Prospect and Potential of *Burkholderia* sp. Against *Phytophthora capsici* Leonian: A Causative Agent for Foot Rot Disease of Black Pepper

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Abstract

Foot rot disease is a very destructive disease in black pepper in Malaysia. It is caused by *Phytophthora capsici* Leonian, which is a soilborne pathogenic protist (phylum, Oomycota) that infects aerial and subterranean structures of many host plants. This pathogen is a polycyclic, such that multiple cycles of infection and inoculum production occur in a single growing season. It is more prevalent in the tropics because of the favourable environmental conditions. The utilization of plant growth-promoting rhizobacteria (PGPR) as a biological control agent has been successfully implemented in controlling many plant pathogens. Many studies on the exploration of beneficial organisms have been carried out such as *Pseudomonas fluorescens*, which is one of the best examples used for the control of *Fusarium* wilt in tomato. Similarly, *P. fluorescens* is found to be an effective biocontrol agent against the foot rot disease in black pepper. Nowadays there is tremendous novel increase in the species of *Burkholderia* with either mutualistic or antagonistic interactions in the environment. *Burkholderia* sp. is an indigenous PGPR capable of producing a large number of commercially important hydrolytic enzymes and bioactive substances that promote plant growth and health; are eco-friendly, biodegradable and specific in their actions; and have a broad spectrum of antimicrobial activity in keeping down the population of phytopathogens, thus playing a great role in promoting sustainable agriculture today. Hence, in this book chapter, the potential applications of *Burkholderia* sp. to control foot rot disease of black pepper in Malaysia, their control mechanisms,

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plant growth promotion, commercial potentials and the future prospects as indigenous PGPR were discussed in relation to sustainable agriculture.

Keywords
Phytophthora capsici Leonian • Foot rot disease • Black pepper • Plant growth-promoting rhizobacteria (PGPR)

Contents

12.1 Introduction

Black pepper (*Piper nigrum* L.) known as "the king of spices" is a historic, traditional spice and one of the most important agricultural produce in Malaysia (Anon 2003). The ~80% of pepper is processed as black pepper, and the remaining ~20% is processed as white pepper. Despite the substantial contribution made by this crop to the socio-economy of Malaysia and other parts of the world, production potentials of the crop are on the trend of decline due to the activities of pests and diseases. For example, a disease known as foot rot caused by *Phytophthora capsici* Leonian is a major obstacle in black pepper production in Malaysia and worldwide. The pathogen was first isolated and identified under *P. palmivora* (Holiday and Mowat 1963) in Malaysia, but later further investigations by Kuch and Khuthubutheen (1985) identified the pathogen as *P. capsici* Leonian (Fig. 12.1a–d). Foot rot is considered as the most serious disease of black pepper causing yield reduction that

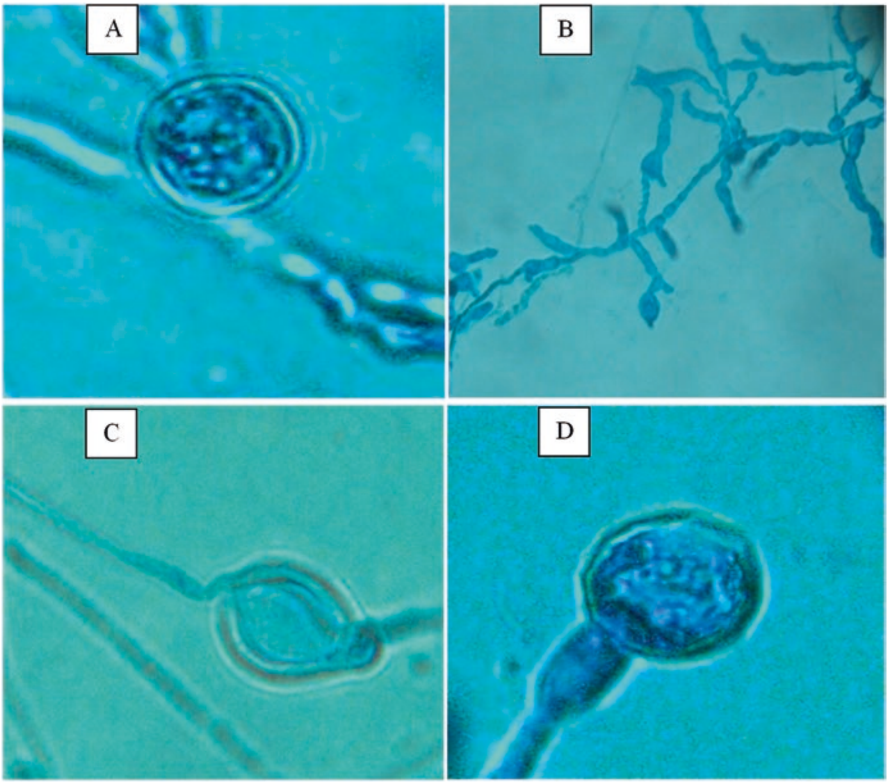

Fig. 12.1 Typical morphological characteristics of *Phytophthora capsici* Leonian isolated from infected black pepper root: chlamydospore (**a**), torulose hyphae (**b**), lemon-shaped sporangium with long pedicel (**c**) and globose oogonia with paragynous antheridia (**d**)

ranges from ~20 to 80 and up to 95% for individual farmers (Manohara et al. 2004). The fungus is a soilborne pathogen that causes infections on roots, leaves and fruits of black pepper (Fig. 12.2a–c) and other crops (Fig. 12.3a–c) in most of the tropical countries. Efforts have been made to check these incessant problems caused by this fungus. Today, the primary means of controlling the disease is through synthetic fungicides applications which have been effective but found to be associated with some drawbacks. Among the drawbacks are their high cost, carcinogenicity, teratogenicity, high and acute residual toxicity, long degradation period, environmental pollution and possible side-effects on human health through the food (Wang et al. 2011; Meena et al. 2013a, 2016a; Bahadur et al. 2014; Maurya et al. 2014; Jat et al. 2015; Kumar et al. 2015, 2016b; Ahmad et al. 2016; Parewa et al. 2014).

These drawbacks coupled with public concern have increased interest in developing further alternative control methods, particularly those that are eco-friendly, biodegradable, feasible to the farmers, non-toxic to human and animals, specific in their actions and have a broad spectrum of antimicrobial activity (Abhishek et al. 2013). Thus, indigenous plant growth-promoting rhizobacteria (PGPR) have been found to

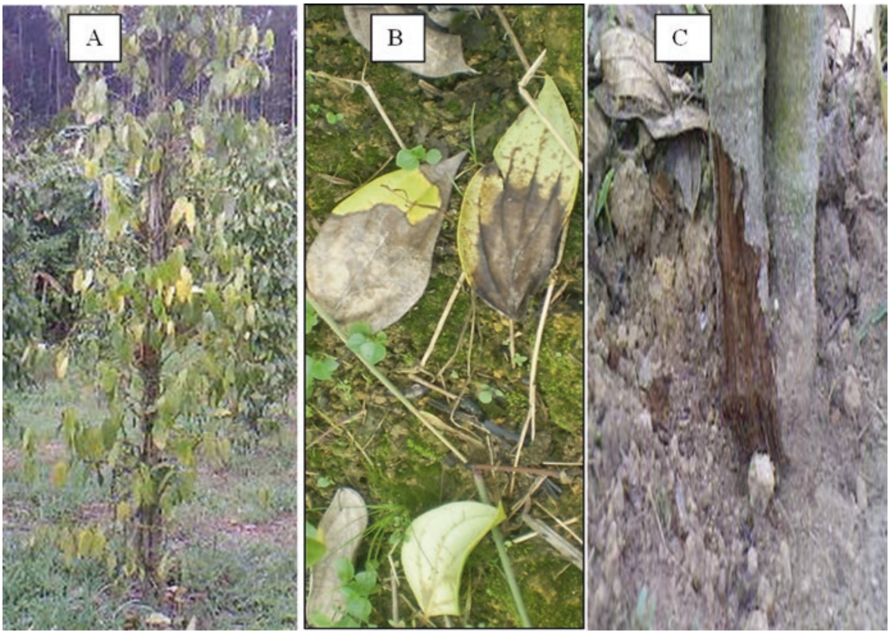

Fig. 12.2 Yellowing symptoms of foot rot disease observed on black pepper foliage (**a**), leaves defoliation (**b**) and collar rot (**c**) symptoms on infected black pepper in Sarawak

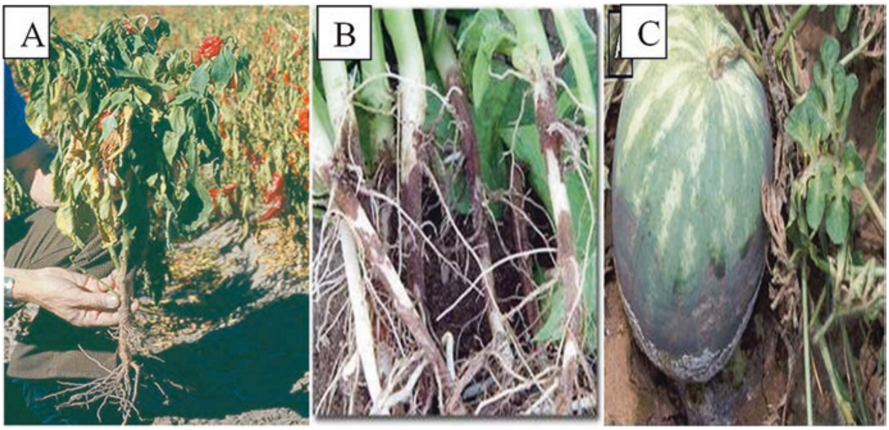

Fig. 12.3 Yellowing symptoms of foot rot disease observed on chili pepper (**a**), infected root of potatoes (**b**) and infected fruit of watermelon (**c**) (Source: Wharton et al. 2007; Sanogo 2003)

play a major role in keeping down the population of pathogen to a low level and can therefore be used as an alternative to synthetic chemicals. Some PGPR, such as *Burkholderia* sp., *Pseudomonas* sp. and *Bacillus* sp., have been found to perform these functions by inducing systemic resistance in plants and showing biological traits like antibiosis and lysis (Eberl and Vandamme 2016; Rahamat Bivi et al. 2010; Prakash and Verma 2016; Priyadharsini and Muthukumar 2016; Kumar et al. 2017; Meena et al. 2015a, 2016b; Jaiswal et al. 2016, 2016a; Jha and Subramanian 2016).

The soil system is a natural body called "pedosphere" that served as a habitat for a quantum of endophytic and rhizospheric microorganisms which in turn modify the complex matrices of the soil especially in the root zone. Recent studies on microbial plant-related interactions revealed that bacterial communities called PGPR belonging to the genus *Burkholderia* are associated with the development of plants and are responsible for a range of physiological activities. In addition to their beneficial features as promoters of plant growth, they also protect plants against pests and pathogens (biocontrol agents) and increase plant fitness by nitrogen fixation, production of phytohormones and antimicrobial substances and induction of systemic resistance (Eberl and Vandamme 2016; Lodewyckx et al. 2002). Additionally, they are involved directly in the plant growth through biofertilization, stimulation of root growth, control of plant stress through host adaptation to environmental stress, sequestration of iron, phosphate solubilization (Raghavendra et al. 2016; Zahedi 2016; Meena et al. 2015b, 2015f, 2016c; Rawat et al. 2016; Yasin et al. 2016; Saha et al. 2016a; Dominguez-Nunez et al. 2016; Dotaniya et al. 2016), ACC deaminase activities and quinolinate phosphoribosyltransferase activity (Barrett and Parker 2006; Janssen 2006; Balandreau and Mavingui 2007; Compant et al. 2008) without conferring pathogenicity (Lugtenberg and Kamilova 2009; Compant et al. 2010; Eberl and Vandamme 2016).

These efficient bacteria are found in the "rhizosphere" which is defined as any volume of soil specifically influenced by plant roots and/or in association with root hairs and plant-produced materials (Dessaux et al. 2009; Silveira et al. 2012; Ahemad and Kibret 2014). The rhizosphere has been identified to consist of three major separates but interacting components that include rhizosphere (soil), the rhizoplane and the root itself. The rhizosphere is the soil zone influenced by roots through the release of substrates that affect microbial activity. The rhizoplane is the root surface that consists of strongly adhering soil particles, and the root itself is a component of the system, where the tissues are colonize by many microorganisms (like endophytes) (Barea et al. 2005; Ahemad and Kibret 2014).

Colonization of the rhizoplane and rhizosphere differs from one another (Kloepper et al. 1991), in that microbial colonization of rhizoplane is termed as root colonization, whereas rhizosphere colonization is microbial colonization of the adjacent volume of soil under the influence of the root (Kloepper 1994; Barea et al. 2005). Hiltner (1904) discovered that the rhizosphere is much richer in bacteria than the surrounding bulk soils, with composition of 10–1000 times higher than that in bulk soil.

The bacteria covered a small part of the root surface (Rovira 1956), and the most popular sites for bacterial growth are junctions between epidermal cells and areas where side roots appear. The effect of rhizosphere is caused by substantial amount of the carbon fixed by the plant, ~5–21% (Marschner 1995), which is secreted mainly as root exudates. In addition to facilitating water and nutrient uptake and providing mechanical support to the plants, a diverse array of compounds is synthesized, accumulated and secreted by plant roots (Walker et al. 2003).

The compounds secreted by the roots are generally referred to as root exudates. They act as attractants on diverse number of active microorganisms in the soil. In addition, they change the physical features and chemical compositions of the soil, therefore, restructuring the microorganisms in the area of the root (Eberl and Vandamme 2016; Dakora and Phillips 2002). They also repel microorganisms, promote symbiosis and control the growth of other unwanted plant species (Nardi et al. 2000). Kang et al. (2010) reported that the compositions of these exudates depend on the species of plants, their physiological status and microorganisms present.

PGPR are species of bacteria collectively found growing around plant tissues in the rhizosphere that enhanced the growth of plant by a number of mechanisms (Vessey 2003; Lemaire et al. 2015). They are distinctively characterized by some inherent features that include the following: they must (i) colonize the surface of the root effectively; (ii) promote plant growth; (iii) be able to survive and multiply, at least for sometimes to exert their protection and growth-promoting activities; and (iv) be able to compete well with other rhizosphere microbes for nutrients secreted by the root and for sites that can be occupied on the root (Kloepper 1994; Lugtenberg and Kamilova 2009). Certain species in this extremely versatile group are capable of causing disease in humans and plants (Eberl and Vandamme 2016), while others are very effective as biological control agents, bioremediation and promotion of plant growth (Perin et al. 2006).

Nowadays, rigorous research are carried out globally with greater aim to explore a vast number of PGPR having novel characteristics that could serve as biocontrol agents (Eberl and Vandamme 2016; Hynes et al. 2008; Joo et al. 2005; Russo et al. 2008) alongside with normal growth promotion characteristics like biofertilization (Tank and Saraf 2010; Ahemad and Khan 2012b), ACC deaminase (1-aminocyclopropane-1-carboxylate), production of ammonia and nitrogenase activities (Khan 2005; Glick 2012), siderophore (Tian et al. 2009; Jahanian et al. 2012), solubilization of phosphate and potentials in heavy metal detoxification (Ma et al. 2011; Ahemad and Khan 2012b), salinity tolerance (Tank and Saraf 2010; Mayak et al. 2004) and pesticide degradation (Ahemad and Khan 2012a). Typical examples of rhizobacteria that showed marvellous plant growth beneficial traits and potential as biological control agents against various root pathogenic microbes that are today used globally as bioinoculants in promoting growth and development of plant under different stresses such as heavy metals (Wani and Khan 2010), herbicides (Ahemad and Khan 2010, 2011a), insecticides and fungicides (Ahemad and Khan 2011b, 2011c, 2012c) and salinity (Mayak et al. 2004) include *Agrobacterium* sp., *Arthrobacter* sp., *Azotobacter* sp., *Azospirillum* sp., *Azomonas* sp., *Bacillus* sp., *Caulobacter* sp., *Chromobacterium* sp., *Erwinia* sp., *Flavobacterium* sp., *Micrococcus* sp., *Pseudomonas* sp., *Serratia* sp., *Allorhizobium* sp., *Azorhizobium* sp., *Bradyrhizobium* sp., *Mesorhizobium* sp., *Rhizobium* sp., *Micromonospora* sp., *Streptomyces* sp., *Streptosporangium* sp., *Thermobifida* sp., *Klebsiella* sp. and *Burkholderia* sp.

The name of the genus *Burkholderia* was derived from "Walter H. Burkholder" who described *Phytomonas caryophylli* (Burkholder 1942) as the first *Burkholderia* sp. which was later known as *Pseudomonas caryophylli*. Burkholder (1950) again described another species named "cepacia" named after onion, which was later called *Pseudomonas cepacia*. Species of *Burkholderia* were included for years in the genus of *Pseudomonas*, but with the advent of molecular rRNA-DNA hybridization analysis, considerable diversity in the genotype was noticed between the genus members (Compant et al. 2008), and as a result they were grouped into five rRNA groups (Palleroni et al. 1973). Later, genomic analysis had shown that five groups are related to one another. Recently, considerable numbers of species are included in the genus of *Burkholderia* (Coenye and Vandamme 2003) known as *Burkholderia cepacia* and representing complex of closely related genotypic species as confirmed by numerous taxonomic studies (Coenye et al. 2001; Vandamme et al. 2003; Vermis et al. 2004; Eberl and Vandamme 2016). The group is called as the *Burkholderia cepacia* complex and recently consists of a total of nine species that include *Burkholderia cepacia* (genomovar I), *Burkholderia multivorans* (genomovar II), *Burkholderia cenocepacia* (genomovar III), *Burkholderia stabilis* (genomovar IV), *Burkholderia vietnamiensis* (genomovar V), *Burkholderia dolosa* (genomovar VI), *Burkholderia ambifaria* (genomovar VII), *Burkholderia anthina* (genomovar VIII) and *Burkholderia pyrrocinia* (genomovar IX). The first discovery of *B. cepacia* by W.H. Burkholder had today led to the identification of many other species of *Burkholderia*.

Currently, the genus *Burkholderia* includes more than 50 species that are found in various ecological niches, rather than in bulk soil (Coenye and Vandamme 2003; Luvizotto et al. 2010), most of which interact with plants in different ways resulting in beneficial effects to the intimate associating hosts. Finally, the potentials of PGPR should not be overemphasized as their application under both normal and stressed conditions has increased the health and productivity of different plant species and decreased global huge reliance on synthetic chemical pesticides that pollute the ecosystem (Yadav and Sidhu 2016; Saha et al. 2016b; Verma et al. 2014, 2015b; Masood and Bano 2016;Teotia et al. 2016; Meena et al. 2015e, 2016d, 2016e; Bahadur et al. 2016b; Das and Pradhan 2016. Therefore, in this book chapter, the potential application of indigenous PGPR (*Burkholderia sp.)* to control foot rot disease of black pepper in Malaysia, their control mechanism and plant growth promotion, the commercial potential application and the future prospects for sustainable agriculture were discussed.

12.2 General Mechanisms of Action for PGPR as a Biological Control Agent

These PGPR generally mediated plant growth promotions in rhizosphere as biocontrol agents by reducing the inhibitory effects of various pathogenic microbes on plant growth and development (Glick 2012), and their utilization to control diseases as biocontrol agents is an eco-friendly approach (Lugtenberg and Kamilova 2009).

The following are the mechanisms that can be distinguished in PGPR as a biocontrol agent.

12.2.1 Competition for Nutrients

The first step in pathogenesis of soilborne microbes is the colonization of rhizosphere and rhizoplane (Lugtenberg et al. 2001; Compant et al. 2010; Eberl and Vandamme 2016). As it is widely believed that root colonization is an important aspect of biocontrol, therefore, PGPR have to be highly competitive to successfully colonize the narrow root zone of the plant to be protected and also be able to exhaust the available nutrients against other microorganisms (Lugtenberg and Kamilova 2009; Compant et al. 2010; Shehata et al. 2016). The roots produce what is known as root exudates which consist of food nutrients that are essentially required by rhizosphere microbes that include sugars, amino acids, organic acids and numerous compounds including enzymes, sterols, vitamins, fatty acids, putrescine, nucleotides, osmoprotectants and signal molecules. In general, PGPR acted by displacing and suppressing the growth and development of pathogens through competition for the nutrients, space and essential elements (Sharma et al. 2016; Verma et al. 2015a; Meena et al. 2013b, 2013c, 2014a, 2015d; Shrivastava et al. 2016;Singh et al. 2015; Bahadur et al. 2016a).

As a mechanism, some of the PGPR secreted siderophores and lytic enzymes that deter the growth of the phytopathogens present in the rhizosphere and rhizoplane. However, some secreted antibiotics that offer them a better chance for rhizosphere and rhizoplane colonization (van Loon and Bakker 2006; Shehata et al. 2016) and typical examples of the antibiotics secreted include 2,4-diacetylphloroglucinol (DAPG), rhamnolipids, hydrogen cyanide, zwittermicin A, oligomycin A, oomycin A, phenazine, pyoluteorin, pyrrolnitrin, thiotropocin, tropolone, cyclic lipopeptides, kanosamine and xanthobaccin, as well as many others (Takeshita et al. 2015; Nielsen et al. 2002; Raaijmakers et al. 2002; de Souza et al. 2003; Compant et al. 2010). Fan et al. (2011) reported that successful colonization of seedlings root was achieved via root dipping in the suspension of *Bacillus* strain (FZB42) before transplanting. The biocontrol ability of *Bacillus* can be understood by the reports of Chen et al. (2009) and Malfanova et al. (2011) that *Bacillus* produces cyclic lipopeptides (cLPs) that are involved in the biological control through ISR (Ongena et al. 2007), in a mechanism that requires rhizosphere colonization only (Dekkers et al. 2000).

12.2.2 Signal Interference

Signal interference is a biocontrol mechanism employed by some PGPR to break the sensing ability of some virulent and/or pathogenic microbes. This is specifically seen in bacteria toward their ability to sense the production level of exoenzymes (cell wall-degrading enzymes) regulated by quorum sensing (QS) molecules such as homoserinelactones (AHLs) (Lugtenberg et al. 2013; Bassler 1999). Inactivation of the molecule called homoserinelactones (AHLs) needed for the production of exoenzyme is one way of controlling the activities of pathogens that can be achieved through signalling interference mechanism (Dong et al. 2004). Lactone ring-hydrolyzing enzymes, AHL lactonases, and the amide linkage-breaking enzymes, AHL acylases, are the two main types of AHL-inactivating enzymes that have been identified (Uroz et al. 2009; Lugtenberg et al. 2013).

Typical example of signal interference mechanism is the production of AHL lactonases by *B. thuringiensis* strains which hydrolyse the lactone ring and/or AHL acylases that break the amide link in the pathosystem (Lugtenberg et al. 2013). Volatile organic compounds (VOCs) produced by rhizospheric strains *P. fluorescens* B-4117 and *S. plymuthica* IC1270 have been demonstrated to be involved in the suppression of crown gall disease in tomato plants caused by *Agrobacterium* (Dandurishvili et al. 2011). Also VOCs produced these strains, which are capable of causing a noticeable decrease in the transcription of phzI and csaI genes capable of AHL synthesis (Chernin et al. 2011; Velazquez et al. 2016; Sindhu et al. 2016; Meena et al. 2014b, 2015c; Singh et al. 2016).

12.2.3 Induced Systemic Resistance (ISR)/Systemic Acquired Resistance (SAR)

The phenomenon induced systemic resistance (ISR) is an activated response immunity by plant that is mediated by some rhizobacteria living on or interacting with roots of host plants (Pierterse et al. 2009, 2014), mediated by the signalling pathway of jasmonic acid (JA), salicylic acid (SA) and ethylene (ET) (Van Wees et al. 2000; Pierterse et al. 2014) within the plant resulting in the host plant's defence responses against a number of bacteria, fungi, viruses, nematodes and insects (Beneduzi et al. 2012; Glick 2012). Labuschagne et al. (2010) showed that PGPR elicited the ISR in the host plants by increasing the mechanical and physical strength of the cell wall of the host plant as well as changing the physiological and biochemical reactions of the host plant. The successes of ISR rely on the plant species or cultivar (van Loon and Bakker 2006) and require only rhizosphere colonization as a competitive mechanism (Dekkers et al. 2000; Lugtenberg et al. 2013).

It is important to note that ISR is not associated with the activation of pathogenesis-related proteins (PRs) as was the case in systemic acquired resistance (SAR). Various individual bacterial-derived compounds were reported to induce ISR, such as bacterial molecules like lipopolysaccharides and salicylic acid; organelles such as flagella; metabolites like siderophores, cyclic lipopeptides and biosurfactants; volatiles such as 2,3-butanediol and acetoin; phenolic compounds; antibiotics; and the signal molecule or quorum sensing molecules (Ahemad and Kibret 2014; Lugtenberg et al. 2013; Beneduzi et al. 2012; Perez-Garcıa et al. 2011).

The term SAR describes a salicylic acid-defendant induced resistance caused by a localized infection (Vleesschauwer and Hofte 2009). Ryals et al. (1996) defined SAR as a defence mechanism activated in the plant following the primary infection

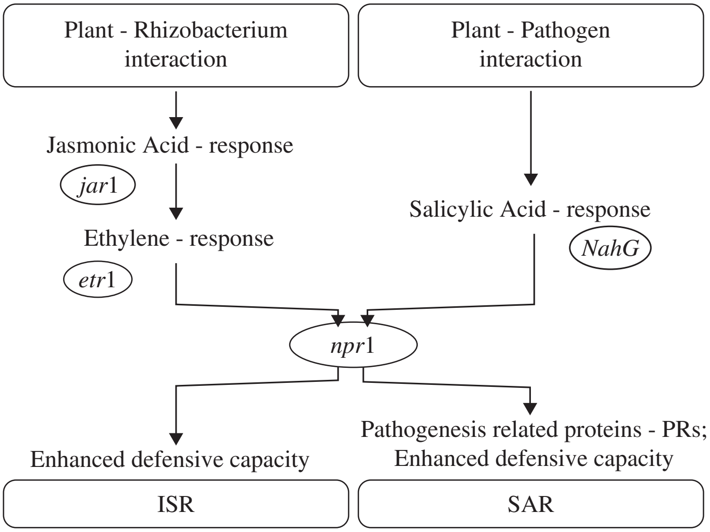

Fig. 12.4 Transduction signal pathways leading to rhizobacteria-mediated induced systemic resistance (*ISR*) and pathogen-induced systemic acquired resistance (*SAR*) in *A. thaliana* (Source: Van Loon et al. 1998)

by pathogens, mediated through the accumulation of salicylic acid signalling pathway (Beneduzi et al. 2012). The plant resists further attacks after the first infection that predisposes the host to subsequent attacks. The defence capacity is linked with the accumulation of PRs. This, therefore, suggested the relevance of these PRs in their contribution to increased defence ability of the infected or induced tissue (Beneduzi et al. 2012). The most important feature of SAR is the activation of SAR genes especially those encoding the PRs that are usually taken as molecular markers for the state of induced resistance attained (Vleesschauwer and Hofte 2009; Mandal and Ray 2011; Shaikh et al. 2016).

Typical examples of PRs that served as hallmarks in several plant species and which have also shown to contribute in the inducement of resistance are 1,3-glucanases and chitinases that are effective in hydrolyzing fungal cell walls. Pieterse et al. (1996) reported that in an experiment conducted on *Arabidopsis* plants inoculated with *Pseudomonas syringae* pv. tomato and/or sprayed with salicylic acid, it developed PRs (PR-1, -2, and -5 mRNAs), and with this conclusion, it could be made that PRs are dominantly associated with induction of SAR (Beneduzi et al. 2012; Meena et al. 2017). Both ISR and SAR can act together in conferring resistance to host against pathogens and exert a protection better than each system alone (Van Wees et al. 2000). Salicylic acid transduction signal needs the activator (regulatory) protein NPR1 which works in the terminal signalling pathway of the SAR, and NPR1 takes part in the defence responses mediated by various signalling ways that act beyond the expression of pathogenesis-related genes, showing ISR and SAR meet at the end of the signalling pathway (Van Loon et al. 1998; Beneduzi et al. 2012). The transduction signal pathways leading to ISR (rhizobacteria) and pathogen-induced SAR in *Arabidopsis thaliana* are shown below (Fig. 12.4).

12.2.4 Siderophores Production to Compete for Ferric Ions

The term siderophores is a ferric ion (Fe^{3+})-chelating compound produced by many rhizobacteria in an attempt to overcome the conditions under Fe^{3+} limitations (Lugtenberg et al. 2013). Virtually, all living organisms essentially need Fe^{3+} for a variety of functions such as synthesis of ATP, formation of heme, reduction of ribotide precursors of DNA and for growth (Saraf et al. 2011; Lugtenberg et al. 2013; Sermwan et al. 2015). The need for iron to support the growth of organism became a challenge to the organisms in a situation of shortage supply. Therefore, survival of the fittest became the rule to survive. As a mechanism of biocontrol agents, siderophore-Fe^{3+} complex is formed by continuous binding to Fe^{3+} limitation receptors, and the Fe^{3+} ion is subsequently conveyed into the cell of bacterial where it becomes active as Fe^{2+}. Those bacteria that secrete siderophores effectively good enough to bind Fe^{3+} to a level that fungal pathogens can no longer grow anymore under iron limitation can act as biological control agents (Leong 1986). Pyoverdine is a good example of a siderophore (Lugtenberg et al. 2013), and examples of bacteria that produced siderophore include *P. fluorescens* strains, *Bacillus*, *Alcaligenes*, *Bradyrhizobium*, *Rhizobium* and *Enterobacter* (Shaikh et al. 2014; Shaikh and Sayyed 2015). *Burkholderia cepacia* was reported to produce siderophore called deferoxamine mesylate salt equivalent. A concentration of 0.64 μg mL^{-1} is sufficient to inhibit 91.1 ± 0.5% of phytopathogen growth on mango (Santos Villalobos et al. 2012). In short, increased concentration siderophore production by the PGPR bacteria could trigger inhibition of phytopathogens due to the starvation of iron.

12.2.5 Antibiosis

The term antibiosis is an antagonistic association between organisms and is the productions of metabolic substances by one organism which is detrimental to the other. In addition to siderophore production, majority of rhizosphere bacteria produced metabolites with antifungal properties which are known in controlling fungal diseases (Shehata et al. 2016; Opelt et al. 2007). These AFMs are also known as antibiotics which are compounds that deter the metabolic processes or growth of other microorganisms (Beneduzi et al. 2012; Duffy et al. 2003). Generally, PGPR produced one or more antibiotic as a mechanism which gave them ability to play the role of antagonism against pathogens (Beneduzi et al. 2012; Glick et al. 2007). Better understanding of the phenomenon of antibiosis as the activity of biocontrol has come to the domain of its peak in the last two decades (Lugtenberg and Kamilova 2009).

The possible mechanisms of action for most of these compounds are discussed by Haas and Defago (2005). Majority of the antibiotics have been isolated and studied, and a great diversity has been observed in their mechanisms to prevent synthesis of pathogen cell walls and inhibit the formation of initiated complexes on the small subunit of the ribosome (Maksimov et al. 2011). The antibiotics best known to involve in biological control by PGPR include bacillomycin D, phenazines, pyocyanin, pyrroles, pyoluteorin, pyrrolnitrin, volatile hydrogen cyanide (HCN), oomycin A, iturins, fengycins, surfactin, mupirocin, bacillomycin, zwittermicin, 2-hexyl-5-propyl resorcinol (Sindhu et al. 2009; Akhtar and Siddiqui 2010; Ahanger et al. 2014; Mabood et al. 2014; Shaikh and Sayyed 2015), volatiles 2,3-butanediol (Ryu et al. 2003), d-gluconic acid (Kaur et al. 2006), 2-hexyl-5-propyl resorcinol (Cazorla et al. 2006), 6-pentyl-α-pyrone (Lorito et al. 2010) and polymyxin, circulin and colistin (Maksimov et al. 2011). Some researchers have proved this through analysis (mutational) followed by studies like complementation studies (Lugtenberg et al. 2013). Majority of these antibiotics were produced by the group of bacteria known as *Bacillus* sp. These antibiotics are found to be effective against phytopathogenic fungi *Aspergillus flavus*, *Fusarium oxysporum*, *Alternaria solani*, *Botryosphaeria ribis*, *Phomopsis gossypii*, *Helminthosporium maydis*, *Colletotrichum gloeosporioides*, etc. (Maksimov et al. 2011).

Nowadays, a detailed investigation has been carried out on the class of antibiotics secreted by numerous species of bacteria, including *Bacillus* known as cyclic lipopeptides (cLPs). The cLPs consist of three major families, namely, the iturins, surfactins and the fengycins. Their mechanisms of beneficial action depend on direct antibiosis of phytopathogens (Borriss 2011; Perez-Garcıa et al. 2011). Several reports have been presented as evidences for the involvement of cLPs in biocontrol activity as exemplified by the fengycins' activity in biological control of *B. cinerea* on apple which was traced in the infected parts of apple at some level of concentrations (Toure et al. 2004). Zeriouh et al. (2011) recently proved the involvement of iturins in the control of *Xanthomonas campestris* and *Pectobacterium carotovorum*. Similarly, Yanez-Mendizabal et al. (2012) observed and reported the involvement of fengycins in the inhibition of peach brown rot disease with mutational analysis. Henry et al. (2011) also enumerated that fengycins combined with surfactins affect defence pathways in tomato and bean. Furthermore, cLPs are involved in biofilm formation, cell differentiation and cannibalism (Lopez et al. 2009).

12.2.6 Bacteriocins Production

Bacteriocins are proteinaceous toxins produced by some bacteria to inhibit the growth of similar or closely related bacterial strains which were first discovered and called colicine in 1925 by A. Gratia because it killed *Escherichia coli* (Gratia 2000). Bacteriocins are narrow in their action and toxic mostly to bacteria related to the producing species, and this is the main difference between bacteriocins and antibiotics (Riley and Wertz 2002). Typical examples of bacteriocins secreted by some bacteria especially gram negative that are lethal to related strains include cloacins derived from *Enterobacter cloacae*, pyocins from *P. pyogenes*, colicin from *E. coli*, megacins from *B. megaterium* and marcescens from *Serratia marcescens* (Beneduzi et al. 2012; Cascales et al. 2007). Abriouel et al. (2011) reported that bacteriocins from *Bacillus* sp. have a broad spectrum against gram-positive species, gram-negative bacteria and fungi or yeast.

12.2.7 Interference with the Activity in Survival, Multiplication, Germination, Sporulation and Spread of the Pathogen

Many bacterial strains have been harnessed and used as biocontrol agents to interfere with growth of some soilborne fungal pathogens. Majority of these strains are from fluorescent pseudomonads including *P. fluorescens*, *P. putida*, *P. aeruginosa and P. aureofaciens* that suppressed soilborne pathogens through antibiosis, rhizosphere competition and iron chelation by siderophores production (Jianbin et al. 2010). *Pseudomonas* strains, *P. fluorescens* WCS365 and *P. putida* PCL1760, have been reported to suppress tomato foot and root rot (TFRR) in stone wool, and their characteristics are well known and documented (Kamilova et al. 2006; Validov et al. 2009). Studies on the control of tomato *Fusarium* root rot disease with the biological control agent *P. fluorescens* strain WCS365 have indicated a positive result through a series of activities that interfere with the cyclic events in the growth of the pathogen including germination, sporulation, multiplication, survival and spread of the pathogen (Lugtenberg et al. 2013).

In the process of biocontrol, the hyphae of the fungus secreted fusaric acid (FA) which is believed to attract the cells of the strain *P. fluorescens* WCS365 with subsequent extensive colonization of hyphae, leading to the formation of biofilms or microcolonies (Lugtenberg et al. 2013; de Weert et al. 2004). Colonization of hyphae and subsequent formation of biofilms make the fungus ineffective and inhibit its growth, reproduction and survival. In a situation where there is nutrient scarcity (nutrient deprivation), biocontrol strain *P. fluorescens* WCS365 used the hyphae as a food source through hyphal colonization with subsequent spore germination inhibition (Kamilova et al. 2008). This conclusively showed that in the presence of *P. fluorescens* WCS365, spore formation will be reduced, and, therefore, this will also reduce pathogen spread, thus, serving as a biocontrol agent (Kamilova et al. 2008; Validov et al. 2009).

12.2.8 Cell Lysis and Degradation

Most of the PGPR produce enzymes such as chitinases, cellulases, glucanases and proteases that hydrolyse polymeric compounds like chitin, cellulose, proteins, hemicellulose and DNA. This will help in the inhibition of phytopathogens (Shaikh et al. 2016). Mabood et al. (2014) reported that these enzymes are known to cause degradation and lysis of cell walls which help in the control of phytopathogens. For example, chitinases and β-1,3-glucanase-producing PGPR such as *B. subtilis* BSK17, *B. suly*, *Paenibacillus illinoisensis*, *P. illinoisensis* KJA-424, *Pseudomonas* sp., *Enterobacter ammrenus*, *Pantoea dispersa* and *Pythium ultimum* are reported to demonstrate some potentials in biocontrol activity (Shaikh et al. 2016). Dubbey et al.

(2014) reported that chitinases and β-1,3-glucanase are produced by *B. subtilis* BSK17 that assist in their root zone competition and antagonistic activity. Similarly, severity of *Fusarium* infections produced under greenhouse conditions is reduced through chitinase production by *B. suly* (Hariprasad et al. 2011). Biocontrol activity by *Paenibacillus illinoisensis* has also been demonstrated against *Phytophthora capsici* causing blight in pepper by the secretion of chitinase (Jung et al. 2005).

12.3 Biological Control Mechanisms in *Burkholderia* sp. Against Phytopathogens

Burkholderia species are considered beneficial in the ecosystem in that they can be used for biological control of diseases caused by fungi in plants, plant growth promotion and bioremediation (Perin et al. 2006; Compant et al. 2008). Several *Burkholderia* species have shown the ability to use different mechanisms such as competition and secretion of allelochemicals, including antibiotics and siderophores known with antimicrobial activity, competition for nutrients, induced systemic resistance (ISR), antagonism as well as hyphal colonization. All these are good features of potential biocontrol agents against phytopathogenic fungi (Baldani et al. 2000; Welbaum et al. 2004; Compant et al. 2005b; Kang et al. 1998; Hu and Young 1998). The efficacy of these *Burkholderia* species as biocontrol agents has been shown by *B. cepacia*, *B. ambifaria*, *B. pyrrocinia*, *B. cenocepacia*, *B. vietnamiensis* and *B. phytofirmans* strains against *Fusarium* sp., *P. capsici*, *Pythium ultimum*, *P. aphanidermatum*, *B. cinerea* and *R. solani* (Compant et al. 2008; Ait Barka et al. 2002; Cain et al. 2000; Parke and Gurian-Sherman 2001; Singh et al. 2006). Several reports have proved these potentials as exemplified by the report of Cuong et al. (2011) by the colonization activity of hyphae-colonizing *Burkholderia* sp. against *R. solani* causing sheath blight in rice. Some traits of *Burkholderia* sp. strains have been shown to encompass antifungal genes which enable members of the group to produce a wide range of secondary metabolites active against *R. solani*. Examples of the metabolites are pyrrolnitrin, phenazine, cepaciamide A (Cartwright et al. 1995; Rosales et al. 1995; El-Banna and Winklemann 1998; Jiao et al. 1996; Mao et al. 2006) and some unknown compounds (Mao et al. 2006).

Bevivino et al. (1994) reported that *Burkholderia* sp. produced very efficient low-molecular-weight iron-chelating compounds known as siderophores which are shown to be involved in antibiosis mechanism against plant pathogens through iron competition under iron-limiting conditions. Ornibactins, cepaciacheline and cepabactine are the predominant siderophores produced by *Burkholderia* strains (Meyer et al. 1995; De Meyer et al. 2015). Recently, it has been reported that 1-am inocyclopropane-1-carboxylate (ACC) deaminase-containing endophyte belonging to *Burkholderia* sp. exhibited antagonistic activity against *R. solani* and *Sclerotinia sclerotiorum* (Pandey et al. 2005).

12.4 PGPR as a Plant Growth Promoter

Generally, plant growth-promoting mechanisms exhibited by PGPR were categorized into two main groups, i.e. direct and indirect mechanisms. In the past, more emphasis has been laid on direct interaction rather than indirect interaction. Direct mechanism may involve nitrogen fixation, phosphate solubilization ability, siderophore production and production of plant growth regulators. On the other hand, indirect mechanisms may include suppression of phytopathogens and enhancement of mutualisms between host plants and other symbionts (Kloepper et al. 1989).

12.4.1 Nitrogen Fixation

Nitrogen-fixing microbes are generally categorized into two main groups (a) symbiotic N_2-fixing bacteria and (b) non-symbiotic bacteria. Diazotrophs are a PGPR that fix N_2 in nonleguminous plants (Glick et al. 1999). Basically, biological nitrogen fixation (BNF) is restricted to prokaryotic organisms. Currently, hundreds of bacterial species were identified, covering most of the different biotrophic energy systems such as photosynthetic bacteria (e.g. *Rhodospirillum rubrum*), anaerobic bacteria (e.g. *Clostridium* sp.), microaerobic (*Burkholderia* sp.) and aerobic bacteria (e.g. *Azotobacter*). Biological nitrogen fixation usually takes place at mild temperatures (Raymond et al. 2004), so that the fixation process can occur everywhere on the earth (Table 12.1). The genus *Burkholderia* was documented as one of the richest N_2-fixing bacteria. Among them *B. vietnamiensis* was the first known N_2-fixing species of this genus and was isolated from the rhizosphere of rice plants in Vietnam. This bacterium has attracted interest of many researchers because of its abilities to fix N_2, promote rice plant growth and enhance grain yield.

12.4.2 Phosphate Solubilization

The search for an ecologically safe and economically reasonable option for improving crop production in low-phosphorus soils becomes the ultimate outcome in soil fertility research. In this context, phosphate-solubilizing bacteria (PSB) are considered as promising biofertilizers since they can supply plants with phosphate from sources otherwise poorly available by various mechanisms (Zaidi et al. 2009). Excellence examples of phosphate-solubilizing bacteria are *Azotobacter*, *Bacillus*, *Beijerinckia*, *Burkholderia*, *Enterobacter*, *Erwinia*, *Flavobacterium*, *Microbacterium*, *Pseudomonas*, *Rhizobium* and *Serratia* (Bhattacharyya and Jha 2012). These bacteria were reported to solubilize inorganic phosphorus through synthesization of the low-molecular-weight organic acids in the soil (Zaidi et al. 2009). The mineralization of organic phosphorus occurs through the synthesis of a variety of different phosphatases, catalysing the hydrolysis of phosphoric esters (Glick 2012). Most importantly, both phosphate solubilization and mineralization can coexist in the same bacterial strain (Tao et al. 2008).

Table 12.1 Distribution of biological nitrogen fixation system

Ecosystem	Nature of BNF	Type	Occurrence
Natural	Symbiotic	Root and stem nodule	Legumes
		Rhizobium, *Frankia*	Actinorhizal trees/shrubs
		Mosses, lichens, pteridophytes	Soil, rock, tree surface
		Insects	Gut of termites
		Gunnera-Nostoc	Base of leaves, cycad root
	Non-symbiotic	Free-living saprophytes (numerous species, aerobes, microaerobes, anaerobes)	Soil and plant root rhizosphere bacteria on litters
		Photosynthetic, *Anabaena*, *Nostoc*, etc.	On plant surfaces cyanobacteria (blue-green algae)
		Photosynthetic bacteria, *Rhodospirillum rubrum*, etc.	Aquatic and marine bacteria
Agriculture/forestry	Symbiotic	Nodulated legumes	Annual, perennial, rotation crops, green manure
		Actinorhizal, angiosperms	Plantation system
		Miscellaneous symbiotic	Pioneer uses, *Azolla*, sugar cane, etc.
	Non-symbiotic	Free-living saprophytes (numerous species, aerobes, microaerobes, anaerobes)	Rice paddies
		Photosynthetic, *Anabaena*, *Nostoc*, etc.	
		Photosynthetic bacteria, *Rhodospirillum rubrum*, etc.	

Adapted from Kennedy and Cocking 1997

12.4.3 Phytohormone Production

Microbial synthesis of the phytohormone, namely, auxin (indole-3-acetic acid/indole acetic acid/IAA), was reported a long time ago. Apart from IAA, PGPR are also capable of synthesizing other plant hormones, such as gibberellins (GAs) and cytokinins (CKs) or affecting plant hormone biosynthesis (homeostasis) *in planta* (Kurepin et al. 2014). IAA plays crucial role in bacteria-host interactions (Spaepen and Vanderleyden 2011). It is well known that IAA affects plant physiological processes such as cell division, extension and differentiation; stimulates seed and tuber germination; increases the rate of xylem and root development; controls processes of vegetative growth; initiates lateral and adventitious root formation; mediates responses to light, gravity and florescence; and affects photosynthesis, pigment formation, biosynthesis of various metabolites and resistance to stressful conditions. *Burkholderia phytofirmans* strain PsJN was reported capable of inducing biomass growth of several crops including potato. This report showed massive root growth increases after inoculation, and this was associated with a twofold to threefold increase in IAA and CK (trans-zeatin or tZ) levels (Kurepin et al. 2015).

12.4.4 Harmonizing Ethylene Production

Many studies show ethylene gas is a crucial growth regulator of numerous aspects of plant development and physiology (Merchante et al. 2013) such as germination, seedling growth and morphology, fruit ripening, organ senescence and stress/defence response (Khalid et al. 2006; Broekgaarden et al. 2015). However, under usual condition the ethylene gas production is always in low concentration. This is due to the biosynthesis of this compound which depends on transcriptional and post-translational mechanisms that regulate the activity levels of the biosynthetic enzymes (Booker and DeLong, 2015). On the other hand, if ethylene present is in high concentration, it may inhibit physiological activities in plant-like root elongation. In this case, PGPR are needed in harmonizing the level of ethylene in plant by converting 1-aminocyclopropane-1-carboxylate (ACC) into ammonia and α-ketobutyrate (Nascimento et al. 2014). Currently, *Achromobacter*, *Agrobacterium*, *Alcaligenes*, *Acinetobacter*, *Azospirillum*, *Bacillus*, *Burkholderia*, *Enterobacter*, *Pseudomonas*, *Ralstonia*, *Serratia* and *Rhizobium* were reported to have ability to harmonize ethylene gas production in plant (Kang et al. 2010; Zahir et al. 2008, 2009). *Burkholderia phytofirmans* PsJN is one of the best-studied *Burkholderia*. This strain was reported to inhabit the rhizosphere and endosphere of plant, thus promoting growth and enhancing stress adaptation in selected herbaceous and woody plant species (Da et al. 2012; Fernandez et al. 2012; Kim et al. 2012; Naveed et al. 2014). According to Poupin et al. (2013) and Zuniga et al. (2013), *B. phytofirmans* PsJN showed excellent capability of promoting growth and accelerating the whole life cycle of *Arabidopsis thaliana*. Moreover, this strain also induces primary root growth and root hair development and promotes aerial growth increasing the epidermal cell size (Poupin et al. 2013) and induces salt stress tolerance (Pinedo et al. 2015) in *A. thaliana*.

12.5 Commercial Potentials of PGPR in Malaysia

Malaysia was the largest pepper-producing country in the world. However, after 1980, Malaysia lost its top position to India and Indonesia (Azmil 1993). Currently, Malaysia is ranked sixth in terms of world pepper production (IPC 2012). Approximately 45,000 families and more than 115,000 workers are involved in the pepper industry in Malaysia. This crop generates about one third of Sarawak's agriculture export earnings, and Sarawak is the main black pepper export producer in

Malaysia. Currently, production of black pepper in Sarawak showed a declining trend. One of the main factors is due to pests and diseases infestation. Foot rot disease is considered the most devastating disease in black pepper.

At present, no effective control measure is available to effectively manage this disease in the world. Application of PGPR might be one of the alternative solutions to chemical control of the disease in the field. Attempt was made to find potential indigenous PGPR strain to control foot rot disease in vitro and in vivo. We found promising PGPR strains that are able to induce systemic resistance in black pepper as well as showing biological control traits like producing antibiotics which caused lysis of the mycelial cells of *P. capsici*. The tested PGPR strains were also found to promote the growth of the treated plants. The use of PGPR should be a preferable method as they are internal colonizers and more efficient to compete in the vascular systems. Thus, this will certainly deprive *P. capsici* in terms of nutrient uptake and space for their proliferation. Based on dual culture test, these three PGPR strains, BPA011, BPA040 and BPA025, exhibited high percentage of inhibition on radial growth with recorded PIRG values as ~81, 83 and 81%, respectively. Furthermore, in culture filtrate test, all the three strains exhibited 100% PIRG (Fig. 12.5 and Table 12.2). These potential strains were successfully identified using GC-FAME as *B. cepacia*, *B. cenocepacia* and *Bacillus alcalophilus*, respectively.

Results from in vivo test demonstrated that application of PGPR resulted in disease suppression and delayed disease onset on treated plant. The present study showed that there were significant differences in terms of disease incidence (DI) and disease severity index (DSI) as compared with control treatment. Our findings showed treated plant with *B. cenocepacia* showed the lowest DSI (1.67%) in the first month, and the severity index was increased gradually in the second month (5.85%), and finally the DSI remained steady at ~10% along the assessment period. A similar trend was observed at *B. cepacia* and *B. alcalophilus* treatments.

Assessment on production of inducible compounds by the host plant was also conducted. Our findings revealed an increased in enzymatic activity of peroxidase (PO), total phenolic content (TPC) and hydrogen peroxidase (H_2O_2) in the treated plants. Significant amount of inducible compounds was expressed in root, stem and leaf parts of the treated plants. Our findings indicated that the systemic protection was offered to the host plant by the tested PGPR strains. This event resulted in limiting and preventing the phytopathogens activities, even at foliar infection by the *P. capsici*. Moreover, the positive effects of PGPR on plant growth are always correlated with a remarkable increase in the root morphology such as lateral root length, root hair number and also shoot length and yield. In our study, we found root, stem and leaf biomass were significantly increased in the treated plants, and this is generally assumed that these developmental responses are triggered by phytohormones such as auxins, cytokinins and gibberellins produced by the PGPR strains.

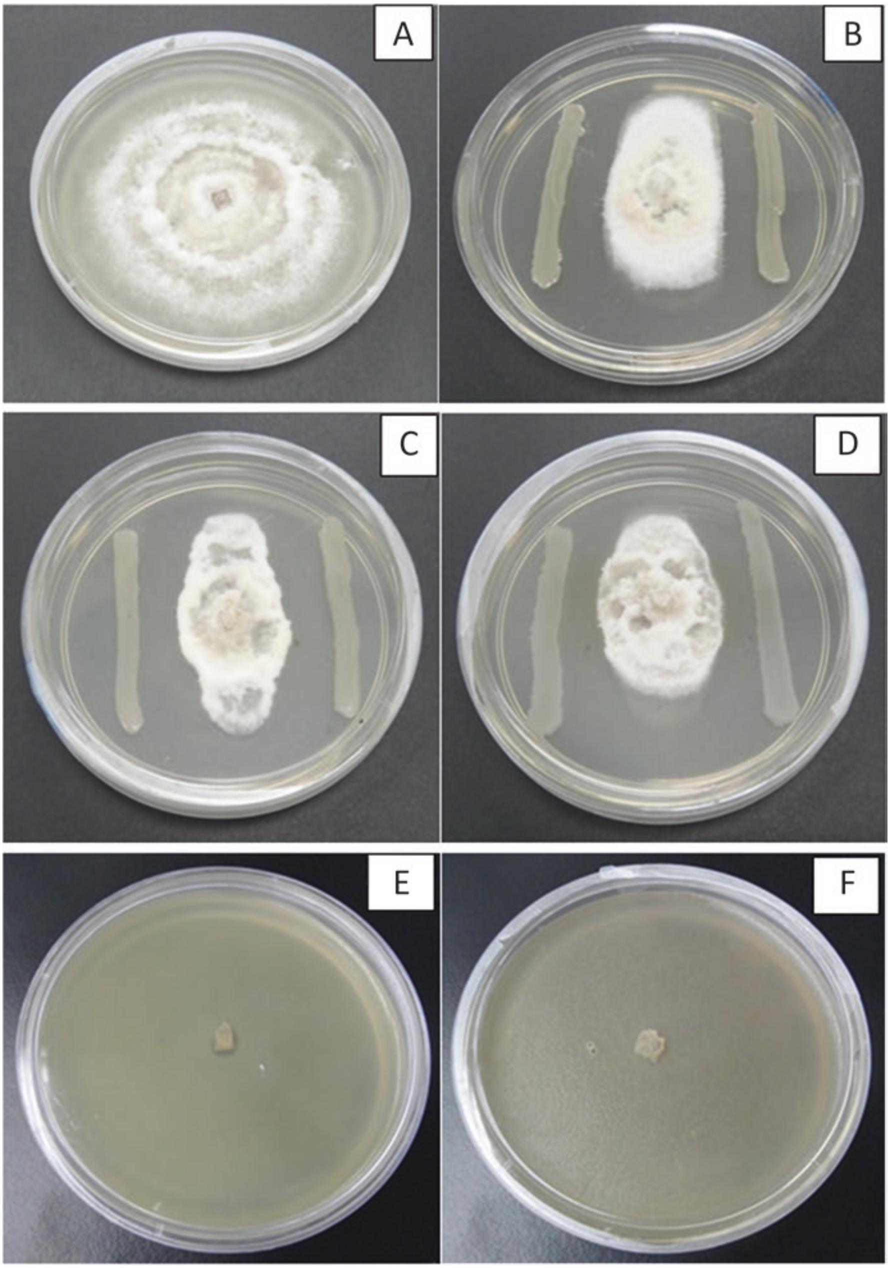

Fig. 12.5 The effect of endophytic bacteria on mycelial growth of *P. capsici* in dual culture and cultural filtrate tests at 7 days after incubation. Pure culture of *P. capsici* in control plate (**a**), BPA011 (**b**), BPA040 (**c**), BPA025 in dual culture test (**d**) and BPA011 and BPA040 in culture filtrate test (**e** and **f**), respectively

Table 12.2 Potential candidates of PGPR were tested using dual culture and culture filtrate tests against *P. capsici* in vitro

Bacteria code	Dual culture test (% PIRG)*	Culture filtrate test (% PIRG)	Identification by CG-FAME
BPA011	81.04 ± 0.59[a]	100 ± 0[a]	*Burkholderia cepacia*
BPA025	80.83 ± 0.09[a]	100 ± 0[a]	*Bacillus alcalophilus*
BPA040	82.97 ± 0.47[a]	100 ± 0[a]	*Burkholderia cenocepacia*

Means in the same column with different alphabet(s) are significantly different ($p \leq 0.05$) according to DNMRT

[a]Percentage inhibition of radial growth (PIRG) of *P. capsici* was assessed at 7 days after incubation

12.6 Future Prospect

Currently, majority of black pepper farmers in Malaysia rely extensively on chemical fungicides to control foot rot disease in black pepper. Heavy reliance on chemical fungicides may lead to numerous biohazards such as environmental pollutions, residual effect in food and pathogen resistance and may be hazardous to beneficial microorganisms. From crop management perspective for sustainable agriculture, the control of foot rot disease in black pepper using PGPR (*Burkholderia*) would best be achieved by combining these two techniques: (i) disease control through the use of biocontrol agents native to black pepper farms involving continuously inoculation of PGPR inoculum to increase their populations and (ii) disease control through application of antifungal metabolites responsible for effectiveness of the biocontrol agent-developed product usually more effective and easier to be used by farmers. Meanwhile, diminishing the biohazards is inherent in the use of intact microbial cells (and the associated potential risk to human health). Application of green technology in agriculture in Malaysia has become more evident in recent year. Implementation of National Green Technology Policy since 2009 contributed huge impact in research and development as well as in agriculture practices in Malaysia. One of the biggest impacts is the ability to achieve reduction in the greenhouse gas intensity of gross domestic product (GDP) of 35% in 2015. Even though many incentives and funds were given by Malaysian government in developing new and effective formulations for effective delivery of PGPR, the process is still very slow. Formulation of biopesticides with PGPR-like *Burkholderia* sp. is a big challenge in practical agriculture especially in the tropical regions where the environmental conditions are favourable for the pathogen to grow. Hence, improvement in the formulation of biopesticides is the key to the success in the development of sustainable agriculture.

In plant protection perspective, integrated pest management (IPM) programme is now adopted widely by commercial planters and farmers. With this regard, PGPR strains tested in this study are showing promising outcomes to be used for sustainable and environmentally friendly horticultural production system. The prospect and potential of manipulating PGPR by direct cell inoculation to increase crop yield and reduce disease pressure have shown considerable promise in laboratory and greenhouse studies. However, this technique is not really successful under field conditions. This might be due to climatic variations, and the soil itself is an unpredictable environment, and an intended result is sometimes difficult to achieve. Hence, development of new formulation biofungicide is urgently needed to overcome the above-mentioned limitations as well as to effectively control phytopathogens in field condition. As reported by many authors, biofungicides are safe or have very small residues and harmless to beneficial organisms, and the most important biofungicides are cost-effective to control many pests and diseases in the field.

12.7 Conclusions

Burkholderia sp. are promising biological control agents against the causal agent of foot rot disease, *P. capsici* Leonian, through the production of antifungal metabolites, induction of disease resistance and promoting plant growth. These results support the potential use of *B. cepacia* or its antifungal metabolites as a microbial alternative to control phytopathogens involved in high losses of agricultural production, diminishing the environmental problems caused by current practices. Government involvement by introducing specific policies or long-term programmes which is associated with "green technology" in order to monitor and protect clean environment is highly recommended for sustainable agriculture.

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