminal and intercalary swellings resulted in reduced disease incidence. Secretion of secondary metabolites and siderophores which was reported to suppress pathogen growth. Thick biological film forming iturin and bacillomycin D and surfactin control growth of pathogen.	Pan et al. (1997), Smith et al. (2003), Thangavelu and Gopi (2015), Sundaramoorthy et al. (2012) and Wang et al. (2013)
4.	Chillies	*Fusarium oxysporum*	BECS7, BECS4 and BECL5 *P. fluorescens* (Pf1) *B. subtilis* (EPCO16 and EPC5) *Pseudomonas* spp.	Inhibition of pathogens through production of hydrolytic enzymes	Amaresan et al. (2014) and Sundaramoorthy et al. (2012)
5.	Potato	*F. Avenaciarum* *F. sambucinum* *F. Oxysporum*	*Bacillus* spp.	In vitro antibiosis	Sturz et al. (1999)
6.	Oak	*C. Fagacearum*	*P. denitrificans* and *P. putida*	In vitro antagonism and competitive colonisation of microbes	Brooks et al. (1994)
7.	Peas (*Pisum sativum* L.)	*F. oxysporum* f. Sp. pisi	*B. pumilus* strain SE34	Strengthening of the epidermal and cortical cell walls	Benhamou et al. (1996)

roborated with the similar findings of the authors. Muthukumar and Bhaskaran (2007) in yet another study screened 12 isolates of *P. fluorescens* and observed that isolates 3 and 4 were found to be very effective against *Pythium* spp. In a similar study carried out a little earlier by Nakkeeran et al. (2006), it was found that two endophytic bacterial strains, namely, *P. chlororaphis* strain PA23 and *B. subtilis* strain BSCBE4, were found to arrest the growth of *P. aphanidermatum*, the causal organism of damping-off disease in chillies.

The studies of Buysens et al. (1996) and Kraus and Loper (1992) reported that restricted growth of damping-off-producing pathogens in tomato and cucumber was attributed to the production of siderophore. The production of antibiotic components like polyphenol oxidase, peroxidases and phenylalanine ammonia-lyase as part of the mechanism of induced systemic resistance exhibited by bacterial species present in the rhizosphere is reported to be behind the suppression of damping off in cucumber caused by *Pythium aphanidermatum* (Chen et al. 2000a).

A study on biological control of damping off caused by *Rhizoctonia solani* in cucumber was taken up by Huang et al. (2012). The authors of the study used an endophytic bacterial strain, *Bacillus pumilus* SQR-N43, for the study. Two experiments were conducted in the study wherein the first experiment has seen the utilisation of only which was applied on the cucumber field. In the second experiment, the researchers added fermented organic fertiliser along with the *Bacillus pumilus* SQR-N43 and applied in the field. The observations were recorded after 20 days, and the results revealed that the second experiment involving the organic manure along with *Bacillus pumilus* SQR-N43 performed better than the first experiment which involves only *Bacillus pumilus* SQR-N43 in terms of number of CFUs, percentage of spores and control efficiency.

Fiddaman and Rossall (1993) and Yangui et al. (2008) observed hyphal vacuolisation and deformation in *R. solani* and in *Pythium ultimum* after treatment with a *B. subtilis* strain and *Bacillus* spp. which resulted in reduced growth of pathogen. Selim et al. (2017) evaluated the antifungal potentialities of three endophytic bacterial strains in greenhouse and found that a significant increase of seed emergence and seedling survival with a clear reduction of disease severity was achieved with the endophytic bacterial treatments.

1.8.3 Endophytic Bacteria Controlling Rot

Disease incidence (DI) (Campbell and Madden 1990) and disease severity (DS) (Liu et al. 1995) were studied in oil palm plants inoculated with two strains of endophytic bacteria, namely, *Burkholderia cepacia* (B3) and *Pseudomonas aeruginosa* (P3), for their ability to reduce the symptoms of basal stem rot caused by *Ganoderma boninense* (Sapak et al. 2008). The study revealed that these endophytic bacteria could keep the *G. boninense* incidence below threshold level through the inhibition of entry and movement of the pathogen into the plant. The epidemic rate of pathogens in treated and control field of 4-month-old oil palm fields was tested, and the results indicated that the selected bacterial species performed better in treated field either solitary or in combination. In 8-month-old oil palm fields inoculated with the two species of endophytic bacteria, the incidence of basal stem rot reduced to 76%. Similar results were already recorded by Dikin et al. (2003) in oil palm fields which were inoculated with the bacterial endophytes *P. aeruginosa* and *B. cepacia.*

Dikin et al. (2003) who recorded that combination of *P. aeruginosa* with *B. cepacia* was less effective than *P. aeruginosa* alone were found to be contradictory to the findings of Lemanceau et al. (1993), Pierson and Weller (1994) and Crump (1998). These researchers established that rather than solitary biocontrol agent, consortia of them would be more beneficial and effective in controlling plant diseases. The biocontrol agents are being tested for their antagonistic behaviour individually instead of testing in combination which was endorsed by earlier studies (Leeman et al. 1996; Meyer and Roberts 2002).

Barka et al. (2002) found *Pseudomonas* sp. strain PsJN, an endophytic bacteria found in onion, suppressed the incidence of *Botrytis cinerea* Pers. (*Botrytis* bunch rot) and enhanced vine growth in colonised grapevines. Jetiyanon (1994) reported that cabbage colonised by endophyte *Xanthomonas campestris* pv. *campestris* in the greenhouse could suppress the symptoms of black rot in the field which is facilitated by inducement of resistance mechanism. The progression of disease in treated field was slow when compared to non-treated fields. The antifungal activity of *B. lentimorbus* was studied, and the bacterium has been reported to produce the antifungal substances alpha- and beta-glucosidase and volatile substances which suppress the pathogenicity of *Botrytis cinerea* Pers. in grapevine and suppressed the development of *Fusarium sambucinum* Fuckel in potato tubers, respectively (Kim et al. 2002; Sadfi et al. 2001).

Torres et al. (2016) in their study, analysed the ability of endophytic bacteria *Bacillus subtilis* subsp. *subtilis* PGPMori7 and *Bacillus amyloliquefaciens* PGPBacCA1 strains against three fungal species of *M. phaseolina* causing the charcoal rot disease in soybean and identified three different mechanisms through which the pathogen get suppressed. They were cell suspension, production of cell-free supernatant and the secretion of lipopeptide fraction. Irrespective of the fungal strains, the mechanism of suspension of the cell wall was found to possess more than 50% of the suppressive ability for the charcoal rot disease in soybean than other mechanisms.

The virulence of *Colletotrichum gloeosporioides* the causal organism of anthracnose in strawberry was found to be drastically reduced by *Bacillus amyloliquefaciens* strain S13–3 (Yamamoto et al. 2015). Colonisation of black pepper vine with endophytic *Pseudomonas* species resulted in 90% reduction in lesion lengths and 60% of plantlets free from infection caused by *P. capsici* (Aravind et al. 2012).

Sian (2013) isolated endophytic bacteria from Australian native plant species and studied their ability to check the infestation of pathogen *Phytophthora cinnamomi.* The in vitro studies revealed that six of the selected bacterial endophytes were found to suppress *P. cinnamomi* infesting *L. augustifolia* effectively by significantly reducing the length of lesions produced by the pathogen. The mechanism of suppression of diseases was found to be the production of antibiotics.

Paenibacillus polymyxa PB71 isolated from the spermosphere of the Styrian oil pumpkin (*Cucurbita pepo* L. subsp. pepo var. styriaca Greb.) was able to reduce disease severity of the Styrian oil pumpkin caused by the phytopathogenic fungus *Didymella bryoniae* (black rot) under greenhouse conditions (Furnkranz et al. 2012).

Sun et al. (2017) reported that out of 19 strains of PGPR strain tested for antifungal ability, LHS11 efficiently antagonised *S. sclerotiorum* in rapeseed and its inhibition rate reached 85.71%. In greenhouse experiments, the control efficiency (LHS11 + FX2) reached 80.51%. Previous studies revealed that the inhibitory rate of *B. subtilis* CKT1 reached 74.71% against *S. sclerotiorum* in vitro.

Yamamoto et al. (2015) studied the effectiveness of the antagonistic endophytic bacterial strain in lessening the virulence of anthracnose in strawberry brought about by the pathogen *Colletotrichum gloeosporioides*. The study results revealed that the spray of *Bacillus amyloliquefaciens* S13–3 on the leaves of strawberry was able to induce the production of chitinase and β-1,3-glucanase which were responsible for suppressing the anthracnose-producing pathogen.

Bacillus amyloliquefaciens PGPBacCA1 was studied to prove its ability to protect common bean seeds from their intrinsic pathogens, and the findings of the study indicated that it had the potential to inhibit the development of the following phytopathogenic fungi *Sclerotium rolfsii* (35%), *Sclerotinia sclerotiorum* (76.5%), *Rhizoctonia solani* (73%), *Fusarium solani* (56.5%) and *Penicillium* spp. (71.5%) (Torres et al. 2017).

1.8.4 Control of Bacterial Diseases Using Endophytic Bacterial Strains

Chen et al. (2016) studied the biocontrol effects of *Brevibacillus laterosporus* AMCC100017 on potato common scab and found that the bacterial strain significantly ($P < 0.05$) reduced the pathogen population of *Streptomyces bottropensis* from 4.54 to 4.28 Log_{10} CFU g^{-1} soil in the harvesting stage of potato and the biocontrol efficacy against common scab reached as great as 70.51%.

Sturz et al. (1999) identified certain strains of endophytic bacteria, namely, *Pantoea agglomerans* and *Pseudomonas* sp. and *Curtobacterium luteum*, which were found to reduce the virulence of *Erwinia carotovora*, a bacterial pathogen causing disease in crops. A recent study conducted by Sharifazizi et al. (2017) with the selected antagonists to reduce the *Erwinia carotovora* found that all antagonists were able to reduce the disease severity on fruit and flowers. On immature fruit assay, isolates Pa21 and En23 with 83% and 25%, respectively, had the highest and lowest effects on disease incidence compared to the control. On flowers, isolates Ps170 with 92% and En23, Ps89 and Se111 with 25% reduction of infection, respectively, had the highest and lowest effects under condition tested. Based on results obtained in this study, Ps170, Ps117, En113 and Pa21 strains have potential to be used for fire blight control.

Crown gall in grapevines, caused by the phytopathogenic bacterium *Agrobacterium vitis*, has been reported to be prevented by endophytes of the xylem sap of vine plants, including *Enterobacter agglomerans*, *R. aquatilis* and *Pseudomonas* spp. strains (Bell et al. 1995). Symptom development of Pierce's disease caused by *Xylella fastidiosa* can be reduced by virulent, endophytic *X. fastidiosa* strains (Hopkins 2005).

Assis et al. (1996) in their paper on the management of *Xanthomonas campestris* pv. *campestris* (Xcc) which is the causal organism of black rot reported to inflict heavy damage in most of crucifer plant species indicated that endophytic bacteria *Bacillus* spp. isolated from disease free cabbage and radish could able to suppress the black rot in the same host plants.

Araujo et al. (2002) identified endophytic bacterial species which brought about resistance to citrus variegated chlorosis (CVC) in citrus and explained that *Curtobacterium flaccumfaciens* could reduce the incidence of CVC. Sturz et al. (1999) argued that endophytic bacterial strains could safeguard potato against soft rot, a disease caused by pathogenic bacterium. Further, Reiter et al. (2002) have identified noteworthy correlation between the incidence of *Erwinia carotovora* and the endophytic bacterial strains present in the soil of potato and colonised in the root zone. It was found that more the presence of such endophytic bacterial strains in the soil of potato, more will be its resistance to the pathogenic bacterial species *Erwinia caratovora.*

Feng et al. (2013) discussed the strength of association between the quantity of endophytic bacteria present in the soil and the resistance of tomato plants against the bacterial wilt caused by *Ralstonia solanacearum* in tomato. The researchers argued that the suppressive ability of endophytic bacterial species towards bacterial wilt varied among resistant and susceptible tomato cultivar at varied stages of tomato plant which was confirmed through traditional MPN counting method. Findings suggested that the population was found to be more in bacterial wilt-resistant tomato cultivar than susceptible cultivar. Further, they found that the antibiotic producing ability of endophytic bacterial species also was higher in resistant cultivar of tomato than susceptible cultivar. This finding of relationship between variety and resistance to disease will go a long way in designing management protocol for bacterial wilt in tomato caused by *Ralstonia solanacearum.*

1.8.5 Endophytic Bacteria Suppressing the Foliar Fungal Diseases

The studies on the antifungal activity of endophytic bacteria on the fungal pathogens of the foliar diseases were found to be scarce and an attempt is made to review those available findings and they are presented below.

The results of the studies conducted by Bargabus et al. (2002) and Bargabus et al. (2004) in successive years revealed that *Cercospora* leaf spot in sugar beets was effectively controlled by the application of two endophytic bacterial strains, namely, *Bacillus mycoides* isolate BacJ and *Bacillus pumilus* isolate 203–7. Despite the plant surfaces of rice were devoid of entophytic bacteria, their presence in internal stem led to the effective curtailing of the pathogen causing sheath blight disease (*Rhizoctonia solani*) in rice through induced systemic resistance as reported by Krishnamurthy and Gnanamanickam (1997). Garita et al. (1988) in their survey identified 8 bacteria and 24 fungi which were found to be antagonistic to *Phytophthora infestans* in the phyllosphere, rhizosphere and endosphere of tomato.

Fifty-five bacterial strains antagonistic to *Phoma tracheiphila* the causal agent of citrus mal secco disease were screened, out of which nine of the most effective antagonistic strains were tested by inoculating them into the stem of sour orange seedlings 15 days before pathogen inoculation. Three isolates of *B. subtilis* and one isolate of *P. fluorescens* significantly lowered the disease symptoms and maintained higher populations in the internal tissues of the plants in which they colonise (Lima et al. 1994).

Shiomi et al. (2006) rust isolated certain endophytic bacterial strains from the phyllosphere of two coffee species, namely, *Coffea arabica* L. and *Coffea robusta* L. They found that two bacterial endophytes, *Bacillus lentimorbus* and *Bacillus cereus*, were reported to inhibit rust development and to control germination of urediniospore responsible for pronouncement of rust in coffee leaves. The study results indicated that the leaf samples collected from coffee were found to exhibit 50% reduced infection of coffee rust due to the suppressive ability of *Bacillus lentimorbus* and *Bacillus cereus.*

Wilhelm et al. (1997) and Yue et al. (2000) in their studies on the suppression of pathogen *Cryphonectria parasitica* causing chestnut blight by bacterial endophytes reported that *Bacillus subtilis* strains isolated from the xylem sap of healthy chestnut trees and cultures of *Epichloe* and *Neotyphodium* species were found to possess inhibitory ability towards blight-causing pathogen *Cryphonectria parasitica* in chestnut. Colonisation of black pepper vine with endophytic *Pseudomonas* species resulted in 90% reduction in lesion lengths and 60% of plantlets free from infection caused by *P. capsici* (Aravind et al. 2012).

Muthukumar and Venkatesh (2013), Karthikeyan et al. (2005) and Rao (2006) who studied the control of *Alternaria* leaf blight in ribbon plant, onion and sunflower, respectively, identified various endophytic bacterial strains which were found to be effective in inhibiting the blight producing pathogens in these crops. In ribbon plant, Muthukumar and Venkatesh (2013) screened ten endophytic bacterial isolates and reported that EBL 5 was found to be efficient in lowering the infection of *Alternaria alternata* which was substantiated by the largest inhibition zone and the least mycelial growth. Similarly, *P. fluorescens* Pf1 and another strain of *P. fluorescens* were found to be effective against *A. palandui* causing leaf blight of onion and *A. helianthi* causing leaf blight of sunflower.

Gao Zhenbeng et al. (2017) studied the volatile organic compounds produced by *Bacillus velezensis* ZSY-1 and tested their suppressive ability towards disease-causing fungus. Volatile organic compounds from ZSY-1 exhibited significant antifungal activity against *Alternaria solani*, *Botrytis cinerea*, *Valsa mali*, *Monilinia fructicola*, *Fusarium oxysporum* f. sp. *capsicum* and *Colletotrichum lindemuthianum*; the inhibition rates were 81.1%, 93.8%, 83.2%, 80.9%, 76.7% and 70.6%, respectively. Based on the study, the antifungal activity of pyrazine (2,5-dimethyl), benzothiazole and phenolic compounds was proved to be significant, and they are promising bioagents for controlling tomato fungal diseases such as early blight and grey mould.

Researchers across the world have been studying the control of leaf blast in rice using beneficial bacterial endophytes. The studies of Krishnamurthy and Gnanamanickam (1998) and later on by Radjacommare et al. (2004) on rice blast in irrigated rice indicated that the virulence of the blast-producing pathogen was drastically reduced and the symptoms of blast disease in rice were minimally observed in the fields inoculated with plant growth-promoting rhizosphere bacterial strains. Lucas et al. (2009) tried seed treatment of rice with two strains of plant growth promoting rhizobacteria found in the root zone of rice in Spain and observed a strong correlation between seed treatment and disease control and enhancement of yield.

Marta Cristina et al. (2011) conducted a study in aerobic rice fields in Brazil to find out the effectiveness of different rhizobacterial culture in controlling the blast causing pathogen (*Magnaporthe oryzae*) in rice. The screening of 18 strains of rhizobacteria which were tested for the suppression of blast pathogen revealed that almost all strains were found to lessen the spore formation and suppress the disease in the range of 16% to 95%. Further evaluation in greenhouse trials with three replications and three application methods revealed that two isolates, namely, Rizo-46 and Rizo-55, were found to be significantly effective and drastically reduced the incidence of blast in rice. Further, the study results showed that there exist marked differences in inhibitory ability of these strains in three application methods. The study indicated that the secretion of enzymes like peroxidase, b-1,3-glucanase and chitinase were accelerated by the inoculation of Rizo-46 and Rizo-55.

1.8.6 Nematode Control Through Endophytic Bacteria

Few studies could be traced about the endophytic bacteria colonising roots of plants and suppressing the growth of nematode. Siddique and Shaukat (2003) in their review indicated that the colonising ability of endophytic bacteria and their traits of easy culturability in vitro, reducing initial root damage and influencing host's response to pathogen attack, accelerated the development of plants and production of abundant root exudates for faster growth of microbes in the soil and offered lot of scope for biological management of nematodes causing damage to plants.

Combined application of endophytic *Fusarium oxysporum* and *Bacillus firmus* resulted in 76.2% reduction in the density of the pathogenic nematode *Radopholus similis* in banana plants (Mendoza and Sikora 2009). Kluepfel et al. (1993) reported reduction of *Criconemella xenoplax* nematode population in peach trees by the antagonistic activity of bacterial strains found in rhizosphere soil. Hallmann et al. (1997) in their study on management of nematodes through biological means indicated that in cotton, gall production in roots due to root-knot nematode, *Meloidogyne incognita*, was considerably reduced by the activity of endophytic bacteria in roots which lowers the infection of nematodes. Further, they reported that the root-knot nematodes in cotton aided the entry of endophytic bacteria in roots and thus helped the establishment of endophytic bacteria in the root system.

Siddiqui and Ehteshamul-Haque (2001) in their research paper published in *Phytopathologia Mediterranea* discussed the control of nematode, *Meloidogyne javanica*, in tomato using bacterial endophytes. The results of the study indicated that inoculation of endophytic bacterial strain *Pseudomonas aeruginosa* strain IE-6 and another strain IE-6SC were found to dent the growth of *Meloidogyne javanica* in tomato which were grown in greenhouse and also in the main field.

Hallmann (2001) identified two potential endophytic bacterial strains *Rhizobium etli* G12 and its genetically modified strain G12 (pGT-trp) in potato which were found to inhibit the gall formation inflicted by the nematode *M. incognita* which was assisted through production of green fluorescent protein by the identified bacterial strains. Reitz et al. (2000) and Hallmann et al. (2001) in their study in potato reported the role of liposaccharides produced by endophytic bacteria *Rhizobium etli* G12 which facilitated the potato plants to defend against cyst nematode *Globodera pallida*.

Siddiqui et al. (2002) found in their study that the population of *M. javanica* nematodes and consequent development of root knot in tomato were considerably reduced by the synergistic effect of combined application of endophytic bacterial strains *E. solani* and P. *aeruginosa* IE-6S+.

1.8.7 Biocontrol of Postharvest Diseases by Endophytic Bacteria

The influence of endophytic bacteria in postharvest disease control has been mostly conducted on fruits and vegetables, and they are found to be limited. A few literatures have been perused and given in this section.

Elshafei et al. (2012) indicated several disease-suppressing endophytic bacteria including *Paenibacillus brasilensis*, *Bacillus subtilis*, *Burkholderia gladioli* pv. *agaricicola* and *Streptomyces* sp. and their antagonistic ability in their study which were reported to control a plethora of pathogens causing postharvest losses in crop plants.

In vitro studies of management of *Penicillium digitatum*, a causal organism of a postharvest disease citrus mould, conducted by Mohammadi et al. (2017) revealed that among ten endophytic bacterial isolates, *Bacillus subtilis* and *Agrobacterium radiobacter* were reported to be superlative in controlling citrus mould. The authors further observed that the two effective bacterial endophytes were found to check the development of mycelium and germination of spores of fungus through the production of important enzymes, namely, chitinase and glucanase.

Parveen et al. (2016) in their recent review on postharvest fungal rots of rosaceous fruits gave an insight into the endophytic bacterial species and their mode of action against pathogens causing postharvest losses especially moulds and rots. Mikani et al. (2008) in their study reported the reduction in the incidence of grey mould caused by *Botrytis* sp. by the antifungal ability of *Pseudomonas fluorescens* applied on the harvested produce. Mari et al. (2014) in their study on postharvest diseases of apple and pear reported that BiosaveTM, trade name of a formulation of an endophytic bacteria *Pseudomonas syringae*, could reduce the incidence of two types of moulds, viz. grey mould and blue mould. It was reported that *Pseudomonas syringae* could take care of Mucor rot, a postharvest disease common in apple and pear.

Smilanick et al. (1993) reported from their study that brown rot in stone fruits, a postharvest disease, could be reduced by the application of *Bacillus subtilis and Pseudomonas* sp. which is effective and safe. Trias et al. (2010) and Wang et al. (2010) identified two endophytic bacterial strains, namely, *Pantoea agglomerans* and *Bacillus subtilis*, which were reported to suppress the activity of a number of fungal pathogens *Botrytis cinerea*, *Alternaria alternata*, *Penicillium expansum* and *P. malicorticis* inflicting fruit rot in damaged apples during harvesting and transit.

Twenty one strains of endophytic bacteria were identified by Pratella et al. (1993) which were drawn from a wide range of fruits, viz. tomato, brinjal, etc., to control a fungal pathogen *M. laxa* which was reported to infect the harvested plum, peach and apricot fruits. The study indicated that *M. laxa* could be controlled effectively than *R. stolonifer.* Calvo et al. (2007) in another study on apple reported that disease producing fungal species of *Penicillium expansum*, *Botrytis cinerea and Alternaria alternata* could be effectively controlled by the application of *Rahnella aquatilis* as biocontrol agent.

1.9 Methods of Application of Endophytic Bacterial Strains

Relevant and appropriate methods of application of endophytic bacteria are to be selected for increasing the efficiency of biocontrol ability. Several methods were used in different crops with different bacterial cultures. The reviews revealed that the methods which are being adopted for the application of microbial inoculants on the various parts of plants including root zone and phyllosphere hold good for endophytic bacteria also (Andrews 1992). An array of methods including seed treatment, soil trenching, stem injecting and spraying on foliage were tried by researchers and reported the differential efficiency of these methods (Fahey et al. 1991).

Musson et al. (1995) conducted experiments to evaluate the effectiveness of several application methods of 15 endophytic bacteria into the stem and root tissues of cotton. Seven application methods were experimented, *viz*. inoculation of bacteria into stem of cotton plants, seed coating with methyl cellulose, cotton seed soaking in bacterial suspensions, application of bacterial suspension on the leaves of cotton, furrow application of granules containing bacterial consortia, vacuum infiltration and application on the pruned-root dip. Among the seven method of application, inoculation into stems or radicles was proved to be effective as ten isolates could be recovered from the cotton plants inoculated with the isolates though the method was labour intensive and the process involves wounding the plant which may reduce the growth of the plants. The pruned-root dip was the most efficient method to deliver bacterial endophytes into maize (Bresson and Borges 2004).

Efforts were made by scientists to find a seed inoculation technique to increase the shelf life of seeds and to improve the compatibility with commonly used fungicides, ensuring the survival and efficacy of bacterial inoculations. In this line, a seed inoculation technique was developed by Crop Genetics International Ltd. in which the seeds were treated with bacterial suspension and redrying of seeds through application of differentiated pressure (Turner et al. 1993). Zakaria et al. (2008) experimented two methods of application of endophytic bacterial culture, *viz.* inoculation in root zone and root tip method, in cultivated and wild rice. Among the two methods experimented, the population of bacterial species increased drastically in root dip method, and the colonisation was found to be more pronounced in cultivated rice than wild rice.

Significant increases in rice yield were achieved by seed inoculation with the endophytic bacterium *Achromobacter xylosoxidans*, which suppressed symptoms of rice blast disease by stimulating production of plant defence-related enzymes (Joe et al. 2012). Similarly, inoculation of seeds with a wide range of putative endophytic bacterial isolates improved shoot dry weights in maize seedlings (Montanez et al. 2012).

Bashan and Holguin (1997) reported that addition of certain nutrients in specific forms may improve the endurance of bacteria present in a formulation. For example, skim milk can improve the survival rate of beneficial microorganisms which can reduce disease risk in crops.

The effective plant colonisation by the endophytic bacteria through inoculation into plant cell suspension and regenerated embryo is a useful option as reported by Bashan and Holguin (1997). Knudsen and Spurr (1987) experimented with lyophilised bacteria which were sprayed in dust formulations or suspensions on fruits and flowers, and the study did not specify the technicalities involved in spraying.

Marta Cristina et al. (2011) in their study tested three methods of application of bacterial cultures to reduce leaf blight in rice. Among the methods studied, soil drenching with isolate Rizo-55, 15 days prior to application of virulent isolate of blast-producing pathogen *M. oryzae*, was found to control 90% of leaf blast, and soil trenching with isolate Rizo-46 applied 2 days before the application of virulent plant pathogen could reduce blast by 95%. The findings of the study indicated that differential method of application resulted in differential control of blast in rice irrespective of the bacterial cultures applied.

Selim et al. (2017) analysed the suppression of damping-off (*Rhizoctonia solani*) disease in cotton through the application of the bacterial strains as a soil drench or talc-based bioformulation, and the results indicated that the soil drench treatment was more efficient than talc-based bioformulation. The foliar application of *Bacillus amyloliquefaciens* S13–3, a bacterial endophyte known for producing antibiotics, was found to suppress anthracnose (*Colletotrichum gloeosporioides)* in strawberry (Yamamoto et al. 2015).

Sundaramoorthy et al. (2012) recorded 17–30% of suppression of *Fusarium* wilt in chilli pepper when compared to control through application of talc-based bioformulation of *P. fluorescens* (Pf1) and *B. subtilis* (EPCO16 and EPC5 strains). Soil application of these bacterial combinations of *Bacillus* and *Pseudomonas* resulted in significant lowering of incidence of *Fusarium* wilt in cv. Grand Naine banana (Thangavelu and Gopi 2015).

Analysing the pros and cons of different methods, Hallman et al. (1997) reported that among different modes of application of bacterial cultures, the most economical, dependable and swift method is seed treatment which will directly let the beneficial bacterial species into the soil and subsequently into the plant system. They also argued that combining of application methods, namely, seed treatment with soil drenching and foliar application, will enhance the colonisation potential of different endophytic bacterial species and could multiply the benefits of these species inside the plant system.

1.10 Conclusion and Future Prospects

The primary objective of this chapter is to sensitise and update the researchers in the field of biological management of plant diseases about the bacterial endophytes; their diversity; mechanism of colonisation in different plant parts; ability to suppress an array of fungal, bacterial and postharvest diseases; mode of action; and method of application. Despite efforts were made to update the literature, it seems unwieldy to include all possible dimensions of plant disease management using endophytic bacteria.

The chapter ellucidated some of the important research areas which need to be explored by scientists in the future. The chapter also suggested that colonisation of endophytic bacteria is the key for the suppression of disease causing pathogen. Much of the research needs to be focussed on how individual species of endophytic bacteria colonise different parts of plants and the traits involved in colonisation. Since majority of the bacterial species are identified in the rhizosphere, enhancing the colonisation of PGPR in other parts of the plants would be a good strategy, though onerous could be a strategic option for controlling foliar diseases. Plant host-specific endophytic bacteria are to be identified; population dynamics are to be studied which should logically culminate in the production of inoculum for specific disease of a specific plant. This means the optimisation of dosage for effective control which would avoid bulk production of inoculum. One step further to this type of research is the genome sequencing and identifying genes responsible for the suppression of plant diseases. Studies suggested that these information will provide a strong base for furthering the studies in plant-microbe interactions. The efforts have already been taken to untangle the biotechnological potential which needs to be further exploited by more meaningful research. Ultimately, more exclusive studies on the endophytic microbiome would reveal useful information on biocontrol of plant diseases.

The information presented in this chapter further informed about the current scope and importance of organic amendment of soil with substances like chitin that would improve the inducement of resistance, and further studies on this line would open up several possibilities. The studies on favourable edaphic factors to suppress plant pathogens would go a long way in identifying appropriate species for appropriate soil conditions. Though the postharvest diseases could inflict huge economic loss, the available literature on controlling them with endophytic bacteria were found to be limited, and research in this area needs to be strengthened. Finally, the application of these endophytic bacteria in appropriate formulations and identifying appropriate method of application are pivotal for effective disease management. Experimental studies on finding effective formulation and method of application of bacterial endophytes are the need of the hour.

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