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## Bacterial endophytes in agricultural crops and their role in stress tolerance: a review

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### Abstract

Bacterial endophytes are a class of endosymbiotic microorganisms widespread among plants that colonize intercellular and intracellular spaces of all plant compartments and do not cause plant disease or significant morphological changes. Plant and endophytic bacteria association includes vast diversity of bacterial taxa and plant hosts and in this review we present an overview of taxonomic composition of endophytes identified in common agricultural crops. Further, during the last decade, new aspects of the microbial diversity have emerged with application of new metagenomic analysis methods in studies of bacterial endophytes. Endophytic bacteria community structure is influenced by plant genotype, abiotic and biotic factors such as environment conditions, microbe – microbe interactions and plant – microbe interactions. Agricultural practices, such as soil tillage, irrigation, use of pesticides and fertilizers have 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 is becoming an important element of sustainable agriculture that could ensure plant productivity and quality of agricultural production. The diverse endophytic microbial communities play integral and unique role in the functioning of agroecosystems. Endophytic bacteria have been shown to have several beneficial effects on their host plant, including growth promoting activity, modulation of plant metabolism and phytohormone signalling that leads to adaptation to environmental abiotic or biotic stress. Use of endophytic bacteria presents a special interest for development of agricultural applications that ensure improved crop performance under cold, draught or contaminated soil stress conditions or enhanced disease resistance.

Key words: agricultural practices, endophytic microbiome, microbial community, microbial diversity, plant adaptation.

### Introduction

Agricultural intensification in the 20<sup>th</sup> century has been largely achieved through the use of farm equipment, high-yielding crop varieties, intensive tillage, irrigation, fertilizers, pesticides and other manufactured inputs (Foley et al., 2005). This is well illustrated by the global use of fertilizers that increased from approx. 27 to 170 million of nutrient tons over the past 50 years before 2010 (Bumb, Baanante, 1996; Heffer, 2013). However, detrimental effects of the agricultural practices on soil ecology, high irrigation needs, as well as effect on human health, have been recognized. Therefore new environmentally benign approaches have to be employed to maintain sustainable agricultural production and to overcome threats that lead to loss of crop yield, including plant stresses associated with unfavourable environmental conditions, such as drought, temperature extremes or soil salinity, as well as biotic stress induced by plant pathogens and pests. In this context, there is a strong case for using microorganisms for improved plant

performance in integrated plant disease management systems (reviewed by Singh et al., 2011 and Jha et al., 2013). Microorganisms can provide beneficial effects on plants directly by enhancing crop nutrition or indirectly by reducing damage caused by pathogens or environmental stress.

Plants live in intimate association with microorganisms that fulfil important functions in agricultural ecosystems. Bacteria may exist as free-living organisms in soils or attached to the surface of roots or phyllosphere, and may establish symbiotic relations with plants (Smith, Goodman, 1999). Endophytic bacteria are a class of endosymbiotic microorganisms that live in internal plant tissues of apparently healthy host plants (Schulz, Boyle, 2006). Unlike phytopathogens, such bacteria do not normally cause any substantial disease symptoms, and occurrence of endophytes is not associated with morphological changes of plant tissues such as caused by root-nodule symbionts. Endophytes

colonize plant apoplast, including the intercellular spaces of the cell walls and xylem vessels of plant roots, stems and leaves, and they are also found in tissues or flowers (Compant et al., 2011), fruits (de Melo Pereira et al., 2012) and seeds (Trognitz et al., 2014). Population densities of endophyte bacteria are extremely variable in different plants and tissues and have been shown to vary from hundreds to reaching as high as  $9 \times 10^9$  of bacteria per gram of plant tissue (Jacobs et al., 1985; Misaghi, Donndelinger, 1990; Chi et al., 2005). Typically, higher density of endophyte populations is found in plant roots and other below-ground tissues as compared to above-ground tissues, and ascending migration of endophytic bacteria from roots to leaves of rice plants has been demonstrated (Chi et al., 2005), suggesting roots as the main entry point of the potential endophytes from soil to the host plant. Although endophytic bacteria are adapted to living inside specific plant genotypes, a variety of reports indicate that structure of endophytic community is influenced by abiotic and biotic factors such as environment conditions, microbe – microbe interactions and plant – microbe interactions (Ryan et al., 2008).

It has been established that tight association between host-plant and endophytes is mediated through action of compounds produced by the microorganisms and the host cells (Reinhold-Hurek, Hurek, 2011; Brader et al., 2014). A large body of literature documented diverse effects of endophytic bacteria on plant health and growth. The endophytes aid nutrient availability and uptake, enhance stress tolerance, and provide disease resistance (Ryan et al., 2008; Hamilton et al., 2012). Plant growth promoting capability of endophytes could be directly established through production of plant growth hormones, interactions that alter endogenous plant hormone production or activity that increases accessibility of nutrients, such as nitrogen and phosphorus (Glick, 2012). Plant disease resistance promoting properties are associated with the ability of endophytic bacteria to produce a wide range of compounds, such as antibiotics or chitinase enzyme, which can inhibit growth of plant pathogens and thus act as biocontrol agents (Raaijmakers, Mazzola, 2012; Christina et al., 2013; Brader et al., 2014; Wang et al., 2014). Endophytes were also shown to stimulate a latent disease defense mechanism, termed as induced systemic resistance (ISR), that confers an enhanced level of protection to a broad spectrum of pathogens (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 as amendments to promote plant growth and health. A number of registered patents that are related to application of endophytic bacteria to enhance host tolerance to fungal pathogens as well as to promote plant growth demonstrate a potential for applications that would benefit development of sustainable agricultural production (Mei, Flinn, 2010).

Here, we provide an overview of the composition of bacterial populations that are found in endosphere of major crop plants grown in agricultural environment and recent advances in analysis approaches used in the endophytic microbiome research. Further, progress in understanding of complex interactions among the

bacterial endophytes, effects of agricultural practices on endophytic bacterial communities and a role of the endophytes in plant adaptation to stress and disease resistance are considered.

## Occurrence and diversity of bacterial endophytes in agricultural crops

Diverse endophytic bacteria play an integral role in ecosystems and plant physiology. These bacteria colonize all plant compartments, generally the intercellular and intracellular spaces of inner tissues. Initial studies on diversity of endophytic bacteria were mostly based on characterization of endophytic isolates obtained from the plant after surface disinfection. Lodewyckx et al. (2002) characterized the main methods used for the bacteria isolation and 81 bacterial species which form endophytic associations with plants. One of the early reviews by Hallman et al. (1997) presented a list of bacterial endophytes isolated from various plant parts of different agricultural crops. The list of endophytes and plants harbouring them was supplemented by later studies (Rosenblueth, Martinez-Romero, 2006; Bacon, Hinton, 2007; Ryan et al., 2008). A summary of most widespread bacterial isolates identified and common agricultural crop plants that serve as host for the bacteria are presented in Table. The list is incomplete as the endophytic bacteria and plant association include a vast diversity of bacterial taxa and plant hosts.

The early studies on composition of endophytic communities revealed that different plant hosts harbour similar community of bacterial endophytes (Mundt, Hinkle, 1976). The genera of *Bacillus* and *Pseudomonas* are identified as frequently occurring in agricultural crops (Seghers et al., 2004; Souza et al., 2013). Presence of different endophytic species depends mostly on plant and bacteria genotype, biotic and abiotic environmental factors. Meanwhile a single host plant species comprises several genera and species of endophytes, the tissue type of plant or season of isolation may determine extent of the endophytic population (Kuklinsky-Sobral et al., 2004; Rosenblueth, Martinez-Romero, 2006). A large study conducted on bacterial endophyte communities revealed that although endophytic bacteria colonize entire plant, the roots usually contain higher number of species. Endophytic species mostly belong to the  $\alpha$ -,  $\beta$ -, and  $\gamma$ -proteobacteria subgroups and are closely related to epiphytic species (Kuklinsky-Sobral et al., 2004). Interestingly, the  $\gamma$ -proteobacteria group is the most diverse and dominant. It has been reported that most of gram-negative endophytes act as agents of biological control (Kobayashi, Palumbo, 2000), while among the gram-positive bacteria the dominant endophytic species primarily those belonging to the *Bacillus* species are found (Gupta et al., 2002; Bacon, Hinton, 2007).

Most of the culturable isolated endophytic bacteria species belong to *Proteobacteria*, meanwhile *Firmicutes*, *Actinobacteria* and also *Bacteroides* are less

**Table.** Endophytic bacteria isolated from common agricultural crop plants

Plant species and organ	Bacterial endophyte taxa	References
1	2	3
Alfalfa ( <i>Medicago sativa</i> L.) roots	<b>γ-proteobacteria:</b> <i>Erwinia</i> sp., <i>Pseudomonas</i> sp. <b>firmicutes:</b> <i>Bacillus megaterium</i> , <i>B. chosinensis</i> <b>actinobacteria:</b> <i>Microbacterium trichothecenolyticum</i>	Gagne et al., 1987; Stajkovic et al., 2009
Black pepper ( <i>Piper nigrum</i> L.) roots	<b>γ-proteobacteria:</b> <i>Pseudomonas</i> sp., <i>Serratia</i> sp. <b>firmicutes:</b> <i>Bacillus</i> sp. <b>actinobacteria:</b> <i>Arthrobacter</i> sp., <i>Micrococcus</i> sp., <i>Curtobacterium</i> sp.	Aravind et al., 2009
Carrot ( <i>Daucus carota</i> L. var. <i>sativus</i> )	<b>α-proteobacteria:</b> <i>Rhizobium (agrobacterium) radiobater</i> <b>γ-proteobacteria:</b> <i>Klebsiella terrigena</i> , <i>Pseudomonas putida</i> , <i>P. fluorescens</i> , <i>P. chlororaphis</i> <b>firmicutes:</b> <i>Bacillus megaterium</i>	Surette et al., 2003
Grape ( <i>Vitis</i> spp.) stems	<b>β-proteobacteria:</b> <i>Comamonas</i> sp. <b>γ-proteobacteria:</b> <i>Pseudomonas cichorii</i> , <i>Enterobacter</i> sp., <i>Klebsiella ozaenae</i> , <i>K. pneumoniae</i> , <i>K. terrigena</i> , <i>Pantoea</i> sp., <i>Xanthomonas</i> sp., <i>Moraxella bovis</i> , <i>Rahnella agquatilis</i> <b>firmicutes:</b> <i>Bacillus fastidiosus</i> , <i>B. insolitus</i> <b>actinobacteria:</b> <i>Curtobacterium</i> sp., <i>Clavibacter</i> sp., <i>Rhodococcus luteus</i>	Bell et al., 1995; West et al., 2010
Maize ( <i>Zea mays</i> L.) stems, roots	<b>α-proteobacteria:</b> <i>Rhizobium etli</i> <b>β-proteobacteria:</b> <i>Bukholderia pickettii</i> , <i>B. cepacia</i> , <i>Achromobacter</i> , <i>Herbaspirillum seropedicae</i> <b>γ-proteobacteria:</b> <i>Erwinia</i> sp., <i>Enterobacter</i> sp., <i>E. cloacae</i> , <i>Stenotrophomonas</i> sp., <i>Klebsiella</i> sp., <i>K. terrigena</i> , <i>K. pneumoniae</i> , <i>K. variicola</i> , <i>Pseudomonas</i> sp., <i>P. aeruginosa</i> , <i>P. fluorescens</i> <b>firmicutes:</b> <i>Bacillus</i> sp., <i>B. mojavensis</i> , <i>B. thuringiensis</i> , <i>B. megaterium</i> , <i>B. subtilis</i> , <i>B. pumilus</i> , <i>Lysinibacillus</i> , <i>Paenibacillus</i> <b>actinobacteria:</b> <i>Corynebacterium</i> sp., <i>Arthrobacter globiformis</i> , <i>Microbacterium testaceum</i>	Lalande et al., 1989; Fisher et al., 1992; McInroy, Kloepper, 1995; Palus et al., 1996; Chelius, Triplett, 2001; Zinniel et al., 2002; Rosenblueth, Martinez-Romero, 2004; Rai et al., 2007
Potato ( <i>Solanum tuberosum</i> L., <i>Ipomoea batatas</i> ) tubers and stems	<b>α-proteobacteria:</b> <i>Agrobacterium</i> sp., <i>Sphingomonas</i> sp., <i>Methylobacterium</i> sp. <b>β-proteobacteria:</b> <i>Acidovorax</i> sp., <i>Alcaligenes</i> sp., <i>Comamonas</i> sp., <i>Enterobacter</i> sp. <b>γ-proteobacteria:</b> <i>Acinetobacter</i> sp., <i>Erwinia</i> sp., <i>Klebsiella</i> sp., <i>Pantoea</i> sp., <i>P. agglomerans</i> , <i>Pasteurella</i> sp., <i>Photobacterium</i> sp., <i>Vibrio</i> sp., <i>Serratia liquefaciens</i> , <i>Xanthomonas</i> sp., <i>Pseudomonas tolaasii</i> , <i>Psychrobacter</i> sp., <i>Shewanella</i> sp., <i>Enterobacter</i> sp., <i>E. asburiae</i> <b>firmicutes:</b> <i>Bacillus alcliphialus</i> , <i>B. pasteurii</i> , <i>B. sphaericus</i> , <i>B. coryneforms</i> , <i>Leuconostoc</i> sp., <i>Paenibacillus odorifer</i> <b>bacteroidetes:</b> <i>Capnocytophaga</i> sp. <b>Actinobacteria:</b> <i>Actinomyces</i> sp., <i>Arthrobacter ureafaciens</i> , <i>Corynebacterium</i> sp., <i>Curtobacterium</i> sp., <i>C. citreum</i> , <i>C. leteum</i> , <i>Micrococcus</i> sp.	Hollis, 1951; De Boer, Copeman, 1974; Sturz et al., 2000; Reiter et al., 2002; Sturz et al., 1998
Radish ( <i>Raphanus sativus</i> L.) leaves and roots	<b>proteobacteria:</b> <i>Proteobacteria</i> sp.	Seo et al., 2010
Red clover ( <i>Trifolium Pratense</i> L.), leaves, stems, roots and fresh nodules	<b>α-proteobacteria:</b> <i>Agrobacterium rhizogenes</i> , <i>A. tumefaciens</i> , <i>Methylobacterium</i> sp., <i>Phyllobacterium</i> sp., <i>Rhizobium</i> sp., <i>Sphingomonas</i> sp. <b>β-proteobacteria:</b> <i>Acidovorax</i> sp., <i>Bordetella</i> sp., <i>Comamonas</i> sp., <i>Variovorax</i> sp. <b>γ-proteobacteria:</b> <i>Enterobacter</i> sp., <i>Aerobacter cloacae</i> , <i>Escherichia</i> sp., <i>Klebsiella</i> sp., <i>Pantoea agglomerans</i> , <i>Xanthomonas compestris</i> , <i>X. oryzae</i> , <i>Pseudomonas cichorii</i> , <i>P. corrugata</i> , <i>P. fulva</i> , <i>P. syringae</i> , <i>P. tolaasii</i> , <i>Serratia</i> sp., <i>Pasteurella</i> sp., <i>Psychrobacter</i> sp., <i>P. immobilis</i> <b>firmicutes:</b> <i>Bacillus brevis</i> , <i>B. megaterium</i> <b>actinobacteria:</b> <i>Arthrobacter ilicis</i> , <i>Cellulomonas</i> sp., <i>Curtobacterium citreum</i> , <i>C. luteum</i> , <i>Micrococcus varians</i>	Sturz et al., 1998

Table continued

1	2	3
Wild rice ( <i>Oryza officinalis</i> , <i>O. barthii</i> , <i>O. rufipogon</i> , <i>O. glandiglumis</i> , <i>O. breviligulata</i> ) and cultivated rice ( <i>O. sativa</i> L.) roots and stems	<b><math>\alpha</math>-proteobacteria:</b> <i>Agrobacterium</i> sp., <i>Azorhizobium</i> sp., <i>Azospirillum</i> sp., <i>A. lipoferum</i> , <i>A. brasilense</i> , <i>Bradyrhizobium</i> sp., <i>Rhizobium leguminosarum</i> , <i>Azorhizobium</i> sp., <i>A. Caulinodans</i> , <i>Bradyrhizobium japonicum</i> <b><math>\beta</math>-proteobacteria:</b> <i>Azoarcus</i> sp., <i>Burkholderia graminis</i> , <i>B. cepacia</i> , <i>Ideonella dechloratans</i> , <i>Chromobacterium violaceum</i> , <i>Herbaspirillum seropedicae</i> , <i>H. rubrisubalbicans</i> , <i>H. seropedicae</i> <b><math>\gamma</math>-proteobacteria:</b> <i>Enterobacter cancerogenus</i> , <i>Pseudomonas</i> sp., <i>Pantoea</i> sp., <i>Serratia</i> sp., <i>S. marcescens</i> , <i>Klebsiella</i> sp., <i>K. variicola</i> , <i>Stenotrophomonas</i> sp. <b>firmicutes:</b> <i>Bacillus</i> sp. <b>actinobacteria:</b> <i>Micrococcus</i> sp.	You, Zhou, 1989; Stolfus et al., 1997; Yanni et al., 1997; Chaintreuil et al., 2000; Engelhard et al., 2000; Elbeltagy et al., 2001; Sandhiya et al., 2005; Mbai et al., 2015
Sugar beet ( <i>Beta vulgaris</i> L.) roots	<b><math>\gamma</math>-proteobacteria:</b> <i>Erwinia</i> sp., <i>Pseudomonas</i> sp., <i>Xanthomonas</i> sp. <b>firmicutes:</b> <i>Bacillus</i> sp., <i>Lactobacillus</i> sp. <b>actinobacteria:</b> <i>Corynebacterium</i> sp.	Jacobs et al., 1985; Dent et al., 2004
Soybean ( <i>Glycine max</i> (L.) Merr.) stems, leaves, roots and nodules	<b><math>\alpha</math>-proteobacteria:</b> <i>Erwinia</i> sp., <i>Agrobacterium</i> sp. <b><math>\gamma</math>-proteobacteria:</b> <i>Pseudomonas citronellolis</i> , <i>P. oryzihabitans</i> , <i>P. staminea</i> , <i>K. pneumoniae</i> , <i>K. oxytoca</i> , <i>Enterobacter</i> sp., <i>Pantoea</i> sp., <i>P. agglomerans</i> <b>firmicutes:</b> <i>Bacillus fastidiosus</i>	Zinniel et al., 2002; Kuklinsky-Sobral et al., 2004
Tomato ( <i>Lycopersicon Esculentum</i> Mill.) stems and fruits	<b><math>\gamma</math>-proteobacteria:</b> <i>Pseudomonas</i> sp., <i>P. syringae</i> , <i>P. aeruginosa</i> , <i>Escherichia coli</i> <b>firmicutes:</b> <i>Brevibacillus brevis</i>	Samish et al., 1961; Pillay, Nowak, 1997; Yang et al., 2011; Patel et al., 2012
Wheat ( <i>Triticum aestivum</i> L.) roots	<b><math>\beta</math>-proteobacteria:</b> <i>Burkholderia cepacia</i> <b><math>\gamma</math>-proteobacteria:</b> <i>Klebsiella</i> sp. <b>firmicutes:</b> <i>Bacillus polymyxa</i> <b>actinobacteria:</b> <i>Mycobacterium</i> sp.	Mavingui et al., 1992; Balandreau et al., 2001; Zinniel et al., 2002; Iniguez et al., 2004

common (Reinhold-Hurek, Hurek, 2011). This suggests that part of communities of bacterial endophytes could be overlooked and others are overrepresented based on their capability to grow on synthetic medium. To draw a more precise picture of the diversity of endophytic microorganisms, recently a number of studies have been focused on identification of unculturable endophytes using novel metagenomic analysis approaches. Direct amplification of microbial DNA from plant tissue samples and application of modern bioinformatics tools allow analysis of a bacterial community composition and its phylogenetic structure inside a variety of plant organs or tissues (Chun et al., 2007; Manter et al., 2010). Sessitsch et al. (2012) analyzed genomic characteristics of bacterial endophytes colonizing rice roots under field conditions. These authors found that the population was dominated by members of  $\gamma$ -proteobacteria, comprising mostly enterobacter-related endophytes. However, application of culture independent methods allowed studies of growing numbers of plant material samples and revealed rarely reported endophyte species of  $\delta$ - and  $\epsilon$ -proteobacteria in rice roots (Sun et al., 2008). Tsurumaru et al. (2015) analyzed a metagenome of the bacterial community associated with the taproot of sugar beet (*Beta vulgaris* L.). The study found that *Alphaproteobacteria* are dominant, followed by the *Actinobacteria* and the *Betaproteobacteria*. Another metagenomic study of the sorghum root and stem microbiome revealed that the two tissues harboured significantly different composition of bacterial communities, but both were dominated by agriculturally important genera such as *Microbacterium*,

*Agrobacterium*, *Sphingobacterium*, *Herbaspirillum*, *Erwinia*, *Pseudomonas* and *Stenotrophomonas* (Maropola et al., 2015).

Metagenomic analysis involves direct isolation of bacterial DNA, library construction and functional analysis (Handelsman, 2004; Jiao et al., 2006). To investigate endophytic bacterial diversity, highly specific methods should be used (Sun et al., 2008). Initial studies on the unculturable bacterial endophyte diversity revealed technical limitation related to separation of endophytic bacteria from plant nuclei, plastids, mitochondria and plant associated microbial DNA (Govindasamy et al., 2014). As plant DNA is much more abundant than bacterial, it is difficult to isolate and sequence only bacterial community at high coverage. In order to avoid plant host DNA, enrichment of endophytic bacteria prior to DNA amplification should be done (Govindasamy et al., 2014). To exclude interference of plant host DNA, Jiao et al. (2006) enriched bacterial endophytes by hydrolysis of the plant cell walls, followed by differential centrifugation. For bacterial DNA ratio enrichment in stems and leaves of soybean and rice, Ikeda et al. (2009) used series of differential centrifugation steps followed by density gradient centrifugation. Another technique suitable for extraction of endophytes from internal tissues of potato tubers was developed by Nikolic et al. (2011) and involved overnight shaking of the small pieces of potato tubers in sodium chloride solution. Although the method allowed bacterial DNA extraction from a large amount of plant material, diversity of rare members of endophytic metagenome could be also reduced.

## Interactions within the population of bacterial endophytes

Endophytic bacteria are known to produce a wide variety of secondary metabolites and hydrolytic enzymes. Discovery of novel endophytic metabolites and investigation of their involvement in plant metabolism is an active field of research (recently reviewed by Brader et al., 2014). A large number of the compounds produced by endophytes possess antibacterial or antifungal activity. So far, the main research on antimicrobial activity of endophytes has been mainly focused on impact of endophytes on pathogenic bacteria and fungi. However, an abundance of endophytic bacteria and potential of metabolic signalling suggests presence of the multidimensional network of competing and symbiotic interactions in plant endosphere, which is difficult to model in *in vitro* experiments. Therefore elucidation of the molecular basis for interactions among the endophytic bacteria and their effect on endophytic fungi largely remains a challenge for future research.

The fact that many endophytic bacteria contain quorum sensing systems suggests a complex interaction between the bacteria in endosphere. Quorum sensing signals are involved in plant colonization by *Methylobacterium* (Dourado et al., 2014). Metagenomic analysis revealed that three quorum sensing systems – autoinducer-2 system, the diffusible signal factor system and N-acyl homoserine lactone (AHL) system are present in endophytic rice microbiome (Sessitsch et al., 2012). The AHL signalling is prevalent in *Populus deltoides* endophytic microbiome (Schaefer et al., 2013). The example of interactions between species based on quorum sensing was revealed in a study on plant pathogen causing olive (*Olea europaea* L.) knot disease *Pseudomonas savastanoi* pv. *Savastanoi*, and enterobacteria *Pantoea agglomerans* and *Erwinia toletana*. All three bacteria produced AHLs and shared one AHL quorum sensing system. *P. savastanoi* AHL quorum sensing mutants had impaired virulence. *E. toletana* knot formation ability by pathogen was regained when olive was co-inoculated with *P. savastanoi* AHL synthase mutant (Hosni et al., 2011). It was demonstrated that plants actively participate in AHL signalling as presence of the AHLs altered expression of number of plant genes including those involved in plant defense responses and plants were shown to mimic bacterial AHLs (reviewed by Hartmann et al., 2014).

Quorum sensing signals can be “intercepted” by signal degrading molecules – the effect known as quorum quenching. Endophytic *Bacillus* isolates from *Cannabis sativa* quenched four different AHLs used by *Chromobacterium violaceum* in violacein production regulation (Kusari et al., 2014). Extracts of endophyte bacteria *Bacillus* and *Enterobacter* from *Pterocarpus* showed AHLs degrading ability when applied on biosensor strains (Rajesh, Ravishankar, 2014). N-acyl-L-homoserine lactone acylase with specificity against medium and long chain AHLs was found in endophytic *Streptomyces* (Chankhamhaengdecha et al., 2013). AHL lactonase gene from *Bacillus thuringiensis* was introduced into endophytic *Burkholderia* which then

was able to attenuate symptoms caused by pathogenic *Burkholderia glumae* in rice and *Erwinia carotovora* in potatoes (Cho et al., 2007).

Recent studies have revealed that bacterial endophytes are involved in complex interactions with endophytic fungi. For example, *Burkholderia rhizoxinica* endosymbiont of endophytic fungus *Rhizopus microsporus* controls vegetative reproduction of the host fungus (Lackner et al., 2011). Endophytic bacteria identified as *Luteibacter* enhances indole-3-acetic acid (IAA) production *in vitro* by endophyte *Pestalotiopsis*, meanwhile bacteria alone fail to produce IAA on medium and endophytic fungi produce significantly smaller amounts of IAA in absence of the bacterium (Hoffman et al., 2013).

## Effect of agricultural practices on endophytic bacterial communities

Agricultural land management greatly alters soil characteristics, including physical, chemical and biological properties (Jangid et al., 2008; Garcia-Orenes et al., 2013). Soil tillage 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. Excessive use of pesticides can induce significant changes in the function and structure of soil microbial populations (Pampulha, Oliveira, 2006). The effect of pesticides may manifest a direct inhibitory effect on microbial growth and metabolism, as well as microbial diversity may change due to overall changes in the structure of agricultural ecosystems. Agricultural management alters the quantity and quality of plant residues entering the soil and their spatial distribution, through changes in nutrients and inputs (Christensen, 1996). Likewise, application of mineral or organic fertilizers has a different effect on composition of microbial community and microbial biomass (Zhong et al., 2010). Microbial diversity and metabolic activity is significantly increased by application of organic manure. However, the application of manures introduces faecal bacteria into soil and has the potential to alter the composition of the endogenous microbial population and to pose environmental hazards (Soupir et al., 2006).

The majority of bacteria in plant endosphere are presumed to have a “facultative endophyte” lifestyle and a stage in their life cycle in which they exist outside the host plants (Hardoim et al., 2008). These endophytes often originate from soil, initially infecting roots of the host plant and colonizing the plant apoplast. Therefore it could be presumed that the endophytic community represents a certain subset of the wider microbial population of rhizosphere and it would reflect differences induced by agronomic practices that are characteristic of soil microbial community. However, research on the effect of agricultural practices on endophyte population dynamics is limited to several studies.

It was demonstrated that colonization ability of nitrogen-fixing endophytic bacterium *Acetobacter diazotrophicus* is largely decreased in the sugarcane plants

fertilized with high levels of nitrogen (Fuentes-Ramirez et al., 1999). Analysis of the endophytic population of maize roots under treatment with herbicides and different fertilizer types revealed that microbial group-specific genetic pattern differentiated the maize plants, cultivated by using mineral fertilizer, from the plants cultivated by using organic fertilizer (Seghers et al., 2004). Meanwhile, no significant effect of herbicide treatment on composition of the root endophyte population was detected. These studies did not reveal if the changes in endophyte population were a consequence of changes in overall soil microbial population upon the fertilizer treatment or the agronomic practices had a direct effect on the root endophytic community. However, another study, demonstrating that application of chitin resulted in changes in bacterial communities in soil, rhizosphere and cotton roots, suggested that the organic amendment supported endophytic species in cotton roots that otherwise did not occur (Hallman et al., 1999). Intriguingly, it was shown that the composition of the endophytic community was largely different from that of the rhizosphere, suggesting that the composition of the endophytic population was not directly determined by microbial diversity of the rhizosphere, but involved other factors related to plant biochemistry. Therefore the amendment of chitin, that enhanced chitinase and peroxidase concentrations, might have changed a preference of the plants for certain bacterial endophytes.

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). Pathogenic bacteria of the family *Enterobacteriaceae* including pathogenic *Salmonella* genus strains, *Escherichia coli* and *Vibrio cholerae* strains, and the human opportunistic pathogen *Pseudomonas aeruginosa* were described as endophytic colonizers of plants (Kutter et al., 2006; Schikora et al., 2008; Deering et al., 2012; Akhtyamova, 2013). The colonization of plants by the human pathogens may be associated with the use of manures contaminated with faecal bacteria (Brandl, 2006; Holden et al., 2009), as well as the use of practices that lead to decline in soil and endophytic microbial populations and a reduced number and abundance of species antagonistic to the human pathogens (Latz et al., 2012).

Another aspect related to the effect of agricultural practices on soil and plant microbiome is reflected by the disease-suppressive soil phenomenon defined as “soils in which plants do not suffer from certain diseases or where disease severity is substantially reduced even though a virulent pathogen is present and the host plant is susceptible to the disease” (Weller et al., 2002; Haas, Defago, 2005). Biological suppression of soil-borne diseases is a function of activity and composition of soil microbiome. 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 build up of host specific microbial community (Scher, Baker, 1980; Whipps, 1997; Lorang et al., 1989). 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 induced systemic resistance (ISR) (Philippot et al., 2013; Pieterse et al., 2014). Specific role of the endophytic bacteria in development of the disease suppressive traits was rarely addressed in the studies on disease suppressive soil communities; however, bacteria of genus *Streptomyces*, *Bacillus*, *Actinomyces*, *Pseudomonas* that lead endophytic lifestyle were shown to contribute to the disease suppressive traits of soils (Siddiqui, Ehteshamul-Haque, 2001; Weller et al., 2002; Haas, Defago, 2005; Mendes et al., 2011; Kinkel et al., 2012).

### Role of endophytes in adaptation of agricultural crops to biotic and abiotic environmental stress

Endophytic bacteria have been shown to have several beneficial effects on their host plant. Plant growth is promoted through improved nutrient acquisition, including nitrogen fixation (Mirza et al., 2001) and production of plant growth enhancing substances such as cytokinins (Garcia de Salamone et al., 2001) and indole acetic acid (IAA) (Naveed et al., 2015). In addition to enhanced growth properties, modulation of plant metabolism and phytohormone signalling by the endophytic bacteria enhances adaptation to environmental abiotic or biotic stress. Endophytic bacteria present a special interest for improved crop adaptation to stress as they have the advantage of being relatively protected from the harsh environment of the soil under draught, high salt or other stress conditions (Sturz et al., 2000).

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 et al., 2006; Fernandez et al., 2012). The bacterium presence 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. Similar positive effect of the bacterium on metabolic balance and reduced effect of drought stress was demonstrated in wheat plants grown under reduced irrigation conditions (Naveed et al., 2014). Endophytic bacteria *Pseudomonas pseudoalcaligenes* was shown to induce accumulation of higher concentrations of glycine betain-like compounds leading to improved salinity stress tolerance in rice (Jha et al., 2011).

Cohen et al. (2009) demonstrated that water stress tolerance in maize plants was alleviated by accumulation of the abscisic acid (ABA) produced by endophytic *Azospirillum* spp. and the effect was further enhanced by plant growth promoting hormones IAA and gibberellins. ABA is the phytohormone critical for plant growth and development and its levels are known to rise under stress condition. Main function of ABA seems to be the regulation of plant water balance and osmotic stress tolerance (Tuteja, 2007).

Ethylene is another important plant hormone that is the extensively studied mediator of plant stress response signalling. Ethylene 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, Kende, 2000). Stress induced accumulation of ethylene is usually deleterious to plant growth and health (Czarny et al., 2006). 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 ethylene precursor ACC (Campbell, Thompson, 1996; Glick, 2014). There are numerous reports on ACC deaminase-containing plant-associated bacteria and their role in improved plant growth and stress tolerance that was recently reviewed by Glick (2014). The effect of endophytic bacteria-derived ACC deaminase activity on salt stress was most studied. Endophytic diazotrophic *Achromobacter xylosoxidans* AUM54 isolated from *Catharanthus roseus* grown in saline soil showed ability to produce ACC deaminase and to reduce ethylene levels (Karthikeyan et al., 2012). Improved plant growth in 150 mM NaCl containing soils was demonstrated for the plants inoculated with the *A. xylosoxidans* AUM54 strain. Recently, the study by Qin et al. (2014) revealed that halophyte plant *Limonium sinense* was naturally associated with ACC deaminase producing putative endophytic bacteria that might play important role in higher salinity tolerance of the plant. Thirteen isolates possessing ACC deaminase activity were obtained that belonged to genera: *Bacillus*, *Pseudomonas*, *Klebsiella*, *Serratia*, *Arthrobacter*, *Streptomyces*, *Isoptericola* and *Microbacterium*. Four of the selected ACC deaminase-producing strains were shown to stimulate growth of the host plants. In another study, tomato plants grown under 165 mM and 185 mM NaCl levels exhibited higher gain of biomass and a greater number of flowers and buds when pretreated with ACC deaminase containing bacterial endophytes *Pseudomonas fluorescens* YsS6 and *P. migulae* 8R6 as compared to treatment with ACC deaminase deficient mutants of the bacteria (Ali et al., 2014). The study revealed that endophytic bacteria affected plants differently under salt stress conditions as compared to other rhizospheric bacteria, such as *Pseudomonas putida* UW4 that was studied by Cheng et al. (2007). Meanwhile the reduced ethylene levels due to ACC deaminase activity were observed in both cases, the later study showed that the rhizospheric bacteria allowed the salt to accumulate in root tissues and presumably partition into the vacuole (Cheng et al., 2007), while the bacterial endophytes limited the concentration of sodium in plant shoots (Ali et al., 2014).

In addition, ACC deaminase producing *Pantoea agglomerans* Jp3-3 and *Achromobacter xylosoxidans* strain Ax 10 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., 2011 a). 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., 2011 b).

The study on cold resistance of vine plants inoculated by *Burkholderia phytofirmans* PsJN revealed

that the colonization of endophytic bacteria placed metabolism of the grapevine in the primed state that enabled higher and faster accumulation of stress related gene transcripts and metabolites leading to more effective resistance to cold stress (Theocharis et al., 2012). This provided insight into the priming phenomenon implicated in stress tolerance induced by plant-associated bacteria. However, so far the role of the priming in resistance to abiotic stress has attracted less attention as compared to the pathogen defense response priming that is proven to be a critical process of the induced systemic resistance (ISR) activated by non-pathogenic plant-associated microorganisms. The protection of cucumber plants against cucumber anthracnose induced by *Pseudomonas fluorescens* strain 89B-61 was the first case demonstrating that endophytic bacteria could elicit ISR in plants and published in 1991 (Wei et al., 1991; Kloepper, Ryu, 2006). Subsequent studies established that the ISR was induced by endophytic bacteria of genus *Bacillus*, *Pseudomonas* and *Serratia* in different plant-pathogen systems and molecular cell signalling mechanisms involved in the defense priming were previously reviewed (Kloepper, Ryu, 2006; Pieterse et al., 2014).

The ISR primes plant defense mechanisms and protects non-exposed plant parts against a future attack by pathogenic microbes and herbivorous insects. Although several plant-associated bacteria have been reported to induce a salicylic acid mediated type of induced systemic resistance, the plant hormones jasmonic acid (JA) and ethylene (ET) play a major regulatory role in the network of interconnected signalling pathways involved in ISR induction (Pieterse et al., 2012). Meanwhile the detailed mechanism of the defense priming during ISR remains elusive, the evidence for role of transcription co-regulator NPR1 in the JA/ET-dependent ISR has been provided and the cytosol specific function of the NPR1, different from the function involved in pathogen induced systemic acquired resistance, has been revealed (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).

## Conclusion and outlook

A vast diversity of endophytic bacteria isolated from a large number of agricultural plants suggests that the bacteria play an integral role in balancing plant physiology and functioning of agroecosystems. Composition of the endosphere microbial populations depends mostly on plant and bacteria genotype, biotic and abiotic environmental factors. Endophytic species have been mostly reported throughout the  $\alpha$ -,  $\beta$ -, and  $\gamma$ -proteobacteria subgroups and the latter is the most diverse and dominant group. The genera of *Bacillus* and *Pseudomonas* are identified as frequently occurring in agricultural crops. During the last decade development of metagenomic analysis techniques has brought to light new information on the diversity of unculturable endophytic bacteria and provided important prospects for understanding complex interactions within the microbial



community and with the plant host. Numerous studies demonstrate beneficial effects of the endophytic bacteria on plant growth and adaptability to biotic or abiotic stresses. Therefore understanding of composition and functioning of plant associated microbial communities as well as control of the structure of endophytic bacterial populations through development of environmentally benign agricultural practices has a large potential for improved plant performance and application of the integrated plant disease management systems required for sustainable agricultural production.

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## **Bakterinių endofitų reikšmė žemės ūkio augalų atsparumui stresui: apžvalga**

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### **Santrauka**

Bakteriniai endofitai yra augaluose plačiai paplitusi endosimbiontinių mikroorganizmų grupė, kuri kolonizuoja visų augalo dalių tarpląstelines bei viduląstelines sritis ir nesukelia augalų ligų ar reikšmingų morfologinių pakitimų. Augalų ir endofitinių bakterijų sąveikai būdinga didelė taksonominė bakterijų ir augalų įvairovė. Apžvalgoje apibendrintos žinios apie ištirtų būdingų žemės ūkio augalų endofitų taksonominę sudėtį. Pastarąjį dešimtmetį naujų duomenų apie šių mikroorganizmų įvairovę pateikė naujų metagenominės analizės metodų taikymas tiriant endofitines bakterijas. Endofitinių bakterijų bendrijų struktūrą lemia augalo genotipas, aplinkos sąlygos, mikroorganizmų tarpusavio sąveika ir jų sąveika su augalais. Tokios žemės dirbimo technologijos kaip dirvos arimas, drėkinimas, pesticidų ir trąšų naudojimas turi didelę įtaką dirvožemio bei endofitinių mikroorganizmų populiacijų funkcijoms ir struktūrai. Todėl natūralią augalų endofitinių bakterijų įvairovę palaikančios žemės ūkio technologijos tampa svarbia darnios žemdirbystės dalimi, užtikrinančia didelį augalų produktyvumą ir žemės ūkio produkcijos kokybę. Įvairios endofitinių mikroorganizmų bendrijos yra neatsiejama agroekosistemų dalis, svarbi jų funkcionavimui. Nustatyta, kad endofitinės bakterijos gali skatinti augalo šeiminko augimą, reguliuoti metabolizmą, fitohormonų signalinius kelius ir tokiu būdu didinti augalų atsparumą aplinkos abiotiniam ar biotiniam stresui. Endofitinių bakterijų panaudojimas sudaro galimybę kurti žemės ūkio technologijas, kurios užtikrintų didesnę augalų atsparumą šalčio, sausros ar užterštų dirvožemių stresui arba padidintų augalų atsparumą ligoms.

Reikšminiai žodžiai: augalų adaptyvumas, endofitinė mikrobioma, mikroorganizmų bendrijos, mikroorganizmų įvairovė, žemės ūkio technologijos.