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Review Article

Diversity and the role of endophytic bacteria: a review

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ABSTRACT:
Endophytes belong to a widespread group of microorganisms that colonise intracellular and intercellular spaces in all known plant parts but do not cause diseases or major morphological changes to the host. Endophytic bacteria ubiquitously colonise plant internal tissues, where they can form a variety of interactions, including commensalistic, symbiotic, trophobiotic and mutualistic. Endophytic bacteria produce pharmaceutically important compounds such as antimicrobials, antioxidants, industrial enzymes, antidiabetics and anti-cancer agents. In addition, endophytes can also support their host by producing a variety of natural products for potential use in medicine, agriculture or industry. This group of bacteria can have a tremendous impact on plant communities, raising their fitness by endowing tolerance to biotic and abiotic stress. There are great prospects for searching, selecting and studying new endophytic bacteria species in order to create new microbial preparations for adaptive crop production, while reducing the environmental impacts of agriculture. The present review summarises studies to date about endophytic bacteria, including topics such as isolation methods, the diversity of these bacteria and their biological roles.

Keywords:
endophytes, biological roles, histological localisation, biocontrol, antimicrobial activity

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INTRODUCTION

The term endophyte was initially introduced by de Bary in 1866 to describe any organism found within the plant´s tissues, distinct from the epiphytes, which reside on the plant's surface (de Bary 1866). Various definitions of endophytes have been used in the literature, terms like endophytic microorganisms, which are described as asymptomatic microbes residing in plants (Carroll 1991), whereas the bacteria that spend part or all of their life cycle colonising intra-cellular or inter-cellular spaces in petiole, leaves, stem and roots within healthy plant tissues are usually considered endophytic bacteria (Wilson 1995). Endophytes are regarded as microbes which are culturable or occupy the inside of plant tissues, do not harm their hosts and therefore do not grow external structures (Araújo *et al.* 2001). This description has been revised by Mendes & Azevedo (2007) who relegate endophytic microorganisms to two groups: group I includes all those that don't generate external structures from the host, and group II includes those that can produce external structures, such as mycorrhytic fungal nodules and nitrogen-fixing bacteria. Different definitions have been suggested, but the most accepted one is "Endophytes are microorganisms which reside in a wide variety of plant tissues without causing any apparent infection to the host" (Hallmann *et al.* 1997). Endophytism is now considered as a universal phenomenon, and it is believed that all plants harbour endophytic bacteria (Compant *et al.* 2010; Dudeja & Giri 2014). The endophytic bacteria can have immense potential in the uptake of nutrients (de Souza *et al.* 2016; Ribeiro *et al.* 2018), growth promotion (Ramanuj & Shelat 2018; Santos *et al.* 2018), as biofertilizers (Ngamau *et al.* 2014; Santos *et al.* 2018), as biocontrol agents (Kandel *et al.* 2017; Selim *et al.* 2017) and in secondary metabolite production (Brader *et al.* 2014; Singh *et al.* 2017; Palanichamy *et al.* 2018).

DIVERSITY OF ENDOPHYTIC BACTERIA

Endophytic bacteria are common to all species of vascular plants (Sturz *et al.* 2000). They are found in both monocotyledon and dicotyledon species (Ryan *et al.* 2008). The colonisation of endophytic bacteria in ferns, algae and bryophytes has already been described (Colombo 1978; Hollants *et al.* 2011; Shcherbakov *et al.* 2013; Liu *et al.* 2014; Das *et al.* 2017a; Tian & Li 2017; Mahlangu & Serepa-Dlamini 2018). All groups of plants ranging from seagrasses (Marhaeni *et al.* 2011; Garcias-Bonet *et al.* 2012) to large trees (Shen & Fulthorpe 2015; Puri *et al.* 2017) harbour endophytic bacteria. They are present in lichens as well (Bates *et al.* 2011). Several attempts have been made to determine the overall number of endophytic bacteria. The number of endophytic bacterial species, however, may vary due to the development of new techniques and methods to identify this diverse group of microorganisms. Previous research on the diversity of endophytic populations has shown that different plant hosts may harbour a similar population of endophytic bacteria (Mundt & Hinkle 1976). Moreover, a single host plant species may house multiple endophytic genera as well as species, and the scope of the endophytic community may be determined by the tissue, plant type or isolation season (Kuklinsky-Sobral *et al.* 2004; Miliute *et al.* 2015).

A database of all 16S rDNA sequences currently allocated to endophytes, along with uncultured and cultured microbes, showed that even though the sequences correspond to a total of 23 different phyla of bacteria, four of them (Firmicutes, Actinobacteria, Bacteroidetes and Proteobacteria) account for 96% of all endophytic sequences of the prokaryotes (Hardoim *et al.* 2015). Among them, more than 50% of the sequences in the database are proteobacteria. Gamma-proteobacteria isolates seem to be the most frequently found as endophytes within this phylum, including genera like *Enterobacter*, *Serratia*, *Pantoea*, *Pseudomonas*, *Stenotrophomonas* and *Acinetobacter*. But on the other hand, *Microbacterium*, *Staphylococcus* (Firmicutes), *Streptomyces*, *Arthrobacter* (within *Actinobacteria*), *Paenibacillus*, *Mycobacterum* and *Bacillus* are all well-identified among endophytic microbes (Hardoim *et al.* 2015). The group of γ-proteobacteria is dominant and most diverse in agricultural crops (Miliute *et al.* 2015).

Endophytic bacteria are traditionally isolated from plant tissues which are surface-sterilised and grown in a nutrient-rich medium. Several endophytes have been recently reported using culture-independent approaches like whole-genome sequencing, sequencing of the 16S rRNA gene or use of the internal transcribed spacer regions ITS1 and ITS2 of endophytic communities (Taghavi *et al.* 2009; Ikeda *et al.* 2010; Sessitsch *et al.* 2012; Turner *et al.* 2013; Yang *et al.* 2017). Typically, endophytic bacteria have been enumerated and characterised by traditional culture-based approaches, although these methods are largely dependent on the isolation medium and incubation conditions, whereas culture-independent 16S rRNA-based techniques, on the other hand, can identify unculturable bacterial colonisers as well as those that are so low in number or grow so slowly that traditional culture-based protocols ignore them.

Endophytic bacteria based on colonisation can be grouped into 'facultative', 'obligate' and 'passive' depending on whether or not tissue of the plant is required for them to reproduce and live. Bacteria obtained from any part of the plant but inside plant tissue and unable to live in the soil are known as obligate endophytic bacteria (Liu *et al.* 2017). Bacteria that are widespread in the soil and carry out infection and colonisation where appropriate conditions are available are known as facultative endophytic bacteria. Many facultative endophytic bacteria are in the cortex, but some also reach the central xylem and phloem as well (Compant *et al.* 2010). The passive mode of colonisation of endophytes is defined as the mode taken by bacteria that are unable to infect and colonise. They can invade endophytic niches of plants through cracks and wounds on the plant (Ambrose *et al.* 2013). Bacteria can thus colonise a plant extracellularly as well as intracellularly. Despite being tracked in all parts of the plant, roots with the most intimate contact with soil are the first ones to attract endophytic bacteria. Endophytic bacteria can have a genetic basis for their different patterns of infection and colonisation, which may correlate with their patterns of interaction in plants (Liu *et al.* 2017). Studies have confirmed the presence of endophytic bacteria in different plants. The detailed list is summarised in Table 1.

HISTOLOGICAL LOCALISATION, ISOLATION AND PURIFICATION OF ENDOPHYTIC BACTERIA

Endophytic bacteria thrive within healthy tissues of the plant; thus disease-free, lesion-free and fresh parts of the plant should be selected at the time of isolation and histological location. Explants must be preserved at 4°C until endophyte isolation. Rapid changes in the colonisation of endophytes are not likely to happen immediately after collection. However, it is important that samples must be processed and handled carefully as soon as possible following collection, generally within 48 hours. Samples should be air-dried before transporting or storing to remove any surface moisture. They should be kept cold and dry during transportation. It is preferred to hold samples in paper envelopes and cotton. The use of plastic bags to hold samples is discouraged, but if used they

Table 1. List of endophytic bacteria isolated from various vascular plants and their biological activity if any.

Plant species	Plant family	Endophytic bacteria isolated (and their bioactivity if any)	Reference
Allium cepa L.	Alliaceae	*Bacillus subtilis*	Pleban *et al.* 1995
Amaranthus spinosus L.	Amaranthaceae	*Exiguobacterium profundum* strain N4	Sharma & Roy 2015
Andrographis paniculata (Burm. f.) Nees	Acanthaceae	*Consortia* spp.	Aziz *et al.* 2013
Andrographis paniculata Nees.	Acanthaceae	*Bacillus thuringiensis* KL1	Roy *et al.* 2016
Artemisia annua L.	Asteraceae	*Streptomyces* sp. (antibacterial and antifungal*)	*Li *et al.* 2012b
Azadirachta indica A. Juss.	Meliaceae	*Nocardia* sp. (antibacterial*), *Streptomyces* sp. (antifungal*)	*Verma *et al.* 2009
Beta vulgaris L.	Amaranthaceae	*Pseudomonas poae* RE 1-1-14	Zachow *et al.* 2015
Boesenbergia rotunda (L.) Mansf.	Zingiberaceae	*Streptomyces* sp. BO-07	Taechowisan *et al.* 2017
Brassica oleracea L.	Brassicaceae	*Enterobacter* sp., *Herbaspirilum* sp.	Zakria *et al.* 2008
Brassica oleracea L. var. *botrytis* L.	Brassicaceae	*Bacillus cereus*	Pleban *et al.* 1995
Bruguiera gymnorrhiza (L.) Lam.	Rhizophoraceae	*Streptomyces* sp. GT2002/1503 (anti-HIV*)	*Ding *et al.* 2010
Capsicum annuum L.	Solanaceae	*Klebsiella oxytoca* AVSCE5 (KM104324) (antibacterial*)	*Syed *et al.* 2017
Capsicum frutescens L.	Solanaceae	*Achromobacter piechaudi,* *Bacillus* spp., *Cupriavidus pauculus,* *Corynebacterium minutissimum,* *Proteus* spp., *P. rettegeri,* *Serratia marcescens,* *Staphylococcus delphini*	Amaresan *et al.* 2012
Catharanthus roseus L.	Apocynaceae	*Bacillus cereus,* *Bacillus* sp. *Brevundimonas* sp., *Curtobacterium* sp., *Erwinia* sp.	Li *et al.* 2012a
Centella asiatica (L.) Urb.	Apiaceae	*Bacillus subtilis,* *Serratia marcescens*	Nongkhlaw & Joshi 2015b
Chenopodium album L.	Amaranthaceae	*Bacillus pumilus*	Beiranvand *et al.* 2017
Citrus nobilis Lour	Rutaceae	*Streptomyces* sp. TQR12-4 (antifungal*)	*Hong-Thao *et al.* 2016
Coffea arabica L.	Rubiaceae	*Paenibacillus amylolyticus*	Sakiyama *et al.* 2001
Curcuma aeruginosa Roxb.	Zingiberaceae	*Bacillus amyloliquefaciens* (antibacterial*), *Bacillus cereus* (antibacterial*)	*Indrawati *et al.* 2018a
Curcuma xanthorrhiza Roxb.	Zingiberaceae	*Bacillus amyloliquefaciens* (antibacterial*), *Lysinibacillus sphaericus* (antibacterial*)	*Indrawati *et al.* 2018a
Curcuma zedoaria (Christm.) Roscoe	Zingiberaceae	*Bacillus spp.* (2) (both isolates antibacterial*)	*Indrawati *et al.* 2018a
Dendrobium sp.	Orchidaceae	*Bacillus megaterium* (antibacterial*)	*Wang *et al.* 2019

Plant species	Plant family	Endophytic bacteria isolated (and their bioactivity if any)	Reference
Fagonia indica L.	Zygophyllaceae	*Bacillus subtilis,* *B. tequilensis,* *Enterobacter cloacae,* *Enterobacter hormaechei,* *Pantoea dispersa* *Stenotrophomonas maltophilia*	Rahman *et al.* 2017 (antibacterial, antifungal and antiprotozoal activity of isolates)
Glycyrrhiza uralensis Fisch. ex DC.	Fabaceae	*Bacillus atrophaeus* (antibacterial*), *B. mojavensis* (antifungal*)	*Mohamad *et al.* 2018
Helianthus sp.	Asteraceae	*Bacillus pumilus*	Pleban *et al.* 1995
Hibiscus rosa-sinensis L.	Malvaceae	*Pseudomonas oryzihabitans*	Bhagat *et al.* 2016
Hyptis suaveolens (L.) Kuntze	Lamiaceae	*Bacillus amyloliquefaciens,* *Bacillus* sp., (antibacterial*) *Pseudomonas* spp. (antibacterial*)	*Das *et al.* 2017b
Lactuca sativa L.	Asteraceae	*Pseudomonas viridiflava* (antifungal*)	*Miller *et al.* 1998
Litsea cubeba (Lour.) Pers.	Lauraceae	*Bacillus siamensis*	Nongkhlaw & Joshi 2015b
Malus domestica Borkh.	Rosaceae	*Bacillus* spp., *Pseudomonas* spp.	Tamošiūnė *et al.* 2018
Mangifera indica L.	Anacardiaceae	*Bacillus clausii,* *B. licheniformis,* *B. pumilus,* *Baccilus* sp.	Kannan *et al.* 2015
Manihot esculenta L.	Euphorbiaceae	*Bacillus pumilus* (antifungal*)	*Melo *et al.* 2009
Medicago sativa L.	Fabaceae	*Bacillus megaterium,* *B. chosinensis,* *Erwinia* sp., *Microbacterium trichothecenolyticum,* *Pseudomonas* sp.	Gagné *et al.* 1987; Stajković *et al.* 2009; López *et al.* 2018
Monstera sp.	Araceae	*Streptomyces* sp. (antibacterial and antifungal*)	*Ezra *et al.* 2004
Moringa peregrina (Frossk.) Fiori	Moringaceae	*Bacillus licheniformis* MpKL1 (antibacterial*)	*Aljuraifani *et al.* 2019
Musa sp.	Musaceae	*Agrobacterium* sp. *Azospirillum brasilense,* *Bacillus amyloliquefaciens, Citrobacter* sp., *Klebsiella variicola*	Weber *et al.* 1999; Martínez *et al.* 2003; Rosenblueth *et al.* 2004
Ocimum sanctum L.	Lamiaceae	*Bacillus subtilis,* *Enterobacter* sp. (antibacterial activity*)	Tiwari *et al.* 2010; *Muhsinin *et al.* 2016
Ophiopogon japonicus (L.f.) Ker Gawl.	Asparagaceae	*Bacillus amyloliquefaciens*	Chen *et al.* 2013
Oryza sativa L	Poaceae	*Agrobacterium* sp., *Azorhizobium caulinodans,* *Bradyrhizobium japonicum,* *Chromobacterium violaceum,* *Pseudomonas stutzeri* A15, *Rhizobium leguminosarum,* *Sphingobacterium* sp.	Yanni *et al.* 1997; Chaintreuil *et al.* 2000; Engelhard *et al.* 2000; Phillips *et al.* 2000; Moronta-Barrios *et al.* 2017; Pham *et al.* 2017;
Phaseolus vulgaris L.	Fabaceae	*Pseudomonas fluorescens*	Pleban *et al.* 1995

Plant species	**Plant family**	**Endophytic bacteria isolated (and their bioactivity if any)**	**Reference**
Pinellia ternata (Thunb.) Berit.	Araceae	*Aranicola proteolyticus*, *Bacillus cereus*, *B. licheniformis*, *B. thuringiensis*, *Serratia liquefaciens*	Liu *et al.* 2015
Plectranthus tenuiflorus (Vatke) Agnew	Lamiaceae	*Acinetobacter calcoaceticus*, *Bacillus licheniformis*, *B. megaterium*, *B. pumilus*, *Baccilus* sp. (antibacterial*), *Micrococcus luteus*, *Paenibacillus* sp., *Pseudomonas* sp. (antifungal*)	*El-Deeb *et al.* 2013
Populus sp.	Salicaceae	*Rhizobium tropici*	Doty *et al.* 2005
Potentilla fulgens Wall. ex Hook.	Rosaceae	*Bacillus methylotrophicus*	Nongkhlaw & Joshi 2015b
Pyrenacantha volubilis Hook.	Icacinaceae	*Bacillus amyloliquefaciens* KY741854, *Bacillus* sp. KP125955 and KP125956, *B. subtilis* KY741853	Soujanya *et al.* 2017
Raphanus sativus L.	Brassicaceae	*Enterobacter* sp. (antifungal*), *B. subtilis* (antibacterial*)	*Seo *et al.* 2010
Saccharum officinarum L.	Poaceae	*Acetobacter diazotrophicus*, *Azospirillum amazonense*, *Burkholderia tropica*, *Gluconacetobacter diazotrophicus*, *Herbaspirillum seropedicae*, *H. rubrisubalbicans*	Dong *et al.* 1994; Olivares *et al.* 1997; Beneduzi *et al.* 2013; Pereira *et al.* 2013; Silva Girio *et al.* 2015
Solanum lycopersicum L.	Solanaceae	*Bacillus* sp.	Tian *et al.* 2017
Taxus brevifolia Nutt.	Taxaceae	*Paenibacillus kribbensis*	Islam *et al.* 2018
Teucrium polium L.	Lamiaceae	*Bacillus cereus*, *B. subtilis*	Hassan 2017
Tridax procumbens L.	Asteraceae	*Bacillus* spp., *Cronobacter sakazakii*, *Enterobacter* spp., *Lysinibacillus sphaericus*, *Pantoea* spp., *Pseudomonas* spp., *Terribacillus saccharophilus*	Preveena & Bhore 2013
Vitis vinifera L.	Vitaceae	*Bacillus atrophaeus* SP13 *B. megaterium* Sof, *B. pumilus* SP7, *Comamonas* sp.	Bell *et al.* 1995; Shcherbakov *et al.* 2009
Withania somnifera (L.) Dunal	Solanaceae	*Bacillus amyloliquefaciens*, *B. horneckiae*, *B. pumilis*, *Bacillus* sp., *Brevibacterium frigoritolerans*, *Micrococcus luteus*, *Pseudomonas putida*, *Rhizobium sullae*, *Staphylococcus haemolyticus*	Pandey *et al.* 2018

should be kept open to prevent the growth of superficial moulds and for circulation of air to prevent condensation (Stone *et al.* 2004). Samples are surface-sterilised by different methods (Zinniel *et al.* 2002; Goryluk *et al.* 2009; Qin *et al.* 2009; Costa *et al.* 2012; Yaish *et al.* 2015; Mahlangu & Serepa-Dlamini 2018). Surface sterilisation procedures vary depending on the preference of the researcher, host tissue type and plant species sampled, but the most often used surface-sterilisation protocol followed is that of Ahmed *et al.* (2012), Anjum & Chandra (2015) and Shukla & Wahla (2019). Explants are washed under running tap water before the isolation of endophytic bacteria, and this is accompanied by surface sterilisation, which differs depending on the form of contaminants and explant. The midrib and lateral stem, roots and leaves are sliced into pieces (0.5-1.0 cm). These surface-sterilised materials are further sterilised with (0.1% w/v) mercuric chloride, different concentrations of ethanol (70%, 80%, 90% and absolute) for some seconds to minutes (30 seconds to 1 minute) in a laminar airflow cabinet and sodium hypochlorite (4%) for 2-3 minutes, which is accompanied by rinsing with sterile water (double-distilled and deionised) to remove sterilisation traces and use of sterile tissue paper to dry the explants by blotting. Bacterial endophytes in the host plants do not cause any signs of disease, and their interaction requires a metabolic exchange. It is therefore difficult to identify their existence externally. As a result, the presence of endophytic bacteria in healthy plant tissues is typically identified by culture-based methods. The surface-sterilised explants are inoculated on sterile Luria Bertani Agar (LB), Tryptic Soy Agar, Rich Media, Nutrient Agar Medium, King B Agar and other media types supplemented with 100 μg/ml of cycloheximide (Zinniel *et al.* 2002; Yan *et al.* 2018) closed with the aid of parafilm and incubated at 37± 2°C in an incubator under controlled conditions to promote bacterial growth. Tryptic Soy Agar and Nutrient Agar are widely used isolation media for the isolation of endophytic bacteria and the incubation temperature and time period most often used for isolation is 28°C for 2-3 weeks (Ferreira *et al.* 2008; Aravind *et al.* 2009; Costa *et al.* 2012; Lumactud *et al.* 2016; Indrawati *et al.* 2018a; Mahlangu & Serepa-Dlamini 2018). The plates are observed regularly for growth of endophytes. The isolated endophytes can be identified based on their morphological, biochemical and molecular characteristics.

BIOLOGICAL ROLES OF ENDOPHYTIC BACTERIA

Endophytes associated with plants of ethnomedicinal importance can be helpful in the production of natural products with novel bioactivities (Nongkhlaw & Joshi 2015a). The ability of endophytic bacteria to produce interesting and new bioactive secondary metabolites of agricultural, industrial and pharmaceutical importance (Strobel 2006; Pandey *et al.* 2017) makes them interesting candidates for research purposes. They play important roles in different fields of life, ranging from their impacts on host plants to their effects on the environment and human life. Endophytic bacteria are capable of synthesizing bioactive compounds that can be used by plants to defend against pathogens or stimulate plant growth, and certain endophytes can be useful in the process of drug discovery. The natural products produced by endophytic bacteria have been shown to have different bioactivities and structures helpful against various diseases. This creates a vast potential of endophytes for the production of secondary metabolites of industrial, agricultural and medicinal importance. For example, endophytic bacteria isolated from the climbing shrub *Miquelia dentate* Bedd. (Icacianaceae) produce camptothecin, an anti-cancer alkaloid. Camptothecin (CPT)-based drugs remain attractive to scientists globally, and more CPT analogues are developing as promising chemotherapeutic agents. It is believed that CPT will continue to attract much attention from the pharmaceutical industry as well as from the academic community. Endophytic bacteria are one of the most diverse and understudied groups of microorganisms. They are omnipresent and found in nearly all plants, including a wide range of hosts in different ecosystems, and thus play a key role in the natural environment. The products of these microorganisms remain poorly characterised despite extensive work in this field. They have appeared as a major boosting factor and have strongly affected human beings in various ways, like their impact on plants and the environment, health care, nutrient cycling, bioremediation, biodegradation and agriculture. It is believed that endophytic bacterial products will be a cheap source of raw material for health, farming and other industries in the future, and more compounds will certainly be isolated from this unique group of bacteria in view of the latest advances in culturing techniques and screening methods used to identify various bioactive molecules.

ROLE OF ENDOPHYTIC BACTERIA IN PHYTOSTIMULATION

As a consequence of increasing growth of the human population worldwide and damage to the environment, world production of food may soon be inadequate to feed all the people of the globe. In this regard, the population of the world, currently around 7.7 billion people, is projected to increase in the next 50 years to about 10 billion (FAO 2017). In order to feed such a large human population, it is essential to significantly increase agricultural productivity over the next few decades. That, however, is not an easy task. We will have to come up with alternative approaches and strategies in order to address this challenge. One such alternative that has been in vogue is the systematic use of plant growth-promoting endophytic bacteria or endophytes (PGPEBs) in agriculture. These PGPEBs have been reported in various studies (Taghavi *et al.* 2009; Weilharter *et al.* 2011; Ali *et al.* 2012; Rashid *et al.* 2012; Jasim *et al.* 2014; Borah *et al.* 2019).

One of the very significant mechanisms that such PGPEBs employ is phytostimulation. Phytostimulation basically involves the production of phytohormones which act as plant growth regulators (Beneduzi *et al.* 2012). Phytohormones such as gibberellins, cytokinins and auxins promote changes in root morphology, absorption of water and uptake of nutrients (Santos *et al.* 2018). It is pertinent to look at how PGPEBs aid in phytostimulation. It has been shown that some PGPEBs like *Arthrobacter* spp., *Bacillus* spp., *Pseudomonas putida* and *Rhodococcus* spp. release the ACC deaminase enzyme (1-aminocyclopropane-1-carboxylic acid), which lowers the ethylene levels of plants, thereby enhancing their growth (Gaiero *et al.* 2013). It should be noted that increased ethylene levels in a plant inhibit cell division, shoot/ root growth and DNA synthesis, which is an impediment to a plant's growth (Gaiero *et al.* 2013).

Phytohormone production is a common characteristic of endophytic bacteria that raises tolerance of the plant to abiotic stresses and promotes plant growth (UmaMaheswari *et al.* 2013; Pieterse *et al.* 2014; Egamberdieva *et al.* 2017). Severe threats to agroecosystems are abiotic stresses such as drought, extreme temperatures, oxidative stress, heavy metal toxicity and salinity (Arora 2015). The expression and induction of stress-responsive genes, the production of scavenger molecules such as ROS and antistress metabolite synthesis are molecular mechanisms adopted by endophytes to improve stress tolerance in host plants (Lata *et al.* 2018). *Enterobacter* sp. (SA187), a desert plant *Indigofera argentea* Brum. f. (Fabaceae) endophyte colonising *Arabidopsis thaliana* (L.) Heynh. (Brassicaceae) shoots and roots, has been shown to induce salt stress tolerance through the formation of bacterial 2-keto-4-methylthiobutyric acid (KMBA), which modulates the ethylene signalling pathway of the plant. *Enterobacter* sp. (SA187) using this novel mechanism was found to be effective in increasing the yield of alfalfa crops (*Medicago sativa* L., Fabaceae) under *in vitro* conditions of salt stress (de Zélicourt *et al.* 2018). *Burkholderia phytofirmans* (PsJNT), an endofungal bacterium isolated from the fungus *Glomus vesiculiferum* (Thaxt.) Gerd. & Trappe (Glomeraceae), showed significant plant growth-promoting effects and was reported to increase resistance and plant vigour in plants like *Solanum tuberosum* L. (Solanaceae) and *Zea mays* L. (Poaceae) exposed to abiotic and biotic stresses (Weilharter *et al.* 2011). *Bacillus pumilus* (2A) isolated from the synanthropic plant *Chelidonium majus* L. (Papaveraceae) was found to produce biosurfactants that can act as plant-growth-promoting agents (Marchut-Mikolajczyk *et al.* 2018). A maximum of 10 endophytic bacteria isolated from wild *Pistacia atlantica* Desf. (Anacardiaceae), belonging to different genera such as *Pseudomonas, Bacillus, Stenotrophomonas, Serratia* and *Pantoea,* were able to produce different amounts of the phytohormone gibberellic acid (GA) (Etminani & Harighi 2018).

Endophytes also play a major role in the absorption of essential nutrients needed for plant growth. For example, endophytic *Bacillus* strains B1920, B2088, B2084 and B1923 isolated from *Zea mays* L. (Poaceae) enhanced nutrient uptake during growth of pearl millet under low-phosphorus conditions (Ribeiro *et al.* 2018). Future use of the strains treated in this study may lead to the creation of robust PGPBE inoculants that are so reliable that minor changes in external environmental factors will not impact the effectiveness of plant growth promotion. With a more comprehensive understanding of the functioning of endophytic bacteria, future generations may be able to design ones that can be used for more efficient crop production.

ENDOPHYTIC BACTERIA AS ANTIMICROBIAL AGENTS

Antimicrobial activity is the process of inhibiting or killing disease-causing microorganisms. Different antimicrobial agents are used for this purpose. Antimicrobials may be anti-viral, anti-bacterial and anti-fungal. At present, bacterial infections are one of the main causes of human and animal mortality and chronic diseases. Antibiotics have been the best method for treating bacterial infections due to powerful outcomes and favourable cost-effectiveness. However, various studies have provided clear proof that the broad use of antibiotics has resulted in the development of multidrug-resistant bacterial strains. Due to the indiscriminate use of antibiotics, so-called superbacteria which are resistant to almost all antibiotics have emerged. For this reason, attention has been focused on the isolation of exciting and new endophytic bacterial strains with antimicrobial activity. Endophytic bacteria are highly suitable for their efficiency and have no unwanted effects. *Bacillus* sp. CY22 (an endophytic bacterium) isolated from *Platycodon grandiflorum* (Jacq.) A. DC. (Campanulaceae) has been reported to have beneficial antimicrobial effects against the fungal plant pathogens *Pythium ultimum, Rhizoctonia solani*, *Phytophthora capsici* and *Fusarium oxysporum* (Cho *et al.* 2002). Endophytic bacteria have received much recognition in recent years for the development of a variety of antimicrobial compounds with a novel mechanism of action due to their non-detrimental and intimate association with plants (Strobel 2003). Various secondary metabolites obtained from endophytic bacteria have found applications in medicine (Adhikari *et al.* 2001; Gunatilaka 2006). A novel family of peptide antimycotics, termed ecomycins (namely ecomycins

Table 2. Endophytic bacteria exhibiting various enhanced enzymatic activities.

Known endophytic bacteria	Enzyme activity reported	Reference
Pseudomonas oryzihabitans	Asparaginase	Bhagat *et al.* 2016
Bacillus clausii, B. licheniformis, B. pumilus, Bacillus sp.	Amylase, cellulase, lipase, protease	Kannan *et al.* 2015
Paenibacillus amylolyticus	Pectin lyase	Sakiyama *et al.* 2001
Pseudomonas sp.	Exo-β-agarase	Gupta *et al.* 2013
Bacillus methylotrophicus, B. siamensis, B. subtilis, Serratia marcescens	L-asparaginase	Nongkhlaw & Joshi 2015b
Alcaligenes faecalis, Burkholderia cepacia, Enterobacter hormaechei	Cellulase, hemicellulase, ligninase	Leo *et al.* 2016
Bacillus amyloliquefaciens	Exopolysaccharase	Chen *et al.* 2013
Bacillus thuringiensis	Anthracene-degrading enzyme	Roy *et al.* 2016
Actinomyces pyogenes, Bacillus circulans, B. coagulans, B. licheniformis, B. megaterium, Bacillus sp., *Corynebacterium renale, Pseudomonas stutzeri, Staphylococcus* sp.	Amalyase, cellulase, pectinase, xylanase	Carrim *et al.* 2006
Bacillus aerophilus, B. anthracis, B. tequilensis, Chryseobacterium indologenes, Enterobacter ludwigii, Macrococcus caseolyticus, Pseudomonas entomophila, P. hibiscicola	Amylase, esterase, lipase, protease	Akinsanya *et al.* 2016
Bacillus licheniformis, B. pseudomycoides, Paenibacillus senitriformus	L-asparaginase	Joshi & Kulkarni 2016
Bacillus sp.	L-asparaginase	Ebrahiminezhad *et al.* 2011
Bacillus amyloliquefaciens	Phytase	Idriss *et al.* 2002
Bacillus sp., *Burkholderia* sp., *Caulobacter* sp., *Chitinophaga* sp., *Curtobacterium* sp., *Kosakonia* sp., *Massilia* sp., *Methylobacterium* sp., *Microbacterium* sp., *Mucilaginibacter* sp., *Pseudorhodoferax* sp., *Pantoea* sp., *Rhizobium* sp., *Sphingomonas* sp.	ACC deaminase, endoglucanase, protease	Chimwamurombe *et al.* 2016
Acinetobacter sp., *Bacillus* sp.	ACC deaminase, amylase, cellulase, pectinase, protease	Joe *et al.* 2016
Bacillus sp., *Curtobacterium* MBR2.20, *Erwinia* sp. MBA2.19	Amylases, cellulases, endoglucanase, esterase, lipases, proteases	Castro *et al.* 2014
Bacillus safensis	Amylases, cellulases, lipases, proteases	Khianngam *et al.* 2013
Bacillus cereus strain 65	Chitinase	Pleban *et al.* 1997
Acenitobacter sp., *Bacillus licheniformis, B. megaterium, B. pumilus, Bacillus* sp., *Micrococcus luteus, Paenibacillus* sp., *Pseudomonas* sp.	Amylase, cellulase, esterase, lipase, pectinase Protease, xylanase	El-Deeb *et al.* 2013
Bacillus cereus, B. licheniformis, B. weihenstephanensis	Amylase, cellulase, lipase, protease.	Amaresan *et al.* 2012

B and C), have been isolated from the endophytic bacterium *Pseudomonas viridiflava* (Miller *et al.* 1998). The molecular masses of Eecomycin B and C are 1153 and 1181, respectively, i.e., different from the molecular masses of other pseudomonad lipopeptide antimycotics (Ballio *et al.* 1994). The ecomycins have significant bioactivities against a wide range of human-pathogenic fungi such as *Cryptococcus neoformans*, *Candida albicans* and plant-pathogenic fungi like *Fusarium oxysporum, Rhizoctonia solani* and *Sclerotinia sclerotiorum*, which are some of the most destructive and widespread of crop pathogens (Miller *et al.* 1998). Four endophytic isolates, viz., *Pseudomonas entomophila*, *Bacillus tequilensis*, *Pseudomonas hibiscicola* and *Chryseobacterium indologenes*, which were isolated from *Aloe barbadensis* Miller (Asphodelaceae), possess a broad spectrum of antimicrobial activities against pathogens like *Staphylococcus aureus, Pseudomonas aeruginosa, Bacillus cereus, Proteus vulgaris, Klebsiella pneumoniae, Salmonella typhimurium, Streptococcus pyogenes* and *Escherichia coli* (Akinsanya *et al.* 2015). Xiamycin, a pentacyclic indolosesquiterpene showing anti-HIV activity, and its methyl ester-derivatives of *Streptomyces* sp. (GT2002/1503), an endophytic bacterium isolated from the mangrove *Bruguiera gymnorrhiza* (L.) Lam. (Rhiyophoraceae)—are novel indolosesquiterpenes isolated from prokaryotes (Ding *et al.* 2010). *Bacillus pumilus* isolated from the South American woody shrub cassava (*Manikhot esculenta* Crantz., Euphorbiaceae) produced the lipopeptide "pumilacidin", an antifungal compound which showed strong inhibitory activity against the plant-pathogenic fungi *Sclerotium rolfsii, Rhizoctonia solani* and *Pythium aphanidermatum* (Melo *et al.* 2009). Endophytic bacteria isolated from *Andrographis paniculata* Nees (Acanthaceae) showed a broad spectrum of activity against clinical pathogens and also against pathogens of fish (Arunachalam & Gayathri 2010).

The endophytic bacterial isolate *Bacillus amyloliquefaciens* isolated from *Curcuma zanthorrhiza* Roxb. (Zingiberaceae) and *Syzygium polycephalum* (Miq.) Merr. & L.M. Perry (Myrtaceae) has been found to block the growth of methicillin-resistant *Staphylococcus aureus* (MRSA), (Indrawati *et al.* 2018a, b). The antimicrobial activities reported from endophytic bacteria are summarised in Table 1. To sum up, the endophytic bacteria have an enormous potential for bioprospecting, and they could serve as one of the potential sources of new antibiotics in the future. Therefore, the current scenario warrants extensive research to explore endophytic bacteria that are untapped, unused and ignored. Effective cross-talk between molecular biologists, chemists, ethnobotanists, pharmacists, taxonomists, toxicologists and microbiologists is essential for exploring endophytic bacteria in the search for new antibiotics.

ENDOPHYTIC BACTERIA AS BIOCONTROL AGENTS

Biocontrol can be defined simply as employing one living organism to control another. This process is also referred to as biological control. Biological control is described as the use of beneficial organisms, their genes and/or products, such as metabolites, to minimise the adverse effects of plant pathogens and promote positive plant responses (Tranier *et al.* 2014). Biological application is mainly launched to reduce a pest's population and produce yields that are pest-free. For the control of invasive plants, it is a long-term treatment and self-sustaining method. The living organism employed in this process is used to prevent the outbreak of weeds and to manage pests, including mosquitoes, bacteria and grazing animals. Endophytic bacteria can reduce or prevent certain pathogenic organisms from having adverse effects. They appear to have significant effects on their plant host via mechanisms similar to those defined for bacteria associated with the rhizosphere (Franks *et al.* 2008).

Certain endophytic bacteria are thought to cause a phenomenon known as induced systemic resistance (ISR), which is phenotypically identical to systemic acquired resistance (SAR). Systemic acquired resistance develops when plants effectively initiate their defence mechanism in reaction to a pathogen's primary infection, particularly when a pathogen induces a hypersensitive reaction through which it is limited in a local necrotic lesion of brown desiccated tissue. Induced systemic resistance is effective against various types of pathogens but is different from SAR because the triggering bacterium does not cause noticeable symptoms in the plant host (van Loon *et al.* 1998). Kloepper & Ryu (2006) analysed endophytic bacteria and their role in ISR (induced systemic resistance). According to their study, selective strains of non-pathogenic endophytic bacteria can induce ISR in plants, resulting in the frequency of various diseases being reduced. In many cases, elicitation of ISR in plants by endophytic *Bacillus* sp. is associated with enhanced plant growth, and further investigation should be conducted in order to clarify the connection between growth promotion and ISR. It has just been unravelled how endophytic bacteria or their determinants account for ISR elicitation, and more work is required to explain why one isolate of a provided bacterial species can elicit ISR, whereas another isolate of the same species cannot.

Vascular wilts are disastrous plant diseases that can impact both woody annual and perennial crops, leading to major food loss and damaging precious natural ecosystems. This could be prevented by endophytic bacteria by modulating various possible disease suppression mechanisms to boost agricultural productivity (Eljounaidi *et al.* 2016). Two unknown isolates of endophytic bacteria (marked as Ps1, Ps8) from healthy tomato plants were shown to inhibit the tomato pathogen *Ralstonia solanacearum,* which causes wilt disease *in vitro* over up to 4-7 mm and *in vivo* significantly suppresses wilt disease by up to 8.07- 9.19% with an incubation period of 15-16 days (Purnawati 2014). It has also been shown that endophytic *Bacillus* sp. isolated from annual crops acts as a potential agent for biocontrol of fungal cacao disease black pod rot of cacao (Melnick *et al.* 2008). Similarly, the endophytic bacterium *Rhodococcus* sp. (KB6 strain) isolated from *Arabidopsis thaliana* (L.) Heynh. (Brassicaceae) minimised signs of black rot disease in leaves of sweet potato [*Impomeoa batatas* (L.) Lam., Convolvulaceae], which is caused by the fungal pathogen *Ceratocystis fimbriata* (Hong *et al.* 2016).

The endophytic bacteria *Burkholderia* sp. and *Bacillus* sp. isolated from soybean [*Glycine max* (L.) Merr., Fabaceae] have been the most active isolates in treating fungal and bacterial pathogens of soybean *in vitro*. Both these bacterial isolates can shield soybean in such a way as to strengthen a sustainable crop management system (de Almeida Lopes *et al.* 2018). Endophytic bacterial isolates of PGPR (plant growth-promoting rhizobacteria), viz., *Bacillus cereus* (RBac-DOB-S24) and *Pseudomonas aeruginosa* (BacDOB-E19), isolated from rhizomes of *Curcuma longa* L. (Zingiberaceae) have been shown to act as biocontrol agents capable of suppressing leaf blight and rhizome rot diseases in the same species (Vinayarani & Prakash 2018).

Endophytes are appealing as a source of chemically produced pesticides because they provide options for plant disease management that contribute to sustainable farming. The Bt toxin synthesized by *Bacillus thuringiensis* is presently one of the most effective, bioinsecticides available on the market (Jeong *et al.* 2016). Endophytic isolates of *Serratia marcescens* and *Escherichia coli* bacterial strains from *Pinus* species (namely *Pinus koraiensis* Siebold & Zucc, *Pinus densiflora* Siebold & Zucc, *Pinus thunbergii* Parl. and *Pinus rigida* Mill., Pinaceae) have been shown to possess important nematicidal activity against the pinewood nematode [*Bursaphelenchus xylophilus* (Steiner & Buhrer) Nickle, 1970, Parasitaphelenchidae] and can be used effectively as agents for the biocontrol of that nematode (Liu *et al.* 2019). Although continuing efforts to screen hypothetical endophytes are routinely carried out via *in vitro* experiments under standardised conditions, field experiments are required in various environmental situations in order to develop commercially successful biocontrol agents. For the commercialisation of biocontrol agents, further research is essential, as this will significantly reduce environmental and economic costs. Future work could be combined with screening, processing of biomass and measuring of antagonistic capacity in greenhouse and field trials, followed by the marketing of biocontrol agents that are essential to ensure global agricultural security.

ENDOPHYTIC BACTERIA AS A SOURCE OF ENZYMES

In different areas such as agriculture, industry and human health, microbial enzymes play a significant role. Endophytic bacteria enter plants through natural openings or injuries with the aid of hydrolytic enzymes such as cellulases and pectinases that enable them to actively penetrate plant tissues. As pathogens also produce these enzymes, more understanding is required to differentiate endophytic bacteria from plant pathogens for their regulation and expression. Limited research has been done on the isolation of endophytic bacteria from indigenous plants and their enzyme production potential (Joshi *et al.* 2018).

Endophytic bacteria are considered to be an important source of extracellular enzymes (Khan *et al.* 2017). They have been documented to produce enzymes like protease, amylase, cellulases, pectinase, phytase, esterase, ACC deaminase, lipase, asparaginase, protease and others (Carrim *et al.* 2006; Joe *et al.* 2016; Vijayalakshmi *et al.* 2016). It has been shown that the endophytic bacterium *Lactobacillus fermentum* isolated from *Vinca rosea* L. (Apocynaceae) exhibits high proteolytic activity superior to that of the protease of non-endophytic bacteria (Jalgaonwala & Mahajan 2011). Some work has already focused on this area of research, and endophytic bacteria producing enzymes of industrial importance are summarised in Table 2. Recently, more attention has been paid to endophytic bacteria, but they remain unexplored and neglected. To date, their capability as producers of enzymes has not been thoroughly studied. At this stage, the question of whether such organisms will be used in the coming years as effective industrial enzyme producers cannot be addressed. Modern and much more detailed research with the aid of well-established methods is required to promote development in the area of enzymes. The huge potential of endophytic bacteria as an industrial source of biocatalysts and characterisation of the chemical and physical properties of such enzymes will be more thoroughly explored in the years to come.

CONCLUSION

Endophytic bacteria contribute to plant adaptation in several habitats and are of considerable ecological significance, since they enhance soil quality and fertility as judged by plant development. Research on the metabolic influence of endophytic bacteria in plant tissues acquaints us with the various biochemical and physiological changes caused by interactions between endophytes and plants. These microorganisms have no bearing on the nutrient rivalry typically found in the rhizosphere and are more significant for reducing the harm brought about by numerous phytopathogens.

Isolation of endophytic bacteria and techniques used to identify them are vital for improving agricultural practices, since many species enhance growth of the plant, promote better nutrient uptake and absorption and induce tolerance of environmental stress, thus representing valuable biological resources that can have a positive effect on agricultural production. Compared to those treating endophytic fungi, studies on endophytic bacteria are generally limited. The appearance of new studies reporting the ability of investigators to isolate beneficial and novel bioactive compounds from endophytic bacteria is therefore significantly much higher. Endophyte research does not rely entirely on microbiologists, but rather involves a network of researchers from multidisciplinary areas such as chemistry, pharmacology, molecular biology, taxonomy and bioinformatics. The focus on existing isolated compounds could be expanded to include topics such as their use for treatment of cancer and other diseases, as well as the problem of emergence of multidrug-resistant pathogens.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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REZIME

Botanica SERBICA

Diverzitet i uloga endofitskih bakterija: pregled

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Endofite pripadaju širokoj grupi mikroorganizama koje naseljavaju unutarćelijske i međućelijske prostore svih poznatih delova biljaka, ali ne uzrokuju bolesti ili veće morfološke promene domaćina. Endofitne bakterije sveprisutno kolonizuju unutrašnja tkiva biljaka, gde mogu da formiraju različite interakcije, uključujući komensalističke, simbiotske, trofobiotske i mutualističke. Endofitne bakterije proizvode farmaceutski važna jedinjenja kao što su antimikrobni lekovi, antioksidanti, industrijski enzimi, lekovi protiv dijabetesa i kancera. Pored toga, endofite mogu da podrže svog domaćina stvaranjem različitih prirodnih proizvoda za potencijalnu upotrebu u medicini, poljoprivredi ili industriji. Ova grupa bakterija ima ogroman uticaj na biljne zajednice poboljšavajući njihovo opšte stanje kroz toleranciju na stres izazvan biotičkim i abiotičkim činiocima. Postoji veliki potencijal pronalaska, odabira i proučavanja novih vrsta endofitskih bakterija sa ciljem stvaranja novih mikrobnih preparata za adaptivno gajenje useva, dok se istovremeno smanjuje uticaj poljoprivrede na životnu sredinu. Ovaj pregled rezimira dosadašnje studije o endofitskim bakterijama, uključujući metode izolacije, njihovu raznolikost i biološku ulogu.

Ključne reči: endofite, biološka uloga, histološka lokalizacija, biokontrola, antimikrobna aktivnost