Role of Endophytic Bacteria in Stress Tolerance of Agricultural Plants: Diversity of Microorganisms and Molecular Mechanisms

1

Inga Tamosiune, Danas Baniulis, and Vidmantas Stanys

Abstract

Bacterial endophytes are a group of endosymbiotic microorganisms widespread among plants. An association of plants with endophytic bacteria includes a vast diversity of bacterial taxa and host plants. In this review we present an overview of taxonomic composition of the bacterial endophytes identified in common agricultural crops with special emphasis on the most recent results obtained using metagenomic analysis. Endophytic microbiome constitutes a part of larger soil microbial community and is susceptible to direct or indirect effect of agricultural practices: soil tillage, irrigation, use of pesticides and fertilizers has a major effect on function and structure of soil and endophytic microbial populations. Therefore, the use of agricultural practices that maintain natural diversity of plant endophytic bacteria becomes important element of sustainable agriculture that ensures plant productivity and quality of agricultural production. On the other hand, the endophytic microbiome itself have been shown to have multiple effects on their host plant, including modulation of phytohormone signaling, metabolic activity, and plant defense response pathways. It has been demonstrated that these effects could be helpful for plant adaptation to abiotic or biotic stresses. Therefore, application of endophytic bacteria to improve crop performance under cold, drought, salinity, and heavy metal contamination stress conditions or to enhance disease resistance presents an important potential for sustainable agricultural production.

I. Tamosiune • D. Baniulis • V. Stanys (✉)
Institute of Horticulture, Lithuanian Research Centre for Agriculture and Forestry,
Kaunas str. 30, Babtai, Kaunas reg, Lithuania
e-mail: i.miliute@lsdi.lt; d.baniulis@lsdi.lt; v.stanys@lsdi.lt

V. Kumar et al. (eds.), *Probiotics in Agroecosystem*,
DOI 10.1007/978-981-10-4059-7_1

1.1 Introduction

An intensification of agricultural production has been crucial in sustaining population growth throughout civilization history (Ellis et al. 2013). During the last century, the agricultural intensification has been largely achieved through improvement in crop productivity and the use of farm equipment, irrigation, intensive tillage, fertilizers, pesticides, and other manufactured inputs (Foley et al. 2005; 2011). However, these agricultural practices often lead to detrimental effects on environment as well as human health. Therefore, new environmentally benign pathways have to be employed to maintain increase in agricultural production while greatly reducing unsustainable uses of water, nutrients, and agricultural chemicals. This requires new means to overcome threats that cause loss of crop yield, including plant stresses associated with unfavorable environmental conditions, such as drought, temperature extremes, or soil salinity, as well as biotic stress induced by plant pathogens and pests. Therefore, the attention is drawn to exploitation of mutualistic and antagonistic biotic interactions within agroecosystems that would increase crop productivity and improve sustainability of pest control technologies (Gaba et al. 2014).

Plants live in intimate association with microorganisms that fulfill important functions in agricultural ecosystems and represent an important resource for improvement of plant performance through enhancing crop nutrition or reducing damages caused by pathogens or environmental stress (Jha et al. 2013; Singh et al. 2011). Bacteria constitute the most numerous group of microorganisms in soil (Whitman et al. 1998). They exist as free-living organisms, attached to the surface of roots or phyllosphere, and establish interactions with plants. The extreme forms of plant–microbe interactions could be categorized into commensal (acquire nutrients from the plant without damaging), mutualistic (positively influence plant health), and pathogenic (damage plant) type, yet many microorganisms exploit different forms of relationship with plants during their life cycles (Newton et al. 2010). Endophytic bacteria are a group of endosymbiotic microorganisms that live in internal plant tissues of apparently healthy host plants and do not normally cause any substantial disease symptoms (Schulz and Boyle 2006).

Endophytic bacteria colonize intercellular spaces of the cell walls and xylem vessels of plant roots, stems, and leaves, and they are also found in tissues of flowers (Compant et al. 2011), fruits (de Melo Pereira et al. 2012), and seeds (Cankar et al. 2005; Johnston-Monje and Raizada 2011; Trognitz et al. 2014). Meanwhile it is generally believed that endophytic bacteria reside in apoplast of plant cells, several studies of intracellular colonization of cytosol have been published (Cocking et al. 2006; Koskimaki et al. 2015; Thomas and Sekhar 2014; White et al. 2014). Plant roots have been established as the main entry point of the potential endophytes from soil and provide a base camp for colonization of other plant organs. Higher density of endophyte populations is characteristic to plant roots and other belowground tissues as compared to phyllosphere, and an ascending migration of endophytic bacteria from roots to leaves of rice plants has been demonstrated (Chi et al. 2005). It has been also shown that plant roots are capable to take up bacteria from surrounding environment (Paungfoo-Lonhienne et al. 2010). Isolation of endophytic bacteria from seeds suggests an alternative transmission route (Cankar et al. 2005; Johnston-Monje and Raizada 2011; Trognitz et al. 2014). Structure of the endophytic community is defined by abiotic and biotic factors such as environmental conditions, microbe–microbe interactions, and plant–microbe interactions (Ryan et al. 2008).

Diverse effects of endophytic bacteria on plant health and growth have been well documented. The endophytes aid nutrient availability and uptake, enhance stress tolerance, and provide disease resistance (Hamilton et al. 2012; Ryan et al. 2008). The plant growth-promoting capability of endophytes is established through activity that increases accessibility of nutrients, such as nitrogen and phosphorus, or is mediated by compounds produced by the microorganisms and the host cells, such as plant growth hormones (Brader et al. 2014; Glick 2012; Reinhold-Hurek and Hurek 2011). Disease protection properties are associated with ability of endophytic bacteria to produce compounds, such as antibiotics and fungal cell-wall lytic enzymes, which can inhibit growth of plant pathogens (Brader et al. 2014; Christina et al. 2013; Raaijmakers and Mazzola 2012; Wang et al. 2014) or priming plant response to pathogens by induced systemic resistance (ISR) mechanism (Pieterse et al. 2014). Owing to their plant growth-promoting and disease control properties, endophytes can be used in the form of bioinoculants in agriculture to benefit development of sustainable agricultural production practices (Mei and Flinn 2010).

The aim of this review is to outline the understanding about diversity of endophytic bacterial communities of agricultural crops and their implication in plant adaptation to stress and disease resistance. We provide a summary of the extensive information on taxonomic composition of bacterial endophytes identified in major agricultural crop plants that has been remarkably expanded due to application of advanced metagenomic analysis methods. Effect of different agricultural practices on the diversity of endophytic bacterial communities is assessed. Further, an implication of endophytes in plant adaptation to stress and disease resistance through modulation of phytohormone balance or induction of stress-related metabolites or systemic resistance signaling pathway is presented.

1.2 Assessment of Diversity of Bacterial Endophytes Using Cultivation Techniques and Metagenomic Analysis

Plants are naturally associated with continuum of other organisms, the majority of which are bacterial endophytes. Population densities of endophytic bacteria are extremely variable in different plants and tissues and have been shown to vary from hundreds to reaching as high as 9×10^9 of bacteria per gram of plant tissue (Chi et al. 2005; Jacobs et al. 1985; Misaghi and Donndelinger 1990). Initial studies of diversity of endophyte community were mostly based on the classic microbial culture techniques; therefore, bacterial endophytes isolated using surface sterilization methods have been reported for most species of agricultural plants (Rakotoniriana et al. 2013). One of the early reviews by Hallman et al. (1997) presented the list of isolated bacterial endophytes from various plant parts of different agricultural crops.

The list was supplemented by latter studies on endophyte diversity (Bacon and Hinton 2007; Lodewyckx et al. 2002; Rosenblueth and Martinez-Romero 2006; Ryan et al. 2008; Sturz et al. 2003).

Innovative culture-independent sequencing technologies allow much deeper assessment of microbial communities and improve our understanding about diverse microbiomes occupying plants. In recent years, extensive information about diversity of endophytic microbiota has been gathered using metagenomic sequencing platforms. Application of hypervariable regions from small subunit ribosomal RNA gene (16S rRNA) for the metagenomic sequencing allows precise taxonomic identification (Turner et al. 2013). Direct amplification of microbial DNA from plant tissue samples and application of modern bioinformatics tools allow analysis of growing numbers of plant material samples, and such studies have revealed rarely reported endophyte species of *δ*- and *ε-Proteobacteria* (Sun et al. 2008). In addition, culture-independent high-throughput sequencing technologies reflect variations of total microbial diversity and their physiological potential and ecological functions (Akinsanya et al. 2015; Turner et al. 2013; van Overbeek and van Elsas 2008). For example, Tian and associates (Tian et al. 2015) used second-generation sequencing technology to assess diversity of bacterial endophytes before and after nematode attack, and the study revealed that nematode infection was associated with variation and differentiation of the endophyte bacterial populations.

Studies of microbial diversity using culture-independent molecular techniques could be limited by relatively low abundance of endophytic bacteria that results in underrepresentation in metagenomic library. This problem is associated with difficulties in separation and high sequence homology of endophytic bacteria, plant nuclei, plastids, mitochondria, and plant-associated microbial DNA (Govindasamy et al. 2014). In recent years, gene enrichment strategies have been broadly used. Bacterial DNA extraction from host plant tissues and enrichment is the key step in preparation of the metagenomic library harboring representative sample of microbial diversity. In order to recover target genes of metagenome, a suitable enrichment method should be used before DNA amplification (Mutondo et al. 2010). Jiao et al. (2006) enriched target genes from a metagenome by optimized hydrolysis of the plant cell walls, followed by differential centrifugation. Wang et al. (2008) efficiently enriched bacterial DNA from medicinal plant by specific enzymatic treatment. The same method increased representation of less abundant grapevine-associated bacteria (Bulgari et al. 2009). Series of differential centrifugation steps followed by a density gradient centrifugation efficiently enriched proportion of microbial DNA in stems of soybean (Ikeda et al. 2009). Maropola and colleagues (2015) analyzed the impact of metagenomic DNA extraction procedures on the endophytic bacterial diversity in sorghum and found that different DNA extraction methods introduce significant biases in community diversities. The authors stated that despite the differences in results of extraction of DNA, the agriculturally important genera such as *Microbacterium*, *Agrobacterium*, *Sphingobacterium*, *Herbaspirillum*, *Erwinia*, *Pseudomonas*, and *Stenotrophomonas* were predominant. An enrichment method useful for extraction of plant-associated bacteria of potato tubers was developed by Nikolic et al. (2011) and involved overnight shaking of small pieces of potato tubers in sodium chloride solution.

Although 16S rRNA gene clone library technique provides efficient means to study different agricultural plant microbiota in detail (genetics and physiology), however, not all endophytes are easily amenable using this method as well (Sessitsch et al. 2012). The methods for microbe enrichment in plant tissues may lead to overrepresentation of high-abundance bacterial species and reduced representation of low-abundance species. Therefore, a combination of microbial cultivation and culture-independent metagenomic analysis methods provides broader perspective of the diversity of endophytes.

A summary of the most widespread bacterial isolates identified in common agricultural crop plants is presented in Table 1.1. Due to a vast diversity of bacterial species and host plants described to this day, the list is not complete and presents a sample of important agricultural crops and overview of associated endophytic bacterial species identified using both, cultivation and metagenomic, analysis methods.

A study of direct comparison of culture-dependent and culture-independent approaches for assessing bacterial communities in the phyllosphere of apple has been published by Yashiro et al. (2011). Among the cultivated isolates only order of *Actinomycetales* has been found, while metagenomic approach has revealed the presence of *Bacteroidales*, *Enterobacteriales*, *Myxococcales*, and *Sphingobacteriales*. Differences between plant-associated microbial phyla are revealed when comparing the niches of rhizosphere, endosphere, and phyllosphere. The largest diversity is found in the roots, as it is the primary site of interaction between plants and soil microorganisms (Hardoim et al. 2011). Maropolla and colleagues (2015) found that diversity of sorghum-associated endophytic bacteria is lower in stems than that of rhizospheric communities. Rhizospheric endophytic species mostly belong to *α*-, *β*-, and *γ-Proteobacteria* subgroups and are closely related to epiphytic species (Kuklinsky-Sobral et al. 2004). The group of *γ-Proteobacteria* is found to be the most diverse. Culture-dependent methods revealed bacteria species that belong to the *Proteobacteria*, meanwhile *Firmicutes*, *Actinobacteria*, and also *Bacteroides* are less common (Reinhold-Hurek and Hurek 2011).

Culture-independent approach suggests a 100–1000-fold higher diversity of the bacterial communities in economically important crops (Suman et al. 2016; Turner et al. 2013). Sessitsch with associates (Chi et al. 2005) investigated genomic characteristics of the most abundant bacterial endophytes colonizing rice roots under field conditions without cultivation bias. In this study, the members of *γ-Proteobacteria*, comprising mostly *Enterobacter*-related endophytes, were predominant. Metagenomic analyses demonstrated that rhizobia (and other *α-Proteobacteria*) were the most abundant plant-associated endophytes, including *β-Proteobacteria*, *γ-Proteobacteria*, and *Firmicutes* (Turner et al. 2013). However, it was found that only culture-independent techniques were able to identify endophytic archaea (*Euryarchaeota*) (Suman et al. 2016). In general, the species of *Pseudomonas*, *Bacillus*, *Enterobacter*, *Klebsiella*, *Rhizobium*, *Sphingomonas*, *Pantoea*, *Microbacterium*, *Acinetobacter*, *Erwinia*, and *Arthrobacter* were defined as the most dominant using both methods.

Table 1.1 Endophytic bacteria isolated from common agricultural crop species plants

Phylum	Subgroup	Genus	Onion	Sorghum	Wheat	Rice	Sugarcane	Maize	Potato	Tomato	Soybean	Strawberry	Sugar beet	Bean	Pepper	Carrot	Grapevine
Proteobacteria	**α**	*Agrobacterium* sp.		■		■		■	■		■						
		Bradyrhizobium sp.				■		■					■	■			
		Brevundimonas sp.			■	■		■	■		■			■			
		Caulobacter sp.				■		■									■
		Devosia sp.						■	■					■			
		Mesorhizobium sp.						■						■			■
		Methylobacterium sp.			■	■		■	■		■			■			
		Novosphingobium sp.				■	■										
		Novosphingobium sp.									■			■			
		Rhizobium sp.			■	■		■	■		■			■		■	
		Rhodopseudomonas sp.				■		■									
		Sinorhizobium sp.			■	■					■			■			
		Sphingomonas sp.				■	■	■	■		■		■	■	■		
		Sphingopyxis sp.				■						■					
	β	*Achromobacter* sp.			■	■	■	■									
		Acidovorax sp.				■			■								
		Burkholderia sp.	■		■	■	■	■							■		■
		Comamonas sp.				■			■		■						■
		Delftia sp.			■	■					■			■			
		Duganella sp.			■	■		■									
		Gallionella sp.			■	■											

		Herbaspirillum sp.		■	■	■	■	■									
		Ralstonia sp.						■	■		■						■
		Variovorax sp.			■	■		■	■		■						
	γ	*Acinetobacter* sp.			■	■		■	■		■			■			
		Azotobacter sp.			■			■									
		Enterobacter sp.			■	■	■	■	■		■	■		■			■
		Erwinia sp.		■			■	■	■		■		■				
		Klebsiella sp.			■	■	■	■	■		■					■	■
		Kluyvera sp.			■			■									
		Pantoea sp.			■	■	■	■	■		■	■					
		Pseudomonas sp.	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
		Psychrobacter sp.			■				■								
		Serratia sp.			■	■		■	■						■		
		Stenotrophomonas sp.		■	■	■		■			■			■	■		■
		Xanthomonas sp.			■			■	■				■				■
		Geobacter sp.			■	■								■			
		Syntrophus sp.						■						■			
Firmicutes		*Bacillus* sp.			■	■	■	■	■	■	■	■	■	■	■	■	■
		Brevibacillus sp.								■				■	■		
		Clostridium sp.			■			■						■			
		Exiguobacterium sp.			■						■						
		Lactobacillus sp.										■	■				
		Lysinibacillus sp.			■			■	■					■	■		
		Paenibacillus sp.			■			■	■		■			■	■	■	■
		Staphylococcus sp.			■			■	■		■			■			■

(continued)

Table 1.1 (continued)

Phylum	Subgroup	Genus	Onion	Sorghum	Wheat	Rice	Sugarcane	Maize	Potato	Tomato	Soybean	Strawberry	Sugar beet	Bean	Pepper	Carrot	Grapevine
Actinobacteria		*Actinomyces* sp.							■								■
		Amycolatopsis sp.				■		■									
		Arthrobacter sp.			■			■	■		■				■		■
		Aureobacterium sp.				■		■									
		Brachybacterium sp.						■									■
		Clavibacter sp.						■			■						■
		Corynebacterium sp.			■	■		■	■				■				
		Curtobacterium sp.				■			■			■			■		■
		Dactylosporangium sp.				■		■									
		Frankia sp.				■		■									
		Kocuria sp.			■			■						■			
		Microbacterium sp.		■		■	■	■	■		■			■	■		■
		Micrococcus sp.			■	■			■					■	■		■
		Micromonospora sp.			■	■		■									
		Mycobacterium sp.			■	■											
		Nocardioides sp.			■	■											
		Rhodococcus sp.				■		■	■					■			■
		Rothia sp.						■									
		Streptomyces sp.			■	■		■					■				■
		Chryseobacterium sp.						■			■				■		

	Cytophagales sp.				■					■						
	Flavobacterium sp.			■	■		■	■		■				■		■
	Pedobacter sp.				■		■	■		■						
	Sphingobacterium sp.		■		■					■			■			

Onion (*Allium cepa* L.) (Frommel et al. 1991; Weilharter et al. 2011), sorghum (*Sorghum bicolor*) (James et al. 1997; Maropola et al. 2015), wheat (*Triticum aestivum*) (Balandreau et al. 2001; Coombs and Franco 2003; Iniguez et al. 2004; Jha and Kumar 2009; Larran et al. 2002; Mavingui et al. 1992; Velazquez-Sepilveda et al. 2012; Verma et al. 2013, 2014, 2015; Zinniel et al. 2002), rice (*Oryza sativa*) (Chaintreuil et al. 2000; Elbeltagy et al. 2001; Engelhard et al. 2000; Govindarajan et al. 2008; Kaneko et al. 2010; Mbai et al. 2013; Naik et al. 2009; Piromyou et al. 2015; Rangjaroen et al. 2014; Sandhiya et al. 2005; Sessitsch et al. 2012; Stoltzfus et al. 1997; Sun et al. 2008; Tian et al. 2007; Yan et al. 2008; Yanni et al. 1997; You and Zhou 1988), sugar cane (*Saccharum officinarum*) (Govindarajan et al. 2007; Mendes et al. 2007; Nutaratat et al. 2014; Quecine et al. 2012; Suman et al. 2001; Tam and Diep 2014), maize (*Zea mays*) (Araujo et al. 2000; Chelius and Triplett 2001; Fisher et al. 1992; Fouts et al. 2008; Hallman et al. 1997; Lalande et al. 1989; Matsumura et al. 2015; Mcinroy and Kloepper 1995; Montanez et al. 2012; Palus et al. 1996; Rai et al. 2007; Rosenblueth and Martinez-Romero 2006; Tam and Diep 2014; Zinniel et al. 2002), potato (*Solanum tuberosum*) (Berg et al. 2005; De Boer and Copeman 1974; Hallman et al. 1997; Han et al. 2011; Hollis 1951; Manter et al. 2010; Pageni et al. 2013; Pavlo et al. 2011; Rado et al. 2015; Reiter et al. 2002; Sessitsch et al. 2004; Sturz et al. 1988, 2003), tomato (*Solanum lycopersicum*) (Hallman et al. 1997; Li et al. 2014; Patel et al. 2012; Pillay and Nowak 1997; Samish et al. 1961; Yang et al. 2011), soybean (*Glycine max*) (Hung and Annapurna 2004; Kuklinsky-Sobral et al. 2004; Mingma et al. 2014; Okubo et al. 2009; Pimentel et al. 2006; Zinniel et al. 2002), strawberry (*Fragaria ananassa*) (de Melo Pereira et al. 2012; Dias et al. 2009; Hardoim et al. 2011, 2012), sugar beet (*Beta vulgaris*) (Dent et al. 2004; Jacobs et al. 1985; Tsurumaru et al. 2015), common bean (*Phaseolus vulgaris*) (de Oliveira Costa et al. 2012; Suyal et al. 2015), pepper (*Piper* sp.) (Aravind et al. 2009; Paul et al. 2013; Sziderics et al. 2007; Xia et al. 2015), carrot (*Daucus carota* L.) (Surette et al. 2003; Wu et al. 2015), grapevine (*Vitis vinifera*) (Baldan et al. 2014; Bell et al. 1995; Bulgari et al. 2009; Campisano et al. 2014a; Compant et al. 2011; West et al. 2010).

1.3 Effect of Agricultural Practices on Diversity of Endophytic Bacterial Communities

Bacteria constitute the most numerous group of microorganisms in soil (Whitman et al. 1998), and many endophytic bacteria originate from the population of plant-associated microorganisms in rhizosphere (Hardoim et al. 2008). Microbial diversity of the plant rhizosphere itself is defined by overall composition of microbial pool of soil and further refined by specific plant–microbe interactions that are largely mediated by root exudates (Sorensen and Sessitsch 2006). It has been demonstrated that endophytic community represents a plant genotype-specific subset of the wider microbial population of soil (Bulgarelli et al. 2012; Lundberg et al. 2012). Agricultural land management, such as tillage or irrigation, greatly alters soil characteristics that may lead to reduction in soil microbial diversity due to mechanical destruction, soil compaction, reduced pore volume, desiccation, and disruption of access to food resources (Garcia-Orenes et al. 2013; Jangid et al. 2008). Several studies have established the effect of tillage systems on soil microbial communities in different soils and cropping systems (Balota et al. 2003; Dorr de Quadros et al. 2012; Mathew et al. 2012). The effect of excessive use of pesticides can induce significant changes in the function and structure of soil microbial populations due to direct inhibition of microbial growth or overall changes in the structure of agricultural ecosystems (Pampulha and Oliveira 2006). Balanced mineral or organic fertilizers have been shown to have positive effect on diversity and metabolic activity of the soil microbial community (Zhong et al. 2010).

The effect of the agronomic practices on the overall soil microbial community could be expected to reflect differences in endophyte populations of agricultural crop plants. However, the research aimed to elicit effect of agricultural practices on composition of the endophytic bacteria populations is limited to several studies. An early study by Fuentes-Ramirez et al. (1999) demonstrated that colonization ability of nitrogen-fixing endophytic bacterium *Acetobacter diazotrophicus* was largely decreased in the sugarcane plants fertilized with high levels of nitrogen. A recent study using automated ribosomal intergenic spacer analysis showed that structure of rice root endophytic community was affected by the nitrogen fertilization level (Sasaki et al. 2013). Another study assessed root bacterial endophyte diversity in maize grown using different fertilizer application conditions. Application of PCR-based group-specific markers revealed that type I methanotroph patterns were different for plants cultivated using mineral and organic fertilizer (Seghers et al. 2004).

Recently, culture-based and metagenomic analyses were employed to assess bacterial endophyte diversity of plants grown using conventional and organic practices. An extensive study by Xia et al. (2015) evaluated diversity of culturable bacterial endophytes in different tissues of corn, tomato, melon, and pepper grown using organic or conventional practices. The endophyte diversity was significantly higher among all the crops grown organically versus those grown using conventional practices. There were 32 species isolated from organically grown plants and 28 species from plants grown using conventional practices.

No significant effect of herbicide treatment on composition of the maize root endophyte population was detected using the PCR-based group-specific markers (Seghers et al. 2004). However, recent study using automated ribosomal intergenic spacer fingerprinting and metagenomic analysis using 16S rDNA pyrosequencing identified differences in the composition of endophytic communities in grapevines cultivated using organic and integrated pest management conditions (Campisano et al. 2014a). While a different outcome of the two studies might be a consequence of improvement in the capability of the analysis methods, it could as well be related to differences specific to the plant species or pesticide treatment conditions.

The studies described in this section showed that agricultural conditions could alter diversity of endophytic bacteria populations; however, further insight would be required to elucidate the mechanisms that mediate such changes. The variation in bacterial diversity could be a consequence of changes in overall soil microbial population upon the fertilizer treatment or application of other agronomic practices. On the other hand, the agronomical conditions potentially had a direct effect on the root endophytic bacterial community as was suggested by Xia et al. (2015). In addition, an important role might be attributed to differences in plant physiological state and changes in composition of the plant root exudates that influence growth of endophytic bacteria (Paungfoo-Lonhienne et al. 2010). This notion that factors related to plant biochemistry regulate endophyte diversity was supported by the study demonstrating that application of chitin resulted in changes in bacterial communities in soil, rhizosphere, and cotton roots, and the organic amendment supported the endophytic species in cotton roots that otherwise did not occur (Hallman et al. 1999). Intriguingly, it was shown that composition of the endophytic community was largely different from that of the rhizosphere; therefore, the amendment of chitin, which enhanced chitinase and peroxidase concentrations, might have changed preference of the plants for certain bacterial endophytes.

Another aspect related to the effect of agricultural practices on soil and plant microbiome is reflected by disease-suppressive soil phenomenon that is associated with the capability of soils to suppress or reduce plant disease of susceptible host plants in the presence of virulent pathogen (Weller et al. 2002). It was shown several decades ago that disease-suppressive properties of soil were largely induced by long-term cultivation of wheat and potato monoculture leading to buildup of host-specific microbial community (Lorang et al. 1989; Scher and Baker 1980; Whipps 1997). Further studies elucidated possible mechanisms of disease suppression that include competition for space and nutrients, antagonism due to production of secondary metabolites, and elicitation of ISR by soil microbiota (Philippot et al. 2013; Pieterse et al. 2014). Specific role of the endophytic bacteria in the development of the disease-suppressive traits was rarely addressed in the studies on disease-suppressive soil communities; however, bacteria of genus *Streptomyces*, *Bacillus*, *Actinomyces*, and *Pseudomonas* that are known to lead endophytic lifestyle were shown to contribute to the disease-suppressive traits of soils (Haas and Defago 2005; Kinkel et al. 2012; Mendes et al. 2011; Siddiqui and Ehteshamul-Haque 2001; Weller et al. 2002).

The importance of agricultural practices that maintain natural diversity of plant endophytic bacteria is emphasized by the observations that agricultural plants may become a niche for human pathogens and a source for outbreaks of food-borne illness (Brandl 2006). Use of manures contaminated with virulent bacteria was identified as a main source of human pathogens (Brandl 2006; Holden et al. 2009; van Overbeek et al. 2014). Other routes included irrigation water (Erickson et al. 2010) or flies (Talley et al. 2009). Meanwhile a decline of species antagonistic to the pathogenic bacteria in soil and endosphere was associated with plant colonization by human pathogen species (Latz et al. 2012); it was also demonstrated that the presence of certain plant pathogens and other species living in soil plays an important role in colonization of plants by human pathogens (Barak and Liang 2008; Brandl 2008; Brandl et al. 2013). On the other hand, typical plant-associated bacteria species belonging to the genera of *Enterobacter*, *Serratia*, and *Klebsiella* could become virulent to humans by acquisition of mobile genetic elements from human pathogens through horizontal gene transfer (van Overbeek et al. 2014). Pathogenic bacteria of the family *Enterobacteriaceae*, including pathogenic *Salmonella* genus strains, *E. coli*, *Klebsiella pneumoniae*, and *Vibrio cholerae* strains, and the human opportunistic pathogens *Pseudomonas aeruginosa* and *Propionibacterium acnes* were described as endophytic colonizers of plants (Campisano et al. 2014b; Deering et al. 2012; El-Awady et al. 2015; Kumar et al. 2013; Kutter et al. 2006; Schikora et al. 2008).

1.4 Role of Endophytic Bacteria in Adaptation of Agriculture Crops to Biotic and Abiotic Environmental Stress

1.4.1 Induction of Accumulation of Stress-Related Metabolites and Enzymes

Plants are capable to acclimate to environmental stresses by altering physiology to attain state adopted to overcome stress factors such as dehydration, mechanical injury, nutrient deficiency, high solar radiation, or stress-induced increase in concentration of reactive oxygen species. This acclimation is associated with enhanced production of compounds that mediate osmotic adjustment, stabilize cell components, and act as free radical scavengers. It has been observed that plant inoculation with endophytic bacteria leads to accumulation of such compounds, including proline, phenolic compounds, carbohydrates, and antioxidants.

It was shown that bacterial endophyte *Burkholderia phytofirmans* PsJN enhances cold tolerance of grapevine plants by altering photosynthetic activity and metabolism of carbohydrates involved in cold stress tolerance (Ait Barka et al. 2006; Fernandez et al. 2012). The presence of the bacterium in the plant promoted acclimation to chilling temperatures resulting in lower cell damage, higher photosynthetic activity, and accumulation of cold-stress-related metabolites such as starch, proline, and phenolic compounds (Ait Barka et al. 2006). Fernandez et al. (2012)

demonstrated that bacterization of grapevine plants resulted in a twofold increase in soluble sugar content, and the plantlets inoculated with the bacterium displayed higher concentrations of the sugars known to be involved in low-temperature tolerance, such glucose, sucrose, and raffinose with its precursor, galactinol.

Positive effect of the *B. phytofirmans* PsJN strain on metabolic balance and reduced effect of drought stress was demonstrated in wheat plants grown under reduced irrigation conditions (Naveed et al. 2014). Inoculation with the bacterium resulted in higher antioxidant activity of plants compared to control under drought stress. However, in contrast to the grapevine plants in the study by Fernandez et al. (2012), the bacterium had no effect on sugar contents of the wheat, and phenolic contents decreased in the bacterized plants as compared to control.

Another endophytic bacterium, *Bacillus subtilis* B26, reduced a phenotypic effect of drought stress in *Brachypodium distachyon* grass compared to plants not harboring the bacterium (Gagne-Bourque et al. 2015). The protection from drought stress was associated with increase in total soluble sugars, glucose, fructose, and starch contents. However, no accumulation of stress response-related raffinose family carbohydrates was observed in either inoculated or control plants.

Pandey et al. (2012) evaluated cross-species stress reducing effect of wheat endophytic bacterium *Pseudomonas aeruginosa* PW09 in cucumber. Application of the PW09 strain induced increase in accumulation of proline and total phenolics under NaCl stress and pathogen *Sclerotium rolfsii* inoculation. Also, increase in activities of the enzymes involved biosynthesis of phenolic compounds, polyphenol oxidase, and phenylalanine ammonia lyase, as well as the antioxidative enzyme superoxide dismutase (SOD) was observed under biotic and abiotic stress conditions. Similarly, effect of six bacterial strains on stress-related biochemical traits of gladiolus plants was assessed in another study (Damodaran et al. 2014). The bacteria strains were shown to induce increase in activities of SOD, phenylalanine lyase, catalase, peroxidase enzymes, and accumulation of higher concentrations of proline and phenolic compounds in gladiolus plants grown in soil with high concentration of sodium. However, the capability of the different bacterial strains, isolated from soil, roots, culms, and leaves of grasses, to colonize endophytic niche was not explicitly confirmed.

A proline accumulation stimulating effect by endophytic strains of *Arthrobacter* sp. and *Bacillus* sp. was reported in pepper (*Capsicum annuum* L.) plants in vitro (Sziderics et al. 2007). Osmotic stress caused a similar increase in the content of free proline in the leaves of both inoculated and non-inoculated plants. However, higher concentration of proline was accumulated in leaves of unstressed plants inoculated with either of the two strains compared with unstressed non-inoculated plants. The bacterization resulted in a significantly reduced upregulation or downregulation of the stress-inducible genes suggesting that both strains reduced abiotic stress in pepper under osmotic stress conditions.

Endophytic bacteria *Pseudomonas pseudoalcaligenes* was shown to induce accumulation of higher concentrations of glycine betaine-like compounds leading to improved salinity stress tolerance in rice (Jha et al. 2011). At higher salinity levels, bacterization with mixture of both *P. pseudoalcaligenes* and rhizospheric

Bacillus pumilus showed better response against the adverse effects of salinity. In this study, bacterization with either *P. pseudoalcaligenes* or both *P. pseudoalcaligenes* and *B. pumilus* resulted in lower levels of proline accumulation under the stress conditions, suggesting that different strategies of accumulation of osmoprotectant proteins in endophyte-inoculated plants were either plant or bacterium genotype-specific phenomena. Related study demonstrated that both of the bacterial strains induced production of defense-related enzymes, chitinase, peroxidase, and polyphenol oxidase, under biotic stress conditions in the presence of *Magnaporthe grisea* pathogen (Jha and Subramanian 2009).

Chen et al. (2014) demonstrated that endophytic bacteria *Sphingomonas SaMR12* influenced the contents of root exudates, which were important for chelating cadmium ions and resulted in alleviation of the toxic metal stress in *Sedum alfredii*. Exudation of oxalic acid, malic acid, and tartaric acid was significantly affected by the inoculation of the endophytic bacterium in a manner dependent on cadmium treatment levels.

1.4.2 Effect on Phytohormone Balance

Ethylene (ET) is important for plant growth and development and has been extensively studied as mediator of plant stress response signaling (Gamalero and Glick 2015). Stress-induced accumulation of ET is usually deleterious to plant growth and health. ET is formed from methionine via S-adenosyl-L-methionine, which is converted into 1-aminocyclopropane-1-carboxylic acid (ACC) by the enzyme ACC oxidase (Bleecker and Kende 2000). ET is a key mediator of the plant defense response pathways that regulate colonization of plant tissue by endophytic bacteria (Iniguez et al. 2005). Endophytes may produce the enzyme ACC deaminase that has no function in bacteria but contributes to plant growth promotion and improved stress tolerance by cleaving the ET precursor ACC (Campbell and Thompson 1996). There are numerous reports on ACC deaminase-containing plant-associated bacteria and their role in improved plant growth and stress tolerance that has been recently reviewed by (Glick 2014).

Qin et al. (2014) isolated 13 ACC deaminase-producing putative endophytic bacteria of genera *Bacillus*, *Pseudomonas*, *Klebsiella*, *Serratia*, *Arthrobacter*, *Streptomyces*, *Isoptericola*, and *Microbacterium* from the halophyte plant *Limonium sinense*. It was suggested that the bacteria might play an important role in higher salinity tolerance of the plant as four of the selected ACC deaminase-producing strains were shown to stimulate growth of the host plants. An improved growth of *Catharanthus roseus* plant in 150 mM NaCl-containing soils was demonstrated for the plants inoculated with the *Achromobacter xylosoxidans* AUM54 strain (Karthikeyan et al. 2012). The bacterium was one of the four isolates isolated from *C. roseus* grown in saline soil and was shown to produce ACC deaminase.

In another study, tomato plants bacterized with ACC deaminase-containing endophytic *Pseudomonas fluorescens* YsS6 and *Pseudomonas migulae* 8R6 strains exhibited higher gain of biomass and a greater number of flowers and buds when grown under 165 mM and 185 mM NaCl levels as compared to the plants treated with ACC deaminase-deficient mutants of the bacteria or control with no bacterial treatment (Ali et al. 2014). Intriguingly, the study suggested the presence of different mechanisms of salt tolerance that might be plant genotype specific or stimulated by ACC deaminase-producing bacteria. It was shown that endophytic *Pseudomonas* sp. used in the study limited the concentration of sodium in tomato plant shoots (Ali et al. 2014). This was in contrast to previously reported rhizospheric *Pseudomonas putida* UW4 strain that was shown to be able to reduce ET levels in canola plants due to ACC deaminase activity (Cheng et al. 2007). In this case, sodium accumulated in root tissues and presumably partitioned into the vacuole.

In addition to salt stress tolerance, ACC deaminase-producing *P. agglomerans* Jp3-3 and *Achromobacter xylosoxidans* strain Ax10 were shown to alleviate stress of *Brassica* sp. plants grown in copper-contaminated soils and improved copper uptake by the plants (Ma et al. 2009; Zhang et al. 2011a). ACC deaminase-producing isolates from *Commelina communis* plants grown on lead and zinc mine soils were shown to improve growth of rape plants in the lead-contaminated soil (Zhang et al. 2011b).

Abscisic acid (ABA) is another phytohormone involved in plant stress response and is important for regulation of plant water balance and osmotic stress tolerance (Tuteja 2007). Information about role of ABA in endophytic bacteria-mediated stress tolerance is limited. It was described that endophytic bacteria *Bacillus licheniformis* Rt4M10 and *Pseudomonas fluorescens* Rt6M10 had drought stress reducing activity on plants grown in vitro that was associated with accumulation of high ABA levels in leaves of bacterized plants (Salomon et al. 2014). Cohen et al. (2009) showed that bacterization with *Azospirillum lipoferum* enhanced ABA accumulation and drought stress tolerance in maize plants. It was also suggested that plant performance under stress conditions was further enhanced by *A. lipoferum*-produced gibberellins (GAs). It is an intriguing observation as it is commonly believed that response to abiotic stress is associated with reduced plant growth-promoting hormone GA levels. However, GA signaling is closely integrated to ABA and ET signaling during the response to abiotic stress (Colebrook et al. 2014), and the interaction of the stress response pathways and exogenous hormone produced by plant growth-promoting bacteria remains ambiguous.

1.4.3 Induced Systemic Resistance and Priming of Response to Biotic Stress

Pathogen defense response priming, termed as induced systemic resistance, is activated by nonpathogenic plant-associated microorganisms. The ISR primes plant defense mechanisms and protects non-exposed plant parts against a future attack by pathogenic microbes and herbivorous insects. Plant hormones jasmonic acid (JA) and ET play a major regulatory role in the network of interconnected signaling pathways involved in ISR induction; however, the details of mechanism of the defense priming during ISR remain vague (Pieterse et al. 2014). There is an evidence for the role of transcription co-regulator NPR1 in the JA-/ET-dependent ISR and its cytosol-specific function that is different from the function involved in pathogen-induced systemic acquired resistance (SAR) (Spoel et al. 2003; Stein et al. 2008). Further, the role of transcription factors MYB72 and MYC2 in establishment of the ISR induced by rhizobacteria and priming of JA-/ET-dependent defense genes has been demonstrated (Pozo et al. 2008; Van Der Ent et al. 2008). In addition to the JA-/ET-mediated ISR activation pathway, an evidence that salicylic acid produced by plant growth-promoting bacteria could elicit ISR response has been discussed (Bakker et al. 2014).

Many studies have been dedicated to the ISR mediated by free-living rhizobacterial strains (Choudhary and Johri 2009); however, a number of endophytic bacteria have been reported to have the ISR-inducing activity as well. The first study demonstrating that endophytic bacteria could elicit ISR in plants was published in 1991 and showed that inoculation of cucumber roots with endophytic *Pseudomonas fluorescens* strain 89B-61 could induce resistance against cucumber anthracnose in the plant leaves (Kloepper and Ryu 2006; Wei et al. 1991). Subsequently attention was drawn to ISR mediated by several other endophytic species of genus *Pseudomonas* and the effect was characterized in different plant–pathogen systems. *Pseudomonas* sp. strain PsJN isolated from onion roots (Frommel et al. 1991) was shown to suppress verticillium wilt (*Verticillium dahliae*) on tomato seedlings and tissue culture plantlets grown in vitro, and it was proposed that the protection was mediated through the ISR activation (Sharma and Nowak 1998). *Pseudomonas* sp. strain 63–28 was shown to induce systemic resistance in tomato and pea plants leading to reduced damage by *Fusarium oxysporum* root pathogen (Benhamou et al. 1996; M’Piga et al. 1997). *Pseudomonas putida* MGY2 was isolated from papaya fruits and had reducing effect on postharvest decay of papaya fruit caused by *Colletotrichum gloeosporioides* (Shi et al. 2011). It was established that bacterization with the endophytic pseudomonad upregulated expression of enzymes involved in plant defense response, phenylalanine ammonia lyase, catalase, and peroxidase. A study by Ardanov et al. (2011) demonstrated that *Pseudomonas* sp. IMBG294 reduced symptoms of soft rot disease caused by bacterial pathogen *Pectobacterium atrosepticum* in potato plants. The assessment of expression of PR2 and PDF1.2, the molecular markers of the SAR and ISR, respectively, in *Arabidopsis–Pseudomonas syringae* model revealed that the endophytic bacterium was able to induce disease resistance via defense priming.

The asporogenous pseudomonads demonstrated poor performance when used in commercial plant protection products due to lack of long-term viability; therefore, subsequently much attention was drawn by plant growth-promoting strains of *Bacillus* sp. (Kloepper et al. 2004). ISR mediated by endophytic *Bacillus pumilus* strain SE34 was described by Benhamou et al. (1996; 1998). The bacterial strain reduced symptoms of root-rotting fungus *Fusarium oxysporum* infection in pea through induction of plant defense mechanism leading to accumulation of callose and phenolic compounds in the root epidermal and cortical cell walls and formation of the barriers beyond the infection sites (Benhamou et al. 1996). The same *B. pumilus* SE34 strain induced resistance to *Fusarium oxysporum* infection in tomato plants (Benhamou et al. 1998).

In addition, ISR mediated by endophytic *Serratia* sp. (Benhamou et al. 2000), *Methylobacterium* sp. (Ardanov et al. 2011), and actinobacteria *Streptomyces* sp. (Conn et al. 2008) was described. The early study by Benhamou et al. (2000) demonstrated that *Serratia plymuthica* strain R1GC4 sensitized susceptible cucumber seedlings to react more rapidly and more efficiently to infection by soilborne pathogen *Pythium ultimum* (Benhamou et al. 2000). The defense reaction was associated with deposition of enlarged callose-enriched wall appositions, also containing pectin, cellulose, and phenolic compounds.

The capability of endophytic actinobacteria *Streptomyces* sp. strains, isolated from wheat tissues, to activate the SAR or ISR pathways was assessed using *Arabidopsis thaliana* (Conn et al. 2008). It was demonstrated that the *Streptomyces* sp. EN27 was able to prime both pathways depending on the infecting pathogen. Resistance to *Erwinia carotovora s*ubsp. *carotovora* occurred via an NPR1-independent pathway and required salicylic acid, whereas the JA/ET signaling molecules were not essential. In contrast, induction of resistance to *Fusarium oxysporum* was mediated by NPR1-dependent pathway but also required salicylic acid and it was JA/ET independent.

Intriguingly, the study on induction of disease resistance to soft rot pathogen *Pectobacterium atrosepticum* in potato plants demonstrated that priming capacities of *Methylobacterium* sp. IMBG290 was inversely proportional to bacterial inoculants size (Ardanov et al. 2011). The difference in plant response mechanisms was associated with different patterns of activity of reactive oxygen species scavenging enzymes SOD and catalase. Plants treated with a low titer of *Methylobacterium* sp. showed higher SOD activity and unchanged catalase activity resulting in the development of ISR; meanwhile higher *Methylobacterium* sp. density caused SOD inactivation and catalase activation after inoculation with the pathogen and was followed by hypersensitive response.

1.5 Concluding Remarks

Several decades of research on endophytes in agricultural plants have revealed an immense taxonomic diversity of the endophytic bacteria. The endophytic species have been mostly reported throughout α-, β-, and γ-subgroups of phylum *Proteobacteria*, the latter being the most diverse and dominant group that includes common soil and endophytic bacteria of *Pseudomonas* sp. Next to the pseudomonads, much attention has been dedicated to members of *Bacillus* sp. that belongs to phylum *Firmicutes*. A number of other species of phyla *Firmicutes* and *Actinobacteria* have been identified as endophytic bacteria as well. During the last decade, development of metagenomic analysis techniques has brought to light new aspects of the diversity of endophytic bacteria including identification of new unculturable species and establishment of the dynamics of endophyte diversity that provide hints about physiological significance and ecological functions of the complex host plant and endophytic bacteria interactions.

Composition of the endophytic microbiome depends on plant genotype as well as environmental factors. Evidence has been presented that agricultural practices play an important role in shaping structure of the endophytic microbial community of agricultural crop plants. Therefore, assessment of the capability of modern agronomical techniques to maintain natural diversity of plant endophytic bacteria should become an important element in the development of sustainable agricultural practices. In addition, numerous studies have demonstrated beneficial effects of the endophytic bacteria on plant growth and adaptability to biotic or abiotic stresses through modulation of phytohormone signaling, production of metabolites involved in stress response, and priming of plant defense response pathways. The endophytes play an integral role in balancing plant physiology and functioning of agroecosystems; thus, understanding of composition and functioning of the plant-associated microbial communities has a large potential for improvement of performance of agricultural crops and development of integrated plant disease management systems.

Acknowledgments This research was funded by the long-term research program "Genetics and directed genotype development of agricultural and forestry plants" implemented by the Lithuanian Research Centre for Agriculture and Forestry.

References

Ait Barka E, Nowak J, Clement C (2006) Enhancement of chilling resistance of inoculated grapevine plantlets with a plant growth-promoting rhizobacterium, *Burkholderia phytofirmans* strain PsJN. Appl Environ Microbiol 72:7246–7252

Akinsanya MA, Goh JK, Lim SP, Ting AS (2015) Metagenomics study of endophytic bacteria in Aloe Vera using next-generation technology. Genom Data 6:159–163

Ali S, Charles TC, Glick BR (2014) Amelioration of high salinity stress damage by plant growth-promoting bacterial endophytes that contain ACC deaminase. Plant Physiol Biochem 80:160–167

Araujo JM, Silva AC, Azevedo JL (2000) Isolation of endophytic actinomycetes from roots and leaves of maize *(Zea mays* L.*)* Braz Arch Biol Technol 43:447–451

Aravind R, Kumar A, Eapen SJ, Ramana KV (2009) Endophytic bacterial flora in root and stem tissues of black pepper (*Piper nigrum* L.) genotype: isolation, identification and evaluation against *Phytophthora capsici*. Lett Appl Microbiol 48:58–64

Ardanov P, Ovcharenko L, Zaets I, Kozyrovska N, Pirttila AM (2011) Endophytic bacteria enhancing growth and disease resistance of potato (*Solanum tuberosum* L.) Biol Control 56:43–49

Bacon CW, Hinton DM (2007) Bacterial endophytes: the endophytic niche, its occupants, and its utility. In: Gnanamanickam SS (ed) Plant-associated bacteria. Springer, Dordrecht, pp 155–164

Bakker PAHM, Ran LX, Mercado-Blanco J (2014) Rhizobacterial salicylate production provokes headaches! Plant Soil 382:1–16

Balandreau J, Viallard V, Cournoyer B, Coenye T, Laevens S, Vandamme P (2001) *Burkholderia cepacia* genomovar III is a common plant-associated bacterium. Appl Environ Microbiol 67:982–985

Baldan E, Nigris S, Populin F, Zottini M, Squartini A, Baldan B (2014) Identification of culturable bacterial endophyte community isolated from tissues of *Vitis vinifera* "Glera". Plant Biosyst 148:508–516

Balota EL, Colozzi-Filho A, Andrade DS, Dick RP (2003) Microbial biomass in soils under different tillage and crop rotation systems. Biol Fertil Soils 38:15–20

Barak JD, Liang AS (2008) Role of soil, crop debris, and a plant pathogen in *Salmonella enterica* contamination of tomato plants. PLoS One 3:e1657

Bell CR, Dickie GA, Harvey WLG, Chan JWYF (1995) Endophytic bacteria in grapevine. Can J Microbiol 41:46–53

Benhamou N, Gagne S, Le QD, Dehbi L (2000) Bacterial-mediated induced resistance in cucumber: beneficial effect of the endophytic bacterium *Serratia plymuthica* on the protection against infection by *Pythium ultimum*. Phytopathology 90:45–56

Benhamou N, Kloepper JW, Quadt-Hallman A, Tuzun S (1996) Induction of defense-related ultrastructural modifications in pea root tissues inoculated with endophytic bacteria. Plant Physiol 112:919–929

Benhamou N, Kloepper JW, Tuzun S (1998) Induction of resistance against *Fusarium* wilt of tomato by combination of chitosan with an endophytic bacterial strain: ultrastructure and cytochemistry of the host response. Planta 204:153–168

Berg G, Krechel A, Ditz M, Sikora RA, Ulrich A, Hallmann J (2005) Endophytic and ectophytic potato-associated bacterial communities differ in structure and antagonistic function against plant pathogenic fungi. FEMS Microbiol Ecol 51:215–229

Bleecker AB, Kende H (2000) Ethylene: a gaseous signal molecule in plants. Annu Rev Cell Dev Biol 16:1–18

Brader G, Compant S, Mitter B, Trognitz F, Sessitsch A (2014) Metabolic potential of endophytic bacteria. Curr Opin Biotechnol 27:30–37

Brandl MT (2006) Fitness of human enteric pathogens on plants and implications for food safety. Annu Rev Phytopathol 44:367–392

Brandl MT (2008) Plant lesions promote the rapid multiplication of *Escherichia coli* O157:H7 on postharvest lettuce. Appl Environ Microbiol 74:5285–5289

Brandl MT, Cox CE, Teplitski M (2013) *Salmonella* interactions with plants and their associated microbiota. Phytopathology 103:316–325

Bulgarelli D, Rott M, Schlaeppi K, van TE VL, Ahmadinejad N, Assenza F, Rauf P, Huettel B, Reinhardt R, Schmelzer E, Peplies J, Gloeckner FO, Amann R, Eickhorst T, Schulze-Lefert P (2012) Revealing structure and assembly cues for *Arabidopsis* root-inhabiting bacterial microbiota. Nature 488:91–95

Bulgari D, Casati P, Brusetti L, Quaglino F, Brasca M, Daffonchio D, Bianco PA (2009) Endophytic bacterial diversity in grapevine (*Vitis vinifera* L.) leaves described by 16S rRNA gene sequence analysis and length heterogeneity-PCR. J Microbiol 47:393–401

Campbell BG, Thompson JA (1996) 1-aminocyclopropane-1-carboxylate deaminase genes from *Pseudomonas* strains. FEMS Microbiol Lett 138:207–210

Campisano A, Antonielli L, Pancher M, Yousaf S, Pindo M, Pertot I (2014a) Bacterial endophytic communities in the grapevine depend on pest management. PLoS One 9:e112763

Campisano A, Ometto L, Compant S, Pancher M, Antonielli L, Yousaf S, Varotto C, Anfora G, Pertot I, Sessitsch A, Rota-Stabelli O (2014b) Interkingdom transfer of the acne-causing agent, *Propionibacterium acnes*, from human to grapevine. Mol Biol Evol 31:1059–1065

Cankar K, Kraigher H, Ravnikar M, Rupnik M (2005) Bacterial endophytes from seeds of Norway spruce (*Picea abies* L. karst). FEMS Microbiol Lett 244:341–345

Chaintreuil C, Giraud E, Prin Y, Lorquin J, Ba A, Gillis M, de LP, Dreyfus B (2000) Photosynthetic bradyrhizobia are natural endophytes of the African wild rice *Oryza breviligulata*. Appl Environ Microbiol 66:5437–5447

Chelius MK, Triplett EW (2001) The diversity of archaea and bacteria in association with the roots of *Zea mays* L. Microb Ecol 41:252–263

Chen B, Zhang Y, Rafiq MT, Khan KY, Pan F, Yang X, Feng Y (2014) Improvement of cadmium uptake and accumulation in *Sedum alfredii* by endophytic bacteria *Sphingomonas* SaMR12: effects on plant growth and root exudates. Chemosphere 117:367–373

Cheng Z, Park E, Glick BR (2007) 1-aminocyclopropane-1-carboxylate deaminase from *Pseudomonas putida* UW4 facilitates the growth of canola in the presence of salt. Can J Microbiol 53:912–918

Chi F, Shen SH, Cheng HP, Jing YX, Yanni YG, Dazzo FB (2005) Ascending migration of endophytic rhizobia, from roots to leaves, inside rice plants and assessment of benefits to rice growth physiology. Appl Environ Microbiol 71:7271–7278

Choudhary DK, Johri BN (2009) Interactions of *Bacillus* spp. and plants - with special reference to induced systemic resistance (ISR). Microbiol Res 164:493–513

Christina A, Christapher V, Bhore SJ (2013) Endophytic bacteria as a source of novel antibiotics: an overview. Pharmacogn Rev 7:11–16

Cocking EC, Stone PJ, Davey MR (2006) Intracellular colonization of roots of *Arabidopsis* and crop plants by *Gluconacetobacter diazotrophicus*. In Vitro Cell Dev - Pl 42:74–82

Cohen AC, Travaglia CN, Bottini R, Piccoli PN (2009) Participation of abscisic acid and gibberellins produced by endophytic *Azospirillum* in the alleviation of drought effects in maize. Botany 87:455–462

Colebrook EH, Thomas SG, Phillips AL, Hedden P (2014) The role of gibberellin signalling in plant responses to abiotic stress. J Exp Biol 217:67–75

Compant S, Mitter B, Colli-Mull JG, Gangl H, Sessitsch A (2011) Endophytes of grapevine flowers, berries, and seeds: identification of cultivable bacteria, comparison with other plant parts, and visualization of niches of colonization. Microb Ecol 62:188–197

Conn VM, Walker AR, Franco CM (2008) Endophytic actinobacteria induce defense pathways in *Arabidopsis Thaliana*. Mol Plant-Microbe Interact 21:208–218

Coombs JT, Franco CM (2003) Isolation and identification of actinobacteria from surface-sterilized wheat roots. Appl Environ Microbiol 69:5603–5608

Damodaran T, Rai RB, Jha SK, Kannan R, Pandey BK, Sah V, Mishra VK, Sharma DK (2014) Rhizosphere and endophytic bacteria for induction of salt tolerance in gladiolus grown in sodic soils. J Plant Interact 9:577–584

De Boer SH, Copeman RJ (1974) Endophytic bacterial flora in *Solanum tuberosum* and its significance in bacterial ring rot disease. Can J Microbiol 54:115–122

de Melo Pereira GV, Magalhaes KT, Lorenzetii ER, Souza TP, Schwan RF (2012) A multiphasic approach for the identification of endophytic bacterial in strawberry fruit and their potential for plant growth promotion. Microb Ecol 63:405–417

de Oliveira Costa LE, de Queiroz MV, Borges AC, de Moraes CA, de Araujo EF (2012) Isolation and characterization of endophytic bacteria isolated from the leaves of the common bean (*Phaseolus vulgaris*). Braz J Microbiol 43:1562–1575

Deering AJ, Mauer LJ, Pruitt RE (2012) Internalization of *E. coli* O157:H7 and *Salmonella* spp. in plants: a review. Food Res Int 45:567–575

Dent KC, Stephen JR, Finch-Savage WE (2004) Molecular profiling of microbial communities associated with seeds of *Beta vulgaris* subsp. *vulgaris* (sugar beet). J Microbiol Methods 56:17–26

Dias ACF, Costa FEC, Andreote FD, Lacava PT, Teixeira MA, Assumpcao LC (2009) Isolation of micropropagated strawberry endophytic bacteria and assessment of their potential for plant growth promotion. World J Microbiol Biotechnol 25:189–195

Dorr de Quadros P, Zhalnina K, Davis-Richardson A, Fagen JR, Drew J, Bayer C, Camargo FAO, Triplett EW (2012) The effect of tillage system and crop rotation on soil microbial diversity and composition in a subtropical acrisol. Diversity 4:375–395

El-Awady MAM, Hassan MM, Al-Sodany YM (2015) Isolation and characterization of salt tolerant endophytic and rhizospheric plant growth-promoting bacteria (PGPB) associated with the halophyte plant (*Sesuvium verrucosum*) grown in KSA. Int J Appl Sci Biotechnol 3:552–560

Elbeltagy A, Nishioka K, Sato T, Suzuki H, Ye B, Hamada T, Isawa T, Mitsui H, Minamisava K (2001) Isolation and characterization of endophytic bacteria from wild and traditionally cultivated rice varieties. Soil Sci Plant Nutr 46:617–629

Ellis EC, Kaplan JO, Fuller DQ, Vavrus S, Klein GK, Verburg PH (2013) Used planet: a global history. Proc Natl Acad Sci U S A 110:7978–7985

Engelhard M, Hurek T, Reinhold-Hurek B (2000) Preferential occurrence of diazotrophic endophytes, *Azoarcus* spp., in wild rice species and land races of *Oryza sativa* in comparison with modern races. Environ Microbiol 2:131–141

Erickson MC, Webb CC, Diaz-Perez JC, Phatak SC, Silvoy JJ, Davey L, Payton AS, Liao J, Ma L, Doyle MP (2010) Surface and internalized *Escherichia coli* O157:H7 on field-grown spinach and lettuce treated with spray-contaminated irrigation water. J Food Prot 73:1023–1029

Fernandez O, Theocharis A, Bordiec S, Feil R, Jacquens L, Clement C, Fontaine F, Barka EA (2012) *Burkholderia phytofirmans* PsJN acclimates grapevine to cold by modulating carbohydrate metabolism. Mol Plant-Microbe Interact 25:496–504

Fisher PJ, Petrini O, Scott HML (1992) The distribution of some fungal and bacterial endophytes in maize (*Zea mays* L.) New Phytol 122:299–305

Foley JA, Defries R, Asner GP, Barford C, Bonan G, Carpenter SR, Chapin FS, Coe MT, Daily GC, Gibbs HK, Helkowski JH, Holloway T, Howard EA, Kucharik CJ, Monfreda C, Patz JA, Prentice IC, Ramankutty N, Snyder PK (2005) Global consequences of land use. Science 309:570–574

Foley JA, Ramankutty N, Brauman KA, Cassidy ES, Gerber JS, Johnston M, Mueller ND, O'Connell C, Ray DK, West PC, Balzer C, Bennett EM, Carpenter SR, Hill J, Monfreda C, Polasky S, Rockstrom J, Sheehan J, Siebert S, Tilman D, Zaks DP (2011) Solutions for a cultivated planet. Nature 478:337–342

Fouts DE, Tyler HL, DeBoy RT, Daugherty S, Ren Q, Badger JH, Durkin AS, Huot H, Shrivastava S, Kothari S, Dodson RJ, Mohamoud Y, Khouri H, Roesch LF, Krogfelt KA, Struve C, Triplett EW, Methe BA (2008) Complete genome sequence of the N_2-fixing broad host range endophyte *Klebsiella pneumoniae* 342 and virulence predictions verified in mice. PLoS Genet 4:e1000141

Frommel MI, Nowak J, Lazarovits G (1991) Growth enhancement and developmental modifications of in vitro grown potato (*Solanum tuberosum* spp. *tuberosum*) as affected by a nonfluorescent *Pseudomonas* sp. Plant Physiol 96:928–936

Fuentes-Ramirez LE, Caballero-Mellado J, Sepulveda J, Martinez-Romero E (1999) Colonization of sugarcane by *Acetobacter diazotrophicus* is inhibited by high N-fertilization. FEMS Microbiol Ecol 29:117–128

Gaba S, Bretagnolle F, Rigaud T, Philippot L (2014) Managing biotic interactions for ecological intensification of agroecosystems. Front Ecol Evol 2:1–9

Gagne-Bourque F, Mayer BF, Charron JB, Vali H, Bertrand A, Jabaji S (2015) Accelerated growth rate and increased drought stress resilience of the model grass *Brachypodium distachyon* colonized by *Bacillus subtilis* B26. PLoS One 10:e0130456

Gamalero E, Glick BR (2015) Bacterial modulation of plant ethylene levels. Plant Physiol 169:13–22

Garcia-Orenes F, Morugan-Coronado A, Zornoza R, Scow K (2013) Changes in soil microbial community structure influenced by agricultural management practices in a mediterranean agroecosystem. PLoS One 8:e80522

Glick BR (2012) Plant growth-promoting bacteria: mechanisms and applications. Scientifica 2012:1–15

Glick BR (2014) Bacteria with ACC deaminase can promote plant growth and help to feed the world. Microbiol Res 169:30–39

Govindarajan M, Balandreau J, Kwon SW, Weon HY, Lakshminarasimhan C (2008) Effects of the inoculation of *Burkholderia vietnamensis* and related endophytic diazotrophic bacteria on grain yield of rice. Microb Ecol 55:21–37

Govindarajan M, Kwoon SW, Weon HY (2007) Isolation, molecular characterization and growth-promoting activities of endophytic sugarcane diazotroph *Klebsiella* sp. GR9. World J Microbiol Biotechnol 23:997–1006

Govindasamy V, Franco CMM, Gupta VVSR (2014) Endophytic actinobacteria: diversity and ecology. In: Verma VC, Gange AC (eds) Advances in endophytic research. Springer, New Dehli, pp 27–59

Haas D, Defago G (2005) Biological control of soil-borne pathogens by fluorescent pseudomonads. Nat Rev Microbiol 3:307–319

Hallman J, Quadt-Hallman A, Mahafee WF, Kloepper JW (1997) Bacterial endophytes in agricultural crops. Can J Microbiol 43:895–914

Hallman J, Rodriguez-Kabana R, Kloepper JW (1999) Chitin-mediated changes in bacterial communities of the soil, rhizosphere and within roots of cotton in relation to nematode control. Soil Biol Biochem 31:551–560

Hamilton CE, Gundel PE, Helander M, Saikkonen K (2012) Endophytic mediation of reactive oxygen species and antioxidant activity in plants: a review. Fungal Div 54:1–10

Han JI, Choi HK, Lee SW, Orwin PM, Kim J, Laroe SL, Kim TG, O'Neil J, Leadbetter JR, Lee SY, Hur CG, Spain JC, Ovchinnikova G, Goodwin L, Han C (2011) Complete genome sequence of the metabolically versatile plant growth-promoting endophyte *Variovorax paradoxus* S110. J Bacteriol 193:1183–1190

Hardoim P, Nissinen R, van Elas JD (2012) Ecology of bacterial endophytes in sustainable agriculture. In: Maheshwari DK (ed) Bacteria in agrobiology: plant probiotics. Springer, Berlin/Heidelberg, pp 97–126

Hardoim PR, Andreote FD, Reinhold-Hurek B, Sessitsch A, van Overbeek LS, van Elsas JD (2011) Rice root-associated bacteria: insights into community structures across 10 cultivars. FEMS Microbiol Ecol 77:154–164

Hardoim PR, van Overbeek LS, Elsas JD (2008) Properties of bacterial endophytes and their proposed role in plant growth. Trends Microbiol 16:463–471

Holden N, Pritchard L, Toth I (2009) Colonization outwith the colon: plants as an alternative environmental reservoir for human pathogenic enterobacteria. FEMS Microbiol Rev 33:689–703

Hollis JP (1951) Bacteria in healthy potato tissue. Phytopathology 41:350–367

Hung PQ, Annapurna K (2004) Isolation and characterization of endophytic bacteria in soybean (*Glycine* sp.) Omonrice 12:92–101

Ikeda S, Kaneko T, Okubo T, Rallos LE, Eda S, Mitsui H, Sato S, Nakamura Y, Tabata S, Minamisawa K (2009) Development of a bacterial cell enrichment method and its application to the community analysis in soybean stems. Microb Ecol 58:703–714

Iniguez AL, Dong Y, Carter HD, Ahmer BM, Stone JM, Triplett EW (2005) Regulation of enteric endophytic bacterial colonization by plant defenses. Mol Plant-Microbe Interact 18:169–178

Iniguez AL, Dong Y, Triplett EW (2004) Nitrogen fixation in wheat provided by *Klebsiella pneumoniae* 342. Mol Plant-Microbe Interact 17:1078–1085

Jacobs MJ, Bugbee WM, Gabrielson DA (1985) Enumeration, location, and characterization of endophytic bacteria within sugar beet roots. Can J Bot 63:1262–1265

James EK, Olivares FL, Baldani JI, Dobereiner J (1997) *Herbaspirillum*, an endophytic diazotroph colonizing vascular tissue of *Sorghum bicolor* L. Moench J Exp Bot 48:785–798

Jangid K, Williams MA, Franzluebbers AJ, Sanderlin JS, Reeves JH, Jenkins MB, Endale DM, Coleman DC, Whitman WB (2008) Relative impacts of land-use, management intensity and fertilization upon soil microbial community structure in agricultural systems. Soil Biol Biochem 40:2843–2853

Jha P, Kumar A (2009) Characterization of novel plant growth promoting endophytic bacterium *Achromobacter xylosoxidans* from wheat plant. Microb Ecol 58:179–188

Jha PN, Gupta G, Jha P, Mehrotra R (2013) Association of rhizospheric/endophytic bacteria with plants: a potential gateway to sustainable agriculture. Greener J Agricult Sci 3:73–84

Jha Y, Subramanian RB (2009) Endophytic *Pseudomonas pseudoalcaligenes* shows better response against the *Magnaporthe grisea* than a rhizospheric *Bacillus pumilus* in *Oryza sativa* (Rice). Arch Phytopathol Plant Protect 44:592–604

Jha Y, Subramanian RB, Patel S (2011) Combination of endophytic and rhizospheric plant growth promoting rhizobacteria in *Oryza sativa* shows higher accumulation of osmoprotectant against saline stress. Acta Physiol Plant 33:797–802

Jiao JY, Wang HX, Zeng Y, Shen YM (2006) Enrichment for microbes living in association with plant tissues. J Appl Microbiol 100:830–837

Johnston-Monje D, Raizada MN (2011) Conservation and diversity of seed associated endophytes in *Zea* across boundaries of evolution, ethnography and ecology. PLoS One 6:e20396

Kaneko T, Minamisawa K, Isawa T, Nakatsukasa H, Mitsui H, Kawaharada Y, Nakamura Y, Watanabe A, Kawashima K, Ono A, Shimizu Y, Takahashi C, Minami C, Fujishiro T, Kohara M, Katoh M, Nakazaki N, Nakayama S, Yamada M, Tabata S, Sato S (2010) Complete genomic structure of the cultivated rice endophyte *Azospirillum* sp. B510. DNA Res 17:37–50

Karthikeyan B, Joe MM, Islam R, Sa T (2012) ACC deaminase containing diazotrophic endophytic bacteria ameliorate salt stress in *Catharanthus roseus* through reduced ethylene levels and induction of antioxidative defense systems. Symbiosis 56:77–86

Kinkel LL, Schlatter DC, Bakker MG, Arenz BE (2012) Streptomyces competition and coevolution in relation to plant disease suppression. Res Microbiol 163:490–499

Kloepper JW, Ryu CM, Zhang S (2004) Induced systemic resistance and promotion of plant growth by *Bacillus* spp. Phytopathology 94:1259–1266

Kloepper JW, Ryu C-M (2006) Bacterial endophytes as elicitors of induced systemic resistance. In: Schulz B, Boyle C, Sieber TN (eds) Microbial root endophytes. Springer, Berlin/Heidelberg, pp 33–52

Koskimaki JJ, Pirttila AM, Ihantola EL, Halonen O, Frank AC (2015) The intracellular scots pine shoot symbiont *Methylobacterium extorquens* DSM13060 aggregates around the host nucleus and encodes eukaryote-like proteins. MBio 6:1–12

Kuklinsky-Sobral J, Araujo WL, Mendes R, Geraldi IO, Pizzirani-Kleiner AA, Azevedo JL (2004) Isolation and characterization of soybean-associated bacteria and their potential for plant growth promotion. Environ Microbiol 6:1244–1251

Kumar A, Munder A, Aravind R, Eapen SJ, Tummler B, Raaijmakers JM (2013) Friend or foe: genetic and functional characterization of plant endophytic *Pseudomonas aeruginosa*. Environ Microbiol 15:764–779

Kutter S, Hartmann A, Schmid M (2006) Colonization of barley (*Hordeum vulgare*) with *Salmonella enterica* and *Listeria* spp. FEMS Microbiol Ecol 56:262–271

Lalande RN, Bissonnette N, Coutlee D, Antoun H (1989) Identification of rhizobacteria from maize and determination of their plant-growth promoting potential. Plant Soil 115:11

Larran S, Perello A, Simon MR, Moreno V (2002) Isolation and analysis of endophytic microorganisms in wheat (*Triticum aestivum* L.) leaves. World J Microbiol Biotechnol 18:683–686

Latz E, Eisenhauer N, Rall BC, Allan E, Roscher C, Scheu S, Jousset A (2012) Plant diversity improves protection against soil-borne pathogens by fostering antagonistic bacterial communities. J Ecol 100:597–604

Li GJ, Dong QE, Ma L, Huang Y, Zhu ML, Ji YP, Wang QH, Mo MH, Zhang KQ (2014) Management of *Meloidogyne incognita* on tomato with endophytic bacteria and fresh residue of *Wasabia japonica*. J Appl Microbiol 117:1159–1167

Lodewyckx C, Mergeay M, Vangronsveld J, Clijsters H, Van der Lelie D (2002) Isolation, characterization, and identification of bacteria associated with the zinc hyperaccumulator Thlaspi Caerulescens subsp. calaminaria. Int J Phytoremediation 4:101–115

Lorang JM, Anderson NA, Lauer FI, Wildung DK (1989) Disease decline in a Minnesota potato scab plot. Am Potato J 66:531

Lundberg DS, Lebeis SL, Paredes SH, Yourstone S, Gehring J, Malfatti S, Tremblay J, Engelbrektson A, Kunin V, del Rio TG, Edgar RC, Eickhorst T, Ley RE, Hugenholtz P, Tringe SG, Dangl JL (2012) Defining the core *Arabidopsis thaliana* root microbiome. Nature 488:86–90

M'Piga P, Belanger RR, Paulitz TC, Benhamou N (1997) Increased resistance to *Fusarium oxysporum* f. Sp. *radicis-lycopersici* in tomato plants treated with the endophytic bacterium *Pseudomonas fluorescens* strain 63-28. Physiol Mol Plant Pathol 50:301–320

Ma Y, Rajkumar M, Freitas H (2009) Inoculation of plant growth promoting bacterium *Achromobacter xylosoxidans* strain Ax10 for the improvement of copper phytoextraction by *Brassica juncea*. J Environ Manag 90:831–837

Manter DK, Delgado JA, Holm DG, Stong RA (2010) Pyrosequencing reveals a highly diverse and cultivar-specific bacterial endophyte community in potato roots. Microb Ecol 60:157–166

Maropola MKA, Ramond JB, Trindade M (2015) Impact of metagenomic DNA extraction procedures on the identifiable endophytic bacterial diversity in *Sorghum bicolor* (L. Moench). J Microbiol Methods 112:104–117

Mathew RP, Feng Y, Githinji L, Ankumah R, Balkcom KS (2012) Impact of no-tillage and conventional tillage systems on soil microbial communities. Appl Environ Soil Sci 2012:1–10

Matsumura EE, Secco VA, Moreira RS, dos Santos OJAP, Hungria M, de Olivera ALM (2015) Composition and activity of endophytic bacterial communities in field grown maize plants inoculated with *Azospirillum brasilense*. Ann Microbiol 65:2187–2200

Mavingui P, Laguerre G, Berge O, Heulin T (1992) Genetic and phenotypic diversity of *Bacillus polymyxa* in soil and in the wheat rhizosphere. Appl Environ Microbiol 58:1894–1903

Mbai FN, Magiri EN, Matiru VN, Nganga J, Nyambati VCS (2013) Isolation and characterization of bacterial root endophytes with potential to enhance plant growth from Kenyan basmati rice. Am Int J Contemp Res 3:25–40

Mcinroy JA, Kloepper JW (1995) Survey of indigenous bacterial endophytes from cotton and sweet corn. Plant Soil 173:337–342

Mei C, Flinn BS (2010) The use of beneficial microbial endophytes for plant biomass and stress tolerance improvement. Recent Pat Biotechnol 4:81–95

Mendes R, Kruijt M, de Bruijn I, Dekkers E, van der Voort M, Schneider JH, Piceno YM, DeSantis TZ, Andersen GL, Bakker PA, Raaijmakers JM (2011) Deciphering the rhizosphere microbiome for disease-suppressive bacteria. Science 332:1097–1100

Mendes R, Pizzirani-Kleiner AA, Araujo WL, Raaijmakers JM (2007) Diversity of cultivated endophytic bacteria from sugarcane: genetic and biochemical characterization of *Burkholderia cepacia* complex isolates. Appl Environ Microbiol 73:7259–7267

Mingma R, Pathom-aree W, Trakulnaleamsai S, Thamchaipenet A, Duangmal K (2014) Isolation of rhizospheric and roots endophytic actinomycetes from *Leguminosae* plant and their activities to inhibit soybean pathogen, *Xanthomonas campestris* pv. *Glycine*. World J Microbiol Biotechnol 30:271–280

Misaghi IJ, Donndelinger CR (1990) Endophytic bacteria in symptom-free cotton plants. Phytopathology 80:808–811

Montanez A, Blanco AR, Barlocco C, Beracochea M, Sicardi M (2012) Characterization of cultivable putative endophytic plant growth promoting bacteria associated with maize cultivars (*Zea mays* L.) and their inoculation effects in vitro. Appl Soil Ecol 58:21–28

Mutondo MS, Huddy RJ, Bauer R, Tuffin MI, Cowan DA (2010) Metagenomic gene discovery. In: Li RW (ed) Metagenomics and its applications in agriculture, biomedicine, and environmental studies. Nova Science Publishers, New York, pp 287–320

Naik BS, Shashikala J, Krishnamurthy YL (2009) Study on the diversity of endophytic communities from rice (*Oryza sativa* L.) and their antagonistic activities in vitro. Microbiol Res 164:290–296

Naveed M, Hussain MB, Zahir ZA, Mitter B, Sessitsch A (2014) Drought stress amelioration in wheat through inoculation with *Burkholderia phytofirmans* strain PsJN. Plant Growth Regul 73:121–131

Newton AC, Fitt BD, Atkins SD, Walters DR, Daniell TJ (2010) Pathogenesis, parasitism and mutualism in the trophic space of microbe-plant interactions. Trends Microbiol 18:365–373

Nikolic B, Schwab H, Sessitsch A (2011) Metagenomic analysis of the 1-aminocyclopropane-1-carboxylate deaminase gene (acdS) operon of an uncultured bacterial endophyte colonizing *Solanum tuberosum* L. Arch Microbiol 193:665–676

Nutaratat P, Srisuk N, Arunrattiyakorn P, Limtong S (2014) Plant growth-promoting traits of epiphytic and endophytic yeasts isolated from rice and sugar cane leaves in Thailand. Fungal Biol 118:683–694

Okubo T, Ikeda S, Kaneko T, Eda S, Mitsui H, Sato S, Tabata S, Minamisawa K (2009) Nodulation-dependent communities of culturable bacterial endophytes from stems of field-grown soybeans. Microbes Environ 24:253–258

Pageni BB, Lupwayi NZ, Larney FJ, Kawchuk LM, Gan Y (2013) Populations, diversity and identities of bacterial endophytes in potato (*Solanum tuberosum* L.) cropping systems. Can J Plant Sci 93:1125–1142

Palus JA, Bonrneman J, Ludden PW, Triplett EW (1996) A diazotrophic bacterial endophyte isolated from stems of *Zea mays* L. and *Zea luxurians* Iltis and Doebley. Plant Soil 186:135–142

Pampulha ME, Oliveira A (2006) Impact of an herbicide combination of bromoxynil and prosulfuron on soil microorganisms. Curr Microbiol 53:238–243

Pandey PK, Yadav SK, Singh A, Sarma BK, Mishra A, Singh HB (2012) Cross-species alleviation of biotic and abiotic stresses by the endophyte *Pseudomonas aeruginosa* PW09. J Phytopathol 160:532–539

Patel HA, Patel RK, Khristi SM, Parikh K, Rajendran G (2012) Isolation and characterization of bacterial endophytes from *Lycopersicon esculentum* plant and their plant growth promoting characteristics. Nepal J Biotechnol 2:37–52

Paul NC, Ji SH, Deng JX, Yu SH (2013) Assemblages of endophytic bacteria in chili pepper (*Capsicum Annuum* L.) and their antifungal activity against phytopathogens in vitro. Plant Omics J 6:441–448

Paungfoo-Lonhienne C, Rentsch D, Robatzek S, Webb RI, Sagulenko E, Nasholm T, Schmidt S, Lonhienne TG (2010) Turning the table: plants consume microbes as a source of nutrients. PLoS One 5:e11915

Pavlo A, Leonid O, Iryna Z, Natalia K, Maria PA (2011) Endophytic bacteria enhancing growth and disease resistance of potato (*Solanum tuberosum* L.) Biol Control 56:43–49

Philippot L, Raaijmakers JM, Lemanceau P, van der Putten WH (2013) Going back to the roots: the microbial ecology of the rhizosphere. Nat Rev Microbiol 11:789–799

Pieterse CM, Zamioudis C, Berendsen RL, Weller DM, Van Wees SC, Bakker PA (2014) Induced systemic resistance by beneficial microbes. Annu Rev Phytopathol 52:347–375

Pillay VK, Nowak J (1997) Inoculum density, temperature, and genotype effects on *in vitro* growth promotion and epiphytic and endophytic colonization of tomato (*Lycopersicon esculentum* L.) seedlings inoculated with a pseudomonad bacterium. Can J Microbiol 43:354–361

Pimentel IC, Glienke-Blanco C, Gabardo J, Stuart RM, Azevedo JL (2006) Identification and colonization of endophytic fungi from soybean (*Glycine max* (L.) Merril) under different environmental conditions. Braz Arch Biol Technol 49:705–711

Piromyou P, Greetatorn T, Teamtisong K, Okubo T, Shinoda R, Nuntakij A, Tittabutr P, Boonkerd N, Minamisawa K, Teaumroong N (2015) Preferential association of endophytic bradyrhizobia with different rice cultivars and its implications for rice endophyte evolution. Appl Environ Microbiol 81:3049–3061

Pozo MJ, Van Der Ent S, Van Loon LC, Pieterse CM (2008) Transcription factor MYC2 is involved in priming for enhanced defense during rhizobacteria-induced systemic resistance in *Arabidopsis thaliana*. New Phytol 180:511–523

Qin S, Zhang Y-J, Yuan B, Xu P-Y, Xing K, Wang J, Jiang J-H (2014) Isolation of ACC deaminase-producing habitat-adapted symbiotic bacteria associated with halophyte *Limonium sinense* (Girard) Kuntze and evaluating their plant growth-promoting activity under salt stress. Plant Soil 374:753–766

Quecine M, Araujo W, Rossetto P, Ferreira A, Tsui S, Lacava P, Mondin M, Azevedo J, Pizirani-Kleiner A (2012) Sugarcane growth promotion by the endophytic bacterium *Pantoea agglomerans* 33.1. Appl Environ Microbiol 78:7511–7518

Raaijmakers JM, Mazzola M (2012) Diversity and natural functions of antibiotics produced by beneficial and plant pathogenic bacteria. Annu Rev Phytopathol 50:403–424

Rado R, Andrianarisoa B, Ravelomanantsoa S, Rakotoarimanga S, Rahetlah V, Fienena FR, Andriambeloson O (2015) Biocontrol of potato wilt by selective rhizospheric and endophytic bacteria associated with potato plant. Afr J Food Agric Nutr Dev 15:9762–9226

Rai R, Dash PK, Prasanna BM, Singh A (2007) Endophytic bacterial flora in the stem tissue of a tropical maize (*Zea mays* L.) genotype: isolation, identification and enumeration. World J Microbiol Biotechnol 23:853–858

Rakotoniriana EF, Rafamantanana M, Randriamampionona D, Rabemanantsoa C, Urveg-Ratsimamanga S, El JM, Munaut F, Corbisier AM, Quetin-Leclercq J, Declerck S (2013) Study in vitro of the impact of endophytic bacteria isolated from *Centella asiatica* on the disease incidence caused by the hemibiotrophic fungus *Colletotrichum higginsianum*. Antonie Van Leeuwenhoek 103:121–133

Rangjaroen C, Rerkasem B, Teaumroong N, Sungthong R, Lumyong S (2014) Comparative study of endophytic and endophytic diazotrophic bacterial communities across rice landraces grown in the highlands of northern Thailand. Arch Microbiol 196:35–49

Reinhold-Hurek B, Hurek T (2011) Living inside plants: bacterial endophytes. Curr Opin Plant Biol 14:435–443

Reiter B, Pfeifer U, Schwab H, Sessitsch A (2002) Response of endophytic bacterial communities in potato plants to infection with *Erwinia carotovora* subsp. atroseptica. Appl Environ Microbiol 68:2261–2268

Rosenblueth M, Martinez-Romero E (2006) Bacterial endophytes and their interactions with hosts. Mol Plant-Microbe Interact 19:827–837

Ryan RP, Germaine K, Franks A, Ryan DJ, Dowling DN (2008) Bacterial endophytes: recent developments and applications. FEMS Microbiol Lett 278:1–9

Salomon MV, Bottini R, de Souza Filho GA, Cohen AC, Moreno D, Gil M, Piccoli P (2014) Bacteria isolated from roots and rhizosphere of *Vitis vinifera* retard water losses, induce abscisic acid accumulation and synthesis of defense-related terpenes in in vitro cultured grapevine. Physiol Plant 151:359–374

Samish Z, Etinger-Tulczynska R, Bick M (1961) Microflora within healthy tomatoes. Appl Microbiol 9:20–25

Sandhiya GS, Sugitha TKC, Balachandar D, Kumar K (2005) Endophytic colonization and in planta nitrogen fixation by a diazotrophic *Serratia* sp. in rice. Indian J Exp Biol 43:802–807

Sasaki K, Ikeda S, Ohkubo T, Kisara C, Sato T, Minamisawa K (2013) Effects of plant genotype and nitrogen level on bacterial communities in rice shoots and roots. Microbes Environ 28:391–395

Scher FM, Baker R (1980) Mechanism of biological control in a Fusarium-suppressive soil. Phytopathology 70:412–417

Schikora A, Carreri A, Charpentier E, Hirt H (2008) The dark side of the salad: *Salmonella typhimurium* overcomes the innate immune response of *Arabidopsis thaliana* and shows an endopathogenic lifestyle. PLoS One 3:e2279

Schulz B, Boyle C (2006) What are endophytes? In: Schulz B, Boyle C, Sieber T (eds) Microbial root endophytes. Springer, Berlin, pp 1–13

Seghers D, Wittebolle L, Top EM, Verstraete W, Siciliano SD (2004) Impact of agricultural practices on the *Zea mays* L. endophytic community. Appl Environ Microbiol 70:1475–1482

Sessitsch A, Hardoim P, Doring J, Weilharter A, Krause A, Woyke T, Mitter B, Hauberg-Lotte L, Friedrich F, Rahalkar M, Hurek T, Sarkar A, Bodrossy L, Brar D, van Elsas JD, Reinhold-Hurek B (2012) Functional characteristics of an endophyte community colonizing rice roots as revealed by metagenomic analysis. Mol Plant-Microbe Interact 25:28–36

Sessitsch A, Reiter B, Berg G (2004) Endophytic bacterial communities of field-grown potato plants and their plant-growth-promoting and antagonistic abilities. Can J Microbiol 50:239–249

Sharma VK, Nowak J (1998) Enhancement of verticillium wilt resistance in tomato transplants by in vitro coculture of seedlings with a plant growth-promoting rhizobacterium (*Pseudomonas* sp. strain PsJN). Can J Microbiol 44:528–536

Shi J, Liu A, Li X, Feng S, Chen W (2011) Inhibitory mechanisms induced by the endophytic bacterium MGY2 in controlling anthracnose of papaya. Biol Control 56:2–8

Siddiqui IA, Ehteshamul-Haque S (2001) Suppression of the root rot–root knot disease complex by *Pseudomonas aeruginosa* in tomato: the influence of inoculum density, nematode populations, moisture and other plant-associated bacteria. Plant Soil 237:81–89

Singh JS, Pandey VC, Singh DP (2011) Efficient soil microorganisms: a new dimension for sustainable agriculture and environmental development. Agric Ecosyst Environ 140:339–353

Sorensen J, Sessitsch A (2006) Plant-associated bacteria lifestyle and molecular interactions. In: van Elsas JD, Jansson JK, Trevors JT (eds) Modern soil microbiology. CRC Press, Boca Raton, pp 211–236

Spoel SH, Koornneef A, Claessens SM, Korzelius JP, Van Pelt JA, Mueller MJ, Buchala AJ, Metraux JP, Brown R, Kazan K, Van Loon LC, Dong X, Pieterse CM (2003) NPR1 modulates cross-talk between salicylate- and jasmonate-dependent defense pathways through a novel function in the cytosol. Plant Cell 15:760–770

Stein E, Molitor A, Kogel KH, Waller F (2008) Systemic resistance in *Arabidopsis* conferred by the mycorrhizal fungus *Piriformospora indica* requires jasmonic acid signaling and the cytoplasmic function of NPR1. Plant Cell Physiol 49:1747–1751

Stoltzfus JR, So R, Malarvithi PP, de Bruijn FJ (1997) Isolation of endophytic bacteria from rice and assessment of their potential for supplying rice with biologically fixed nitrogen. Plant Soil 194:25–36

Sturz AV, Chriestie BR, Matheson BG (1988) Association of bacterial endophyte populations from red clover and potato crops with potential for beneficial allelopathy. Can J Microbiol 44:162–167

Sturz AV, Christie BR, Nowak J (2003) Bacterial endophytes: potential role in developing sustainable systems of crop production. Crit Rev Plant Sci 19:1–30

Suman A, Shasany AK, Singh M, Shahi HN, Gaur A, Khanuja SPS (2001) Molecular assessment of diversity among endophytic diazotrophs isolated from subtropical Indian sugarcane. World J Microbiol Biotechnol 17:39–45

Suman A, Yadav AN, Verma P (2016) Endophytic microbes in crops: diversity and beneficial impact for sustainable agriculture. In: Singh DP, Singh AB, Prabha R (eds) Microbial inoculants in sustainable agricultural productivity. Springer India, New Delhi, pp 117–143

Sun L, Qiu F, Zhang X, Dai X, Dong X, Song W (2008) Endophytic bacterial diversity in rice (*Oryza sativa* L.) roots estimated by 16S rDNA sequence analysis. Microb Ecol 55:415–424

Surette MA, Sturz AV, Lada RR, Nowak J (2003) Bacterial endophytes in processing carrots (*Daucus carota* L. Var. *sativus*): their localization, population density, biodiversity and their effects on plant growth. Plant Soil 253:381–390

Suyal DC, Yadav A, Shouche Y, Goel R (2015) Bacterial diversity and community structure of western Indian Himalayan red kidney bean (*Phaseolus vulgaris*) rhizosphere as revealed by 16S rRNA gene sequences. Biologia 70:303–313

Sziderics AH, Rasche F, Trognitz F, Sessitsch A, Wilhelm E (2007) Bacterial endophytes contribute to abiotic stress adaptation in pepper plants (*Capsicum annuum* L.) Can J Microbiol 53:1195–1202

Talley JL, Wayadande AC, Wasala LP, Gerry AC, Fletcher J, DeSilva U, Gilliland SE (2009) Association of *Escherichia coli* O157:H7 with filth flies (Muscidae and Calliphoridae) captured in leafy greens fields and experimental transmission of *E. coli* O157:H7 to spinach leaves by house flies (Diptera: Muscidae). J Food Prot 72:1547–1552

Tam HM, Diep CN (2014) Isolation, characterization and identification of endophytic bacteria in sugarcane *(Saccharum* sp. L.*)* cultivated on soils of the Dong Nai province, southeast of Vietnam. Am J Life Sci 2:361–368

Thomas P, Sekhar AC (2014) Live cell imaging reveals extensive intracellular cytoplasmic colonization of banana by normally non-cultivable endophytic bacteria. AoB Plants 6:1–12

Tian BY, Cao Y, Zhang KQ (2015) Metagenomic insights into communities, functions of endophytes, and their associates with infection by root-knot nematode, *Meloidogyne incognita,* in tomato roots. Sci Rep 5:1–15

Tian X, Cao L, Tan H, Han W, Chen M, Liu Y, Zhou S (2007) Diversity of cultivated and uncultivated actinobacterial endophytes in the stems and roots of rice. Microb Ecol 53:700–707

Trognitz F, Piller K, Nagel M, Borner A, Bacher C-F, Rechlik M, Mayrhofer H, Sessitsch A (2014) Isolation and characterization of endophytes isolated from seeds of different plants and the application to increase juvenile development. In: Brandstetter A, Geppner M, Grausgruber H, Buchgraber K (eds) Tagung Zukünftiges Saatgut - Produktion, Vermarktung, Nutzung und Konzervierung (future seed - production, marketing, use and conservation). Hohere Bundeslehr und Forschungsanstalt, Raumberg-Gumpenstein, pp 25–28

Tsurumaru H, Okubo T, Okazaki K, Hashimoto M, Kakizaki K, Hanzawa E, Takahashi H, Asanome N, Tanaka F, Sekiyama Y, Ikeda S, Minamisawa K (2015) Metagenomic analysis of the bacterial community associated with the taproot of sugar beet. Microbes Environ 30:63–69

Turner TR, James EK, Poole PS (2013) The plant microbiome. Genome Biol 14:209

Tuteja N (2007) Abscisic acid and abiotic stress signaling. Plant Signal Behav 2:135–138

Van Der Ent S, Verhagen BW, Van Doorn R, Bakker D, Verlaan MG, Pel MJ, Joosten RG, Proveniers MC, Van Loon LC, Ton J, Pieterse CM (2008) MYB72 is required in early signaling steps of rhizobacteria-induced systemic resistance in *Arabidopsis*. Plant Physiol 146:1293–1304

van Overbeek L, van Elsas JD (2008) Effects of plant genotype and growth stage on the structure of bacterial communities associated with potato (*Solanum Tuberosum* L.) FEMS Microbiol Ecol 64:283–296

van Overbeek LS, van DJ, Wichers JH, van AA, van Roermund HJ, Willemsen PT (2014) The arable ecosystem as battleground for emergence of new human pathogens. Front Microbiol 5:104

Velazquez-Sepilveda I, Orozco-Mosqueda MC, Prieto-Barajas CM, Santoyo G (2012) Bacterial diversity associated with the rhizosphere of wheat plants (*Triticum aestivum*): toward a metagenomic analysis. Int J Exp Bot 81:81–87

Verma P, Yadav AJ, Khannamkazy S, Saxera AK, Suman A (2013) Elucidating the diversity and plant growth promoting attributes of wheat (*Triticum aestivum*) associated acidotolerant bacteria from southern hills zone of India. Natl J Life Sci 10:219–227

Verma P, Yadav AN, Kazy SK, Saxena AK, Suman A (2014) Evaluating the diversity and phylogeny of plant growth promoting bacteria associated with wheat (*Triticum aestivum*) growing in central zone of India. Int J Curr Microbiol App Sci 3:432–447

Verma P, Yadav AN, Khannam S, Panjiar N, Kumar S, Saxena AK, Suman A (2015) Assessment of genetic diversity and plant growth promoting attributes of psychrotolerant bacteria allied with wheat *(Triticum aestivum)* from the northern hills zone of India. Appl Environ Microbiol 65:1885–1899

Wang M, Xing Y, Wang J, Xu Y, Wang G (2014) The role of the *chi1* gene from the endophytic bacteria *Serratia proteamaculans* 336x in the biological control of wheat take-all. Can J Microbiol 60:533–540

Wang M, Xing Y, Xu Y, Wang G (2008) The role of the chi1 gene from the endophytic bacteria *Serratia proteamaculans* 336x in the biological control of wheat take-all. Can J Microbiol 60:533–540

Wei G, Kloepper JW, Tuzun S (1991) Induction of systemic resistance of cucumber to *Colletotrichum orbiculare* by select strains of plant growth-promoting rhizobacteria. Phytopathology 81:1508–1512

Weilharter A, Mitter B, Shin MV, Chain PS, Nowak J, Sessitsch A (2011) Complete genome sequence of the plant growth-promoting endophyte *Burkholderia phytofirmans* strain PsJN. J Bacteriol 193:3383–3384

Weller DM, Raaijmakers JM, Gardener BB, Thomashow LS (2002) Microbial populations responsible for specific soil suppressiveness to plant pathogens. Annu Rev Phytopathol 40:309–348

West ER, Cother EJ, Steel CC, Ash GJ (2010) The characterization and diversity of bacterial endophytes of grapevine. Can J Microbiol 56:209–216

Whipps JM (1997) Developments in the biological control of soil-borne plant pathogens. Adv Bot Res 26:1–134

White JF Jr, Torres MS, Somu MP, Johnson H, Irizarry I, Chen Q, Zhang N, Walsh E, Tadych M, Bergen M (2014) Hydrogen peroxide staining to visualize intracellular bacterial infections of seedling root cells. Microsc Res Tech 77:566–573

Whitman WB, Coleman DC, Wiebe WJ (1998) Prokaryotes: the unseen majority. Proc Natl Acad Sci U S A 95:6578–6583

Wu Q, Zhu L, Jiang L, Xu X, Xu Q, Zhang Z, Huang H (2015) Draft genome sequence of *Paenibacillus dauci* sp. nov., a carrot-associated endophytic actinobacteria. Genom Data 5:241–253

Xia Y, DeBolt S, Dreyer J, Scott D, Williams MA (2015) Characterization of culturable bacterial endophytes and their capacity to promote plant growth from plants grown using organic or conventional practices. Front Plant Sci 6:490

Yan Y, Yang J, Dou Y, Chen M, Ping S, Peng J, Lu W, Zhang W, Yao Z, Li H, Liu W, He S, Geng L, Zhang X, Yang F, Yu H, Zhan Y, Li D, Lin Z, Wang Y, Elmerich C, Lin M, Jin Q (2008) Nitrogen fixation island and rhizosphere competence traits in the genome of root-associated *Pseudomonas stutzeri* A1501. Proc Natl Acad Sci U S A 105:7564–7569

Yang CJ, Zhang XG, Shi GY, Zhao HY, Chen L, Tao K, Hou TP (2011) Isolation and identification of endophytic bacterium W4 against tomato *Botrytis cinerea* and antagonistic activity stability. Afr J Microbiol 5:131–136

Yanni YG, Rizk RY, Corich V, Squartini A, Ninke K, Philip-Hollingsworth S, Orgambide G, de Bruijn F, Stoltzfus J, Buckley D, Schmidt TM, Mateos PF, Ladha JK, Dazzo FB (1997) Natural endophytic associations between *Rhizobium leguminosarum* bv. *trifolii* and rice roots and assessment of its potential to promote rice growth. Plant Soil 194:114

Yashiro E, Spear RN, McManus PS (2011) Culture-dependent and culture-independent assessment of bacteria in the apple phyllosphere. J Appl Microbiol 110:1284–1296

You C, Zhou F (1988) Non nodular endophytic nitrogen fixation in wetland rice. Can J Microbiol 35:408

Zhang YF, He LY, Chen ZJ, Wang QY, Qian M, Sheng XF (2011a) Characterization of ACC deaminase-producing endophytic bacteria isolated from copper-tolerant plants and their potential in promoting the growth and copper accumulation of *Brassica napus*. Chemosphere 83:57–62

Zhang YF, He LY, Chen ZJ, Zhang W-H, Wang QY, Qian M, Sheng XF (2011b) Characterization of lead-resistant and ACC deaminase-producing endophytic bacteria and their potential in promoting lead accumulation of rape. J Hazard Mater 186:1720–1725

Zhong W, Gu T, Wang W, Zhang B, Lin X, Huang Q, Shen W (2010) The effects of mineral fertilizer and organic manure on soil microbial community and diversity. Plant Soil 326:511–522

Zinniel DK, Lambrecht P, Harris NB, Feng Z, Kuczmarski D, Higley P, Ishimaru CA, Arunakumari A, Barletta RG, Vidaver AK (2002) Isolation and characterization of endophytic colonizing bacteria from agronomic crops and prairie plants. Appl Environ Microbiol 68:2198–2208