Bacterial Endophytes Associated to Crops: Novel Practices for Sustainable Agriculture

Giuliano Degrassi1*, Valeria Carpentieri-Pipolo2

1Industrial Biotechnology Group, International Centre for Genetic Engineering and Biotechnology (ICGEB), Parque Tecnológico Miguelete, San Martin, Buenos Aires, República Argentina
2Embrapa Trigo, Rodovia BR-285, Km 294, 99050-970, Passo Fundo, Rio Grande do Sul, Brazil.

*Corresponding author: Giuliano Degrassi, Industrial Biotechnology Group, International Centre for Genetic Engineering and Biotechnology (ICGEB), Parque Tecnológico Miguelete, Av. General Paz N° 5445, B1650WAB San Martín, Buenos Aires, República Argentina

Citation: Degrassi G and Carpentieri-Pipolo V (2020) Bacterial Endophytes Associated to Crops: Novel Practices for Sustainable Agriculture. Adv Biochem Biotechnol 5: 1099. DOI: 10.29011/2574-7258.001099

Received Date: 16 April, 2020; Accepted Date: 20 May, 2020; Published Date: 25 May, 2020

Abstract

For many decades, rhizosphere bacteria have been studied for their potential to promote crop growth and control certain pathogens. Compared to the studies conducted, there are relatively few examples of microbial inoculants based on rhizosphere bacteria that have had commercial success, mainly due to the strong competition present in the rhizosphere. In the last twenty years, studies on endophytes have multiplied, also and above all as a possible alternative to rhizobacteria, for the development of microbial inoculants capable of replacing some agrochemicals and reducing the environmental impact of agronomic management of crops. This minireview summarizes the most important characteristics and qualities of endophytic bacteria and describes the path that can be followed to identify and deepen the knowledge of candidates suitable for the development of microbial inoculants. The nature of endophytes requires careful isolation methods; the growth promotion potential can be identified by evaluating some traits-related phenotypes and metabolic capacities; relations with the host plant and capacity of colonization, the influence of the external environment and sensitivity to agronomic practices are pivotal factors in establishing the endophytic population in the different parts of the plant. All of this must be taken into consideration in selecting the most promising endophytes for field trials.

Keywords: Bacterial endophytes; Microbial inoculants; Plant-bacteria interactions; Plant growth promoting bacteria

Introduction to plant bacterial endophytes

Rising global population increases demand for food and drives the need for improved crop productivity over the next 30 years. This requires an increase in the current ability of agriculture to produce sufficient food to meet demand of providing food security and feeding the expanding population using efficient and sustainable crops management practices. The yield improvements need to be achieved without significant costs increases and still maintaining acceptable yields. Thus, crop enhanced productivity is needed without significant increases in land, water, or fertilizer use as these are all becoming limited and pose additional threats to the environment. In this regard, the soil microbial diversity and plant-microbe associations is considered one of the most researched areas to exploit and develop sustainable agriculture production systems. In the last ten years many studies have been published regarding the endophytic bacterial populations living associated with crops such as soybean, maize, sugarcane, wheat and many others. The aim of these studies was to identify the bacteria associated to crops which were not pathogenic and could have been beneficial, such as the Plant Growth Promoting Bacteria (PGPB) and which were living inside the plant tissues, such as the endophytes, with the purpose of assessing the mechanisms of plant-bacteria interaction and the potential beneficial effects of these bacteria on growth and health of hosting crops. Among the microorganisms living in close associations with plants, the Plant Growth Promoting Bacterial Endophytes (PGPBEs) could be more successful in plant growth promotion through the combined action of mechanisms enhancing the plants growth and protecting them from diseases and abiotic stresses [1-4]. Besides the genotypic characterization, the main and most important metabolic activities within the plant were also investigated, with the purpose of assessing the mechanisms
of plant-bacteria interaction and the potential beneficial effects of these bacteria on growth and health of hosting crops. In this respect the definition of endophytes becomes relevant. The most commonly accepted definition for endophytic bacteria, as well as fungi, is “Bacteria that are detected from inside surface-disinfected plants or extracted from inside plants and have no visibly harmful effects on the plants” [5]. The purpose of this minireview is to highlight the potential of these endophytes as plant growth promoting bacteria to be used to improve crop production in a sustainable agronomic management system.

Isolation and biodiversity of bacterial endophytes

Although the list of isolated endophytes from crop plants is considerable, the most studied and most predominant endophytes belong to the three major phyla (Actinobacteria, Proteobacteria and Firmicutes) and the most commonly found genera are Azoarcus [6], Acetobacter (renamed as Gluconobacter) [7], Bacillus [8], Enterobacter [9], Burkholderia [10], Herbaspirillum [11], Pseudomonas and Serratia [9], Stenotrophomonas, Micrococcus, Pantoea, Microbacterium and Streptomyces [12]. Species of these genera are ubiquitous in soil/rhizosphere and this is not a coincidence since soil and rhizosphere represent the main sources of endophytic colonizers [5,13-18]. All of these genera, described as bacterial endophytes, are also common inhabitants of the rhizosphere. Therefore, it has been suggested that the endophyte microbiome may be a subpopulation of the rhizosphere inhabiting bacteria [17,19,20].

PGPBEs have extended colonization on the host plant organs and tissues which reflects the ability of bacteria to selectively adapt to these specific ecological niches and consequently, intimate associations between bacteria and host plants can be formed [21]. The plant colonization by endophytes may occur mainly through the roots if the bacteria can hydrolyse the epidermal, hypodermal, endodermal and other cortical cells barriers [22]. Once inside, the colonization can be either local in specific plant tissues such as cortex, or systemic or transported across or through the conductor apoplastic elements [23]. Plant colonization by bacterial endophytes is preferably intercellular [24], with only a few reports of intracellular colonization, such as in the case of banana [25] or Arabidopsis [26]. It is also suggested that the endophytic bacteria are evolutionarily intermediate between saprophytic and pathogenic bacteria, speculating on the possibility that endophytic bacteria are more evolved than pathogenic, being able to take nutrients from the host without killing it [5]. According to Azevedo, et al. [27], the difference between endophytes, epiphytes and pathogens is purely didactic since there is a gradient between them that makes complex to discriminate each category. Endophytic bacteria may, depending on the conditions and the genotype of the host, become a pathogen; and may, depending on the phase of the lifecycle, live in harmony with the host [28].

Based on the original definition of bacterial endophytes given by Hallmann, et al. [5] and broadly accepted, the importance of methods and criteria of endophytes isolation results clear. As the character of endophytic bacteria is attributed to bacteria isolated exclusively from plant tissues superficially sterilized, surface disinfection processes have to be well defined to retain the concept and limit the endophytic habitat. Errors may arise as result of either incomplete disinfection of the surface or adsorption of bacteria through plant cell structure or penetration of sterilant within the tissues of the plant cells, resulting in loss of endophytism [5].

There are two main methods for identification and characterization of endophytic bacterial populations, depending on the possibility of culturing the bacteria. Culture dependent methods for identification of culturable endophytes involve the isolation and growth of the bacteria from surface-sterilized root, stem and leaves sections [29-33]. This step is usually followed by the phenotypic characterization of these bacteria focused mainly on properties and metabolic activities such as the secretion of hydrolytic enzymes, production of indole acetic acid and siderophores for iron uptake, phosphate solubilization, biofilm formation and exopolysaccharides production, nitrogen fixation, antimicrobial activity, different types of motility as well as other characteristics related to competitiveness, plant growth promotion, antagonism and capacity of plant colonization (Figure 1).
Figure 1: Flow chart summarizing method for isolation and characterization of bacterial endophytes, development of bacterial inoculants and benefits to agricultural crops. Sampling and sterilization of tissues (A), maceration and growth of bacteria on solid media (B), and isolation of pure cultures (C). Characterization of isolates in relation to Plant Growth Promoting (PGP) traits (D) such as phosphates solubilization (1), production of exopolysaccharides (2), siderophores (3) and indolacetic acid (4), and antimicrobial activity (5). Characterization of the endophytic bacterial population (E) by amplification and sequence analysis of the 16SrRNA gene (6), composition of bacterial population in different agronomic managements (7) and localization of bacteria in different tissues (8). Field trials (9) to establish colonization and growth promotion capabilities (10). Release to industry (G), followed by development of proper formulations and different crop-specific bioproducts.
On the other hand, some endophytes are obligate because they are unable to proliferate outside of plants and require the plant for survival, thus are often nonculturable [34]. Obligate endophytes can be studied by means of culture-independent techniques [35] based on molecular tools as Polymerase Chain Reaction (PCR) for amplification of variable regions of DNA, often from the 16S rRNA gene. This step is followed by downstream methods to analyze the endophyte community composition, which may include cloning or other community fingerprinting techniques. Considering the implications in identifying and measuring endophyte diversity and community structure, the complementarity of both culture-dependent and independent methodologies has received a broad consensus [31-33].

The Next Generation Sequencing (NGS) technology and bioinformatic tools allow the characterization of many endophyte communities from a broad variety of plant species, including their structure and dynamics based on information regarding endophyte genomes, proteomes, and transcriptomes. The complete genomes of *Glucanacetobacter diazotrophicus* [9], *Bacillus subtilis* [8], *Burkholderia* sp. [36], *Kosakonia oryzae* [37], *Enterobacter* sp. [9], *Burkholderia phytofirmans* [10], *Azospirillum* sp. [38], *Pseudomonas stutzeri* [39], *Herbaspirillum seropedicae* [11], *Azorarcus* sp [6], among others, have been sequenced and analysed. Bioinformatic analysis of genomes provides additional information on the role of these bacteria and their effects inside the plant, and represents an important tool for further studies such as the regulation of gene expression also in relation to the mechanisms of plant-microbes interaction [40,41]. In addition, the comparisons between the endophytic bacterial genomes and the genomes of rhizospheric plant growth-promoting bacteria could shed light on potential genetic factors specifically responsible of the endophytic lifestyle, therefore contributing to a better understanding of the functioning of complex interactions between bacterial endophytes and plants [20].

**Mechanisms of plant growth promotion**

Plant growth promotion by bacterial endophytes is usually the result of direct or indirect mechanisms. Direct promotion occurs either by increased acquisition of essential nutrients which involve nitrogen, phosphorus and iron or by modulation of hormone levels synthesizing auxin, cytokinin or gibberellins. In addition, some endophytes can lower levels of the phytohormone ethylene by synthesizing an enzyme, 1-Aminocyclopropane-1-Carboxylate (ACC) deaminase that cleaves the compound ACC, the immediate pre-cursor of ethylene in all higher plants. Indirect mechanisms of growth promotion occur by production of substances that inhibit bacterial or fungal pathogens and by indirect effects such as antagonism against pathogens and competition for iron [20,42-46]. For example, siderophores such as pyochelin from *Pseudomonas* sp., chelate iron and can indirectly contribute to suppression and control of disease by competing with phytopathogens for trace metals [47]. Endophytes also contribute to the control of phytopathogens primarily for their ability to induce plant defense reactions through a mechanism called Induced Systemic Resistance (ISR), that leads to a higher tolerance of pathogens [48]. Systemic resistance develops when plants successfully activate their defense mechanism in response to primary infection by a pathogen, notably when the latter induces a hypersensitive reaction through which it becomes limited in a local necrotic lesion of brown, desiccated tissue. Bacterial strains of the genera *Pseudomonas* and *Bacillus* can be considered the most common groups inducing ISR [49], although induction of resistance is not exclusive to these groups and to this mechanism. For example, the shoot endophyte *Methyllobacterium* sp. strain IMBG290 induced resistance against the pathogen *Pectobacterium atrosepticum* in potato, in an inoculum-density-dependent manner. The observed resistance was accompanied by changes in the structure of the innate endophytic community. Endophytic community changes were shown to correlate with disease resistance, indicating that the endophytic community as a whole, or just fractions, can play a role in disease suppression [50]. Bacterial factors responsible for ISR induction were identified to include flagella, antibiotics, N-acylhomoserine lactones, salicylic acid, jasmonic acid, siderophores, volatiles (e.g., acetoin), and lipopolysaccharides [51].

The potential of bacterial endophytes to Promote Plant Growth (PGP) by means of abiotic stress tolerance and disease protection is associated with their ability to produce different compounds such as secondary metabolites that are involved in mechanisms of signaling, defense and genetic regulation of the establishment of symbiosis. It has been observed that plant inoculation with endophytic bacteria leads to accumulation of “protective” compounds, such as proline, carbohydrates and antioxidants, in addition to antibiotics and fungal cell-wall lytic enzymes, which can inhibit growth of plant pathogens. Plants acclimate to environmental stresses by altering their physiology to be able to overcome stress factors such as dehydration, mechanical injury, nutrient deficiency, high solar radiation, or biotic/abiotic factors. Proline accumulation stimulating effect by endophytic strains of the actinobacteria *Arthrobacter* sp. and the Firmicutes *Bacillus* spp. were reported in pepper (*Capsicum annuum*) plants *in vitro* where their synthesis was related to osmotic stress responses. In addition, plants inoculated with bacterial endophytes could tolerate abiotic stresses by increasing enzymatic activity. *B. cereus* CSR-B-1, *B. marisflavi* CSR-G-4, *B. pumilus* CSR-B-2, *B. saffisens* CSR-G-5, *B. subtilis* CSR-G-1 and *B. thuringiensis* CSR-8, induced increment of superoxide dismutase, phenylalanine lyase, catalase, and peroxidase enzymes activity in gladiolus plants under high sodium concentration conditions [19]. Tolerance to low temperatures and growth promotion by bacterial endophytes activity has also been reported by Verma, et al. [52] that found
psychrotolerant *Bacillus* and *Bacillus* derived genera as wheat (*Triticum aestivum*) endophytes, among others. Phosphate and iron are major essential nutrients, but soluble phosphate and iron concentrations in soil for plant intake are usually very low; their acquisition can be facilitated by plant-associated bacteria [20].

The benefits of plant growth promotion mechanisms by bacterial endophytes colonization was investigated for the main crops by several authors [6,7,10-13,23,31-34,36-39,53-85]. Table 1 illustrates examples of PGPBEs in plants and crops such as Banana, Canola, Citrus, Coffee, Common Bean, Grapevine, Maize, Potato, Rice, Soybean, Sugar beet, Sugar cane, Tomato and Wheat.

**Table 1:** Some crop-associated bacterial endophytes and their plant-growth promoting traits.

| Host plant | Endophyte species | Plant growth- promoting traits | Reference |
|------------|-------------------|--------------------------------|-----------|
| Potato     | *Bacillus* spp.   | ACC deaminase activity, phosphate solubilization, siderophore production. | [53]      |
|            | *Streptomyces* spp. | PGP and biological control | [12]      |
|            | *Pseudomonas putida* and *Serratia plymuthica* | Production of the antibiotic 2,4-diacyl-phloroglucinol (*Pseudomonas*) and antagonism (*Serratia*) | [13]      |
|            | *Burkholderia phytofirmans* PsJN | ACC deaminase activity and production of indole acetic acid (IAA) | [10]      |
| Rice       | *Streptomyces* sp. strain A20 | Production of three antibiotics: streptomycins D, E and F; production of siderophores and IAA, and P solubilization. | [54]      |
|            | *Bacillus* sp.     | multiple PGP and antagonistic activity | [56]      |
|            | *Azooarcus* sp. BH72 | N-fixation | [6]       |
|            | *Azospirillum* sp. | Production of IAA and ACC deaminase | [118, 38] |
|            | *Pseudomonas stutzeri* | N-fixation | [39]      |
|            | *Burkholderia* sp., | Antifungal activity | [36]      |
|            | *Herbaspirillum seropedicae* | N-fixation | [11]      |
|            | *Kosakonia oryzae* | Siderophore production, auxin biosynthesis and N-fixation | [37]      |
|            | *Azospirillum* sp. | Promotion of rice growth |         |
|            | *Rhizobium* spp. | Growth promotion | [119]     |
|            | *Herbaspirillum, Pseudomonas,* | IAA, N-fixing, P solubilization, ACC deaminase, etc | [23]      |
|            | *Pantoea, Methylobacterium,* | | [55]      |
|            | *Kosakonia, Burkholderia,* | | |
|            | *Rhodococcus, Ralstonia,* | | |
|            | *Brevibacillus, Bacillus* | | |
| Soybean    | *B. subtilis and B. thuringiensis:* | Production of siderophores, IAA synthesis and ACC-deaminase | [57]      |
|            | *Pseudomonas, Ralstonia, Enterobacter, Pantoea and Acinetobacter* | Antifungal activity; phytases; N-fixation; phosphate solubilization; | [58]      |
|            | *Bacillus* spp. | Cellulase, pectinase and motility | [59]      |
|            | *Agrobacterium, Enterobacter, Kosakonia, Pantoea, Pseudomonas, Ralstonia, Serratia, Rhizobiun, Stenotrophomonas,* etc | Production of IAA and exopolysaccharides, P solubilization, etc. | [31, 33] |
|            | *Enterobacter sp., Bacillus sp., Variovorax sp., Serratia sp., Burkholderia sp., Pantoea sp., Kosakonia sp.* | Antimicrobial activity | [32]      |
| Crop          | Bacterial Species                        | Activity/Trait                                                                 | Reference(s) |
|--------------|------------------------------------------|-------------------------------------------------------------------------------|--------------|
| Wheat        | *Bacillus subtilis*                      | Antifungal activity against *Puccinia*                                         | [60]         |
|              | *Bacillus cereus*                        | Biofilm formation, colonization and biocontrol                                 | [61]         |
|              | *Bacillus thuringiensis*                 | Biocontrol                                                                     | [62]         |
|              | *Azospirillum sp.*                       | Phytormone synthesis: IAA, GA, ABA; phosphate solubilization                   | [38]         |
|              | *Arthrobacter sp.*                       | Siderophore-production and Zn solubilization                                   | [63]         |
|              | *Burkholderia cepacia*                   | Plant growth promotion                                                          | [64]         |
| Sugar Beet   | *Bacillus pumilus,* *Chryseobacterium indologene,* *Acinetobacter johnsonii* | Increased concentration of carbohydrates and growth photosynthetic efficiency   | [65]         |
| Sugar Cane   | *Gluconacetobacter diazotrophicus*       | N-fixation, plant growth promotion, secretion of organic acids, synthesis of auxin and bacteriocins | [7]          |
|              | *Azospirillum amazonense,* *Burkholderia tropica,* *Herbaspirillum seropedicae,* *H. rubrisubalbicans,* *Gluconacetobacter diazotrophicus* | Acceleration of budding; increase in biomass; N-fixation; production of siderophores and IAA; phosphate solubilization | [66, 67]    |
| Tomato       | *Bacillus subtilis*                      | Control of *Alternaria solani* and *Phytophthora infestans*                    | [68]         |
|              | *Burkholderia phytofirmans PsJN*         | IAA synthesis, ACC deaminase                                                   | [10]         |
|              | *Sphingomonas sp.*                       | Production of gibberellins and IAA                                             | [69]         |
| Common Bean  | *Microbacterium testaceum*               | Inhibition of bacterial pathogens and quorum sensing                           | [70]         |
|              | *Rhizobium endophyticum*                | Solubilization of phytate                                                      | [71]         |
|              | *Bacillus, Delfta, Methylobacterium, Microbacterium, Paenibacillus, Staphylococcus and Stenotrophomonas* | To be determined                                                                 | [72]         |
| Citrus       | *Bacillus sp.*                          | IAA production and P solubilization                                            | [73]         |
| Maize        | *Bacillus spp.*                          | Production of lipopeptides active against *Fusarium moniliforme*               | [74]         |
|              | *Azospirillum brasilense*                | Plant growth promotion                                                          | [75]         |
|              | *Enterobacter sp.*                       | Improved photochemical efficiency and flowering anticipation; N-fixation        | [76]         |
|              | *Paenibacillus polymyxa*                | N-fixation and growth promotion                                                | [77]         |
|              | *Pseudomonas spp.*, *Enterobacter asburiae,* *Sinorhizobium meliloti* | PGP traits and antifungal activity                                             | [78]         |
| Canola       | *Bacillus subtilis*                      | Antibacterial and antifungal activity                                          | [79]         |
|              | *Burkholderia phytofirmans*             | ACC deaminase activity and production of IAA                                   | [10]         |
| Coffee       | *Escherichia fergusonii,* *Acinetobacter calcoaceticus,* *Salmonella enterica,* *Brevibacillus choshinensis,* *Pectobacterium carotovorum,* *Bacillus megaterium,* *Microbacterium testaceum,* *Cedecea davisae* | Production of phosphatase and indol acetic acid; control of coffee leaf rust, *Hemileia vastatrix* | [80]         |
| Grapevine    | *Bacillus pumilus,* *Paenibacillus sp.* | Biocontrol of fungal pathogen *Phaeomoniella chlamydospora*                    | [81]         |
|              | *Bacillus subtilis,* *Curtobacterium sp.* | Biocontrol of *Agrobacterium vitis* crown gall disease                        | [82]         |
Plant growth promotion

Antagonism against pathogen

Enterobacter, Stenotrophomonas, Variorvax, Micrococcus, Agrococcus

To be determined

[83]

Pseudomonas aeruginosa

Stenotrophomonas malthophilia, Pseudomonas putida, Serratia proteamaculans

Antagonism against pathogen

Plant growth promotion

Acetoin and 2,3-butanediol synthesis; production of IAA and ACC deaminase;

[84][85]

Importance of endophytes and potential use as inoculants

The potential of PGPBEs to improve plant health has led to a great number of studies examining their application as inoculants, primarily in agricultural crops [67,86-88]. Development and use of microbial inoculants can lead to a reduction of the need and use of agrochemicals such as pesticides and fertilizers [89] and help to promote sustainable agricultural practices. Several studies are being conducted in order to identify possible candidates for crops inoculation [58,59,90]. However, plant growth promotion and protection remain priorities in studying bacteria associated to crops, and the development of new inoculants could provide a sustainable biotechnological approach as demonstrated by those already on the market [91]. In this respect, Azospirillum brasilense as well as Bradyrhizobium japonicum are examples of efficient plant growth promoting bacteria widely used in Brasil in soybean and maize [86]. However, it happens that many PGBP with good properties in the laboratory or greenhouse conditions, poorly behave when delivered in the field, mainly due to the high competitions for and complex mechanisms involved in colonization of the rhizosphere [92].

Endophytic bacteria are not subject to competition for nutrients that typically occurs in the rhizosphere, and can have higher efficiency than the rhizosphere colonizing bacteria in promoting growth, water absorption and the elimination of harmful microorganisms which are in the inside of the root system [93,94].

Endophytes, which are protected by the host against environmental stresses and competition with other organisms, are normally found in low densities compared to pathogenic bacteria or rhizobacteria [5,16]. Therefore, the potential of PGPBEs can be a valid alternative to the PGP rhizobacteria, since the competition inside the plant is lower and, once the plant is colonized by means of mechanisms involving motility, attachment, plant-polymer degradation, iron uptake and evasion of plant defenses [20,24,95], these bacteria could exploit their PGP functions in a more efficient manner.

Despite the fact that endophytes are protected inside the plants, there are several factors that can affect the type and density of the endophytic bacterial population in the interior of the host such as plant genotype and the type of farming, the tissue where they are located and the stage of plant development; in addition, also environmental factors such as variations in temperature and humidity, agronomic management adopted and application of agrochemicals can have significant effects. However, there are probably other limiting factors that may be relevant during the establishment of populations in the plant tissues. Thus, the establishment and maintenance of the bacterial population could be limited and influenced by the same factors that affect the health of the plant [5]. Currently it is unclear whether plants benefit more from the colonization by endophytic bacteria or rhizobacteria. However, both can promote plant growth. Therefore, there is an increasing interest in studying these bacteria and in the development of biofertilizers to increase crop yields [96].

Plants growth promoting bacterial endophytes and crop management

Plant genotype can have a direct influence on plant-associated bacteria, as this can change the exudates released by the roots and made available to bacterial groups, affecting colonization by rhizobacteria [97] and, consequently, entry into the plant and colonization by endophytes. Besides the genotype, the stage of development of the host may also influence the bacterial population. In endophytic bacteria associated with soybean the population increases with the development of the plant and start to decrease at the beginning of the reproductive stage [98]. However, a major influence is determined by environmental factors such as variations in temperature (heat or cold depending on the season in which the samples were collected) and the observed tissue (roots, stems or leaves) [99]. Furthermore, the soil was found to be the main factor in determining the population variance of Burkholderia cepacia associated with maize roots [100].

Crop agronomic management is a factor of great importance and impact on the microbial community, mainly due to the use of agrochemicals. The bacterial community and the density of bacteria populations in transgenic and non-transgenic sugarcane plants were found to be affected by crop management; the density of bacterial population associated with the rhizosphere of transgenic sugarcane plants treated with the herbicide Imazapyr was found reduced if compared with the non-trangenic one [101].
The most important herbicide used in herbicide-resistant soybean and maize fields is glyphosate. Glyphosate is a systemic herbicide with wide spectrum of activity, recommended for post-emergence control of a wide range of plants, and not selective in its action on mono and dicotyledons since it inhibits the enzyme 5-Enolpyruvylshikimate-3-Phosphate Synthase (EPSPS) involved in the synthesis of aromatic amino acids, therefore causing developmental delay, imbalance of amino acids and eventual death of the plants [102]. The use of herbicide-tolerant soybean yielded several benefits to farmers, including a decreased use of more toxic herbicides, and the ease of management. According to Cerdeira and Duke [103], glyphosate would have a much smaller residual effect in the soil if compared with the replaced active ingredients used for broad and narrow leaf plant control, therefore representing an option with less impact on soil, water and subsequent cultures in the area.

Despite its advantages, the use of glyphosate has some impacts on crops and also on the soil biota. It is reported that the application of glyphosate produces a shift in the microbial community [104,105]. In addition, glyphosate may be toxic to certain organisms or, in others, be used as a source of energy and nutrients [106]. de Almeida Lopes, et al. [31] found that the bacterial endophytic population associated to conventional and glyphosate-tolerant soybean in Brazil is significantly different both in term of composition and density, suggesting the importance of weed control strategy in determining the crop-bacterial endophyte association. Dallmann, et al. [107] found that the use of herbicides in herbicide-tolerant soybeans reduced the fungal flora of the soil and did not significantly alter the bacterial count. However, Arantes, et al. [108] found that glyphosate reduced microbial activity in two types of soil (Psamnet and Oxisol), whether or not the use of liming. A similar result was reported by Andrea, et al. [109], which found that the biomineralization of glyphosate decreased with increasing applications, suggesting an effect of the herbicide on soil microbial activity. Studying fungi and soil bacteria, Busse, et al. [106] found that there was toxic effect on population growth and metabolic diversity for continuous use (9-13 years) of glyphosate in the same area.

Regarding the endophytic populations associated to crops, herbicides has a significant influence on their composition [110] and contribute to select those endophytes that are able to withstand the adopted weed control strategy or those able to metabolize the used herbicide. This observation represents a pivotal starting point for the isolation of endophytes that can degrade herbicides with the aim of using them to inoculate crops and confer herbicide tolerance as an alternative approach to genetic modification [111].

The promotion of plant growth through protection from phytopathogens is known as biocontrol. Several mechanisms may be involved [112], including the production of antibiotics or secondary metabolites, the acquisition of iron by siderophores, and the secretion of enzymes such as chitinases and proteases. Crops are exposed to many microbial diseases whose agents come in contact with the endophytic population during the infection of inner parts of plant tissues. The development of competitive factors in endophytes is therefore highly probable in such conditions as a necessary step to be competitive and survive. Therefore, the isolation and characterization of these bacteria could lead to the identification of suitable candidates to be used for the development of biological control agents [113]. In the work of de Almeida Lopes, et al. [32] bacteria of genera Bacillus and Burkholderia isolated from soybean in Brazil were found to have antimicrobial properties against several soybean bacterial and fungal pathogens, and the molecules responsible for this activity produced by these bacteria were secondary metabolites, peptides, lipopeptides and bacteriocins. Among the bacterial endophytes reported to have antimicrobial activity, the endophyte Enterobacter sp. strain 638 produces antibiotic substances, including 2- phenylethanol and 4-hydroxybenzoate [9]. Endophytic Streptomyces sp. are known producers of antimicrobial compounds such as kakadumycins [114], coronamycin [115] and multicyclic indolosesquiterpenes [116]. Recently, Streptomyces sp. was found able to inhibit the growth of Burkholderia glumae, a bacterial rice pathogen, and other bacterial and fungal pathogens. Interestingly, this strain produced three small antibiotics, streptotrichins D, E and F, in addition to colonization of rice plants and growth promotion [54]. These and other similar reports suggest further investigation to assess the ability of antimicrobial compounds-producing bacterial endophytes to efficiently colonize the plant from where they have been isolated and the ability to control the pathogens sensitive to their antimicrobial molecules from inside the plant.

As discussed previously, many bacterial endophytes have been found to have PGP properties and are potential candidates for the development of biofertilizers. However, they are sensitive to the agronomic management, including soil and plant fertilization. Therefore, the study of compatibility with mineral and organic fertilizers is advisable to optimize their use in combination and reduce the use of chemical fertilizers and the loss of fertilization potential of both components [117-119].

**Conclusion and future perspectives**

In conclusion, the current knowledge about the actual role of endophytes associated with crops, their beneficial effects and the influence of the environment as well as the agronomic management on the bacterial population suggest additional effort to explore the potential of endophytes as new biological tools for a range of applications in agriculture mainly as biofertilizers and biocontrol agents. More investigations on the effects of agronomical practices on endophytes and the differences between the populations associated to transgenic and conventional crops...
could also help in this direction. Biotechnology can be applied to further improve strains that have prized qualities. All these aspects should be further investigated and put together to the development of commercially viable PGPBE inoculant strains to be utilized in agriculture, able not to lose PGP qualities under the environment variation, as sustainable strategies to promote growth and to protect crops.

References
1. Dimkpa C, Weinand T, Asch F (2009) Plant-rhizobacteria interactions alleviate abiotic stress conditions. Plant Cell Environ 32: 1682-1694.
2. Grover M, Ali SZ, Sandhya V, Shaik R (2011) Role of microorganisms in adaptation of agriculture crops to abiotic stresses. World J Microbiol Biotechnol 27: 1231-1240.
3. Glick BR (2012) Plant growth-promoting bacteria: mechanisms and applications. Scientifica.
4. Coutinho BG, Licastro D, Mendonça-Previali L, Câmara M, Venturi V (2015) Plant-influenced gene expression in the rice endophyte Burkholderia kururiensis M130. Mol Plant-Microb Interact 28: 10-21.
5. Hallmann J, Quadt-Hallmann A, Mahaffee WF, Kloeper JW (1997) Bacterial endophytes in agricultural crops. Can J Microbiol 43: 895-914.
6. Krause A, Ramakumar A, Barlets D, Battistoni F, Bekał et al. (2006) Complete genome of the mutualistic, N2-fixing grass endophyte Azorhizus sp. strain BH72. Nat Biotechnol 24: 1385-1391.
7. Bertalan M, Albano R, de Pádua V, Rouws L, Rojas C, et al. (2009) Complete genome sequence of the sugarcane nitrogen-fixing endophyte Gluconacetobacter diazotrophicus Pa15. BMC Genomics. 10: 450.
8. Deng Y, Zhu Y, Wang P, Zhu L, Zheng J, et al. (2011) Complete genome sequence of Bacillus subtilis BS54, an endophytic bacterium of Amorphophallus konjac with antimicrobial activity for the plant pathogen Erwinia carotovora subsp. carotovora. J Bacteriol 193: 2070-2071.
9. Taghavi S, van der Lelie D, Hoffman A, Zhang YB, Walla MD, et al. (2011) Genome sequence of an antagonistic bacterial endophyte on native bacterial community and its survival in soil: a case study with Pseudomonas aeruginosa from banana. Front Microbiol 7: 493.
10. McCully ME (2001) Niches for bacterial endophytes in crop plants: a plant biologist’s view. Funct Plant Biol 28: 983-990.
11. Chi F, Shen SH, Cheng HP, Jing YX, Yanni YG, et al. (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.
12. Kandel SL, Joubert PM, Doty SL (2017) Bacterial endophyte colonization and distribution within plants. Microorganisms 5: 77.
13. Thomas P, Sekhar AC (2016) Effects due to rhizospheric soil application of an antagonistic bacterial endophyte on native bacterial community and its survival in soil: a case study with Pseudomonas aeruginosa from banana. Front Microbiol 7: 493.
14. Cocking EC, Stone PJ, Davey MR (2006) Intracellular colonization of roots of Arabidopsis and crop plants by Gluconacetobacter diazotrophicus. In Vitro Cell Dev Biol-Plant 42: 74-82.
15. Azevedo JL, Maccheroni Jr. W, Pereira JO, de Araújo W (2000) Endophytic microorganisms: a review on insect control and recent advances on tropical plants. Electron J Biotechnol 3: 15-16.
16. Misaghi IJ, Donndelinger CR (1990) Endophytic bacteria in symptom-free cotton plants. Phytopathology, 80: 808-811.
17. Hallmann J, Berg G (2006) Spectrum and population dynamics of bacterial root endophytes. In: Schulz BJ, Boyle CJC, Sieber TN (eds) Microbial Root Endophytes. Soil Biology, Springer, Berlin, Heidelberg.
18. Qin S, Xing K, Jiang JH, Xu LH, Li WJ (2011) Biodiversity, bioactive natural products and biotechnological potential of plant-associated endophytic actinobacteria. Appl Microbiol Biotechnol 89: 457-473.
19. de Almeida Lopes KB, Carpentieri-Pipolo V, Oro TH, Pagliosa ES, degrassi G (2016). Culturable endophytic bacterial communities associated with field-grown soybean. J Appl Microbiol 120: 740-755.
32. de Almeida Lopes KB, Carpentieri P, Pipolo V, Fira D, Balatti PA, López SMY, et al. (2018) Screening of bacterial endophytes as potential biocontrol agents against soybean diseases. J Appl Microbiol 125: 1466-1481.

33. Carpentieri-Pipolo V, de Almeida Lopes KB, Degrassi G (2019) Phenotypic and genotypic characterization of endophytic bacteria associated with transgenic and non-transgenic soybean plants. Arch Microbiol 125: 1466-1481.

34. Thomas P, Sekhar AC (2014) Live cell imaging reveals extensive intracellular cytoplasmic colonization of banana by normally non-cultivable endophytic bacteria. AoB Plants 6: plu002.

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

36. Kwak M-J, Song JY, Kim SY, Jeong H, Kang SG, et al. (2012) Complete genome sequence of the endophytic bacterium Burkholderia sp. Strain KJ006. J Bacteriol 194: 4432-4433.

37. Meng X, Bertani I, Abbruscato P, Piffanelli P, Licastro D, et al. (2015) Draft genome sequence of rice endophyte-associated isolate Kosakonia oryzae KO348. Genome Announc 3: 15.

38. Wisniewski-Dyë F, Borziak K, Khalsa-Moyers G, Alexandre G, Sukharnikov LO, et al. (2011) Azospirillum genomes reveal transition of bacteria from aquatic to terrestrial environments. PLoS Genet 7: e1002430.

39. Yan Y, Yang J, Dou Y, Chen M, Ping S, et al. (2008) Nitrogen fixation island and rhizosphere competence traits in the genome of root-associated Pseudomonas stutzeri A1501. Proc Nat Acad Sci 105: 7564-7569.

40. Farrar K, Bryant D, Copeland Sebly N (2014) Understanding and engineering beneficial plant–microbe interactions: plant growth promotion in energy crops. Plant Biotechnol J 12: 1193-1206.

41. Hardoim PR, van Overbeek LS, van Elsas JD (2008) Properties of bacterial endophytes and their proposed role in plant growth. Trends Microbiol 16: 437-447.

42. Kang SH, Cho H, Cheong H, Ryu CM, Kim JF, Park SH (2007) Two bacterial endophytes eliciting both plant growth promotion and plant defense on pepper (Capsicum annuum). J Microbiol Biotechnol 17: 96-103.

43. Goes K, Fisher MLC, Cattelan AJ, Nogueira MA, Portela de Carvalho CG, et al. (2012) Biochemical and molecular characterization of high population density bacteria isolated from sunflower. J Microbiol Biotechnol 22: 437-447.

44. Brader G, Campant S, Mitter B, Trognotz F, Sessitsch A (2014) Metabolic potential of endophytic bacteria. Curr Opin Biotechnol 27: 30-37.

45. Chaturvedi H, Singh V, Gupta G (2016) Potential of bacterial endophytes as plant growth promoting factors. J Plant Pathol Microbiol 7: 376.

46. Ek-Ramos MJ, Gomez-Flores R, Orozco-Flores AA, Rodríguez-Padilla C, González-Ochoa G, et al. (2019) Bioactive products from plant-endophytic gram-positive bacteria. Front Microbiol 10: 463.

47. Mercado-Blanco J, Bakker PAHM (2007) Interactions between plants and beneficial Pseudomonas spp.: exploiting bacterial traits for crop protection. Antonie van Leeuwenhoek 92: 387-389.

48. Eljounaidi K, Lee SK, Bae H (2016) Bacterial endophytes as potential biocontrol agents of vascular wilt diseases. Review and future prospects. Biological Control 103: 62-68.

49. Santoyo G, del Carmen Orozco-Mosqueda M, Govindappa M (2012) Mechanisms of biocontrol and plant growth-promoting activity in soil bacterial species of Bacillus and Pseudomonas: a review. Biocontrol Sci Technol 22: 855-872.

50. Ardanov P, Sessitsch A, Häggman H, Kozyrovska N, Anna Maria Pirtilă AM (2012) Methylobacterium-induced endophyte community changes correspond with protection of plants against pathogen attack. PLoS One 7: e46802.

51. De Vleeschaauwer D, Höfte M (2009) Rhizobacteria-induced systemic resistance. Adv Botanical Res 51: 223-281.

52. Verma P, Yadav AN, Khannam KS, Panjjar N, Kumar S, et al. (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. Ann Microbiol 65: 1885-1899.

53. Gururani MA, Upadhyaya CP, Baskar V et al. (2013) Plant growth-promoting rhizobacteria enhance abiotic stress tolerance in Solanum tuberosum through inducing changes in the expression of ROS-scavenging enzymes and improved photosynthetic performance. J Plant Growth Regul 32: 245-258.

54. Suárez-Moreno ZR, Vichuna-Villarraga DM, Vergara-Morales DI, Castellanos L, Ramos F, et al. (2019) Plant growth-promotion and biocontrol properties of three Streptomyces spp. isolates to control bacterial rice pathogens. Front Microbiol 10: 290.

55. Bertani I, Abbruscato P, Piffanelli P, Subramoni S, Venturi V (2016) Rice bacterial endophytes: isolation of a collection, identification of beneficial strains and microbiome analysis. Environ Microbiol Rep 8: 388-389.

56. Etesami H, Alikhani HA (2017) Evaluation of Gram-positive rhizosphere and endophytic bacteria for biological control of fungal rice (Oryza sativa L.) pathogens. Eur J Plant Pathol 147: 7-14.

57. Bai Y, Zhou X, Smith DL (2003) Enhanced soybean plant growth resulting from coinoculation of Bacillus strains with Bradyrhizobium japonicum. Proc Nat Acad Sci 102: 4571-4576.

58. Kuklinsky-Sobral J, Araújo WL, Mendes R, Geraldí IO, Pizzirani-Klein er AA, et al. (2004) Isolation and characterization of soybean-associated bacteria and their potential for plant growth promotion. Environ Microbiol 6: 1244-1256.

59. Hung PQ, Annapurna K (2004) Isolation and characterization of endophytic bacteria in soybean (Glycine spp.). Oomycetes 12: 92-101.

60. Li H, Zhao J, Feng H, Huang L, Kang Z (2013) Biological control of wheat stripe rust by an endophytic Bacillus subtilis strain E1R-j in greenhouse and field trials. Crop Protection 43: 201-206.

61. Xu Y, Chen M, Zhang Y, Wang M, Wang Y, et al. (2014) The phosphotransferase system gene ptsI in the endophytic bacterium Bacillus cereus is required for biofilm formation, colonization, and biocontrol against wheat sharp eyespot. FEMS Microbiol Lett 354: 142-152.

62. Tao A, Pang F, Huang S, Yu G, Li B, Wang T (2014) Characterisation of endophytic Bacillus thuringiensis strains isolated from wheat plants as biocontrol agents against wheat flag smut. Biocontrol Sci Technol 24: 901-924.
Citation: Degrassi G and Carpentieri-Pipolo V (2020) Bacterial Endophytes Associated to Crops: Novel Practices for Sustainable Agriculture. Adv Biochem Biotechnol 5: 1099. DOI: 10.29011/2574-7258.001099

63. Singh D, Geat N, Rajawat MVS, Mahajan MM, Prasana R, et al. (2018) Deciphering the mechanisms of endophyte-mediated biofortification of Fe and Zn in wheat. J Plant Growth Regul 37: 174-182.

64. Wang Y, Li H, Zhao W, He X, Chen J, et al. (2010) Induction of toluene degradation and growth promotion in corn and wheat by horizontal gene transfer within endophytic bacteria. Soil Biol Biochem 42: 1051-1057.

65. Shi Y, Lou K, Li C (2010) Growth and photosynthetic efficiency promotion of sugar beet (Beta vulgaris L.) by endophytic bacteria. Photosynth Res 105: 5-13.

66. Oliveira ALM, Stoffers M, Schmid M, Reis VM, Baldani JI, et al. (2009) Colonization of sugarcane plantlets by mixed inoculations with diazotrophic bacteria. Eur J Soil Biol 45: 106-113.

67. da Silva MF, de Souza a, de Oliveira C, et al. (2012) Survival of endophytic bacteria in polymer-based inoculants and efficiency of their application to sugarcane. Plant Soil 356: 231-243.

68. Chowdappa P, Mohan Kumar SP, Jyothi Lakshmi M, Upreti KK (2013) Growth stimulation and induction of systemic resistance in tomato against early and late blight by Bacillus subtilis OTPB1 or Trichoderma harzianum OTPB3. Biological Control 65: 109-117.

69. Khan AL, Waqas M, Kang S, Al-Harrasi A, Hussain J, et al. (2014) Bacterial endophyte Sphingomonas sp. LK11 produces gibberellins and IAA and promotes tomato plant growth. J Microbiol 52: 689-695.

70. Lopes RB, Costa LE, Vanetti MC, de Araújo EF, de Queiroz MV (2015) Endophytic bacteria isolated from common bean (Phaseolus vulgaris) exhibiting high variability showed antimicrobial activity and quorum sensing inhibition. Curr Microbiol 71: 509-516.

71. Lopes-Lopes A, Rogel MA, Ormeno-Orrillo E, Martinez-Romero J, Martinez-Romero E (2010) Phaseolus vulgaris seed-borne endophytic community with novel bacterial species such as Rhizobium endophyticum sp. nov. Syst Appl Microbiol 33: 322-327.

72. Costa L, Queiroz MV, Borges AC, Moraes CA, 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.

73. Giassi V, Kiritani C, Kupper KC (2016) Bacteria as growth-promoting agents for citrus rootstocks. Microbiol Res 190: 46-54.

74. Gond SK, Bergen MS, Torres MS (2015) Endophytic Bacillus spp. produce antifungal lipopeptides and induce host defence gene expression in maize. Microbiol Res 172: 79-87.

75. Ferreira AS, Pires RP, Rabelo PG, Oliveira RC, Luz JMQ, et al. (2013) Implications of Azospirillum brasilense inoculation and nutrient addition on maize in soils of the Brazilian Cerrado under greenhouse and field conditions. Appl Soil Ecol 72: 103-108.

76. Naveed M, Mitter B, Yousaf S, Pastor M (2014) The endophyte Enterobacter sp. FD17: a maize growth enhancer selected based on rigorous testing of plant beneficial traits and colonization characteristics. Biol Fertil Soils 50.

77. Puri A, Padda KP, Chanway CP (2016) Seeding growth promotion and nitrogen fixation by a bacterial endophyte Paenibacillus polymyxa P2b-2R and its GFP derivative in corn in a long-term trial. Symbiosis 69: 123-129.

78. Sandhya V, Shrivastava M, Ali SZ, Prasad VSSK (2017) Endophytes from maize with plant growth promotion and biocontrol activity under drought stress. Russ Agricult Sci 43: 22-34.

79. Lahiali R, Peng G, Gossen BD, McGregor L, Yu FQ, et al. (2013) Evidence that the biofungicide Serenade (Bacillus subtilis) suppresses clubroot on canola via antibiosis and induced host resistance. Phytopathology 103: 245-554.

80. Silva HSA, Tozzi JPL, Terrasan CRF, Bettiol W (2012) Endophytic microorganisms from coffee tissues as plant growth promoters and biocontrol agents of coffee leaf rust. Biol Control 63: 62-67.

81. Haidar R, Roudet J, Bonnard O, Dufour MC, Corio-Costet MF, et al. (2016) Screening and modes of action of antagonistic bacteria to control the fungal pathogen Phaeoanomella chlamydospora involved in grapevine. Microbiol Res 192: 172-184.

82. Ferrigo D, Causin R, Raiola A (2017) Effect of potential biocontrol agents selected among grapevine endophytes and commercial products on crown gall disease. BioControl 62: 821-833.

83. Baldan E, Nigri S, Populin F, Zotti M, Squartini A, et al. (2014) Identification of cultivable bacterial endophyte community isolated from tissues of Vitis vinifera “Glera”. Plant Biosys 148: 508-516.

84. Ting ASY, Moon S, Kadir J et al. (2008) Endophytic microorganisms as potential growth promoters of banana. BioControl 53: 541-553.

85. Taghavi S, Garafola C, Monchy S, Newman L, Hoffman A, et al. (2009) Genome survey and characterization of endophytic bacteria exhibiting a beneficial effect on growth and development of poplar trees. Appl Environ Microbiol 75: 748-757.

86. Marks BB, Megías M, Nogueira MA, Hungria M (2013) Biotechnological potential of rhizobial metabolites to enhance the performance of Bradyrhizobium spp. and Azospirillum brasilense inoculants with soybean and maize. AMB Express 3: 21.

87. Bashan Y (1998) Inoculants of plant growth-promoting bacteria for use in agriculture. Biotechnology Advances 16: 729-770.

88. Vessey JK (2003) Plant growth promoting rhizobacteria as biofertilizers. Plant and Soil 255: 571-586.

89. Horrigan L, Lawrence R, Walker P (2002) How sustainable agriculture can address the environmental and human health harms of industrial agriculture. Environ Health Perspect 110: 445-456.

90. Assumpção LC, Lacava PT, Dias ACF, Azvedo JL, Menten JOM (2009) Diversidade e potencial biotecnológico da comunidade bacteriana endofítica de sementes de soja. Pesq Agropec Bras 44: 503-510.

91. Timmusk S, Behers L, Muthoni J, Muraya A, Aronsson AC (2017) Perspectives and challenges of microbial application for crop improvement. Front Plant Sci 8: 49.

92. lugtenberg B, Kamilova F (2009) Plant-growth-promoting rhizobacteria. Biotechnology Advances 16: 729-770.

93. Amorim E, Melo I (2002) Ação antagônica de rizobactérias contra Phytophthora parasitica e P. citrophthora e seu efeito no desenvolvimento de plântulas de citros. Revista Brasileira de Fruticultura, SciELO Brazil 24: 1-8.

94. Santos MHLC, Mariano RLR, Camara TR, Andrade AG, Willadino L, et al. (2005) Bactérias promotoras de crescimento no desenvolvimento de Heliconia psittacorum L.f. Hoehnea 32: 1-8.
95. Afzal I, Shinwari ZK, Sikandar S, Shahzad S (2019) Plant beneficial endophytic bacteria: mechanisms, diversity, host range and genetic determinants. Microb Res 221: 36-49.

96. Dudeja SS, Giri R, Saini R, Suneja-Madan P, Kothe E (2012) Interaction of endophytic microbes with legumes. J Basic Microbiol 52: 248-260.

97. Kozdrój J, Dirk van Elsas J (2000) Response of the bacterial community to root exudates in soil polluted with heavy metals assessed by molecular and cultural approaches. Soil Biol Biochem 32: 1405-1417.

98. Dalal J (2013) Population dynamics and diversity of endophytic bacteria associated with soybean (Glycine max (L) Merril). Microbiol Res J Intern 3: 96-105.

99. Mocali S, Bertelli E, Di Cello F, Mengoni A, Sfalanga A, et al. (2003) Fluctuation of bacteria isolated from elm tissues during different seasons and from different plant organs. Res Microbiol 154: 105-114.

100. Dalmastri C, Chiarini L, Cantale C, Bevivino A, Tabacchioni S (1999) Soil type and maize cultivar affect the genetic diversity of maize root-associated Burkholderia cepacia populations. Microb Ecol 38: 273-284.

101. Dini-Andreote F, Andreote FD, Costa R, Araujo WL (2010) Bacterial soil community in a Brazilian sugarcane field. Plant Soil 336: 337-349.

102. Yamada T, Castro PRC (2007) Efeito do glifosato nas plantas: implicações fisiológicas e agronômicas. Informações Agronômicas 119: 1-39.

103. Cerdeira AL, Duke SO (2006) The current status and environmental impacts of glyphosate-resistant crops. J Environ Qual 35: 1633-1658.

104. Newman MM, Hoillet N, Lorenz N, Dick RP, Liles MR, et al. (2016) Glyphosate effects on soil rhizosphere-associated bacterial communities. Sci Total Environ 543: 155-160.

105. Kuklinsky-Sobral J, Araújo WL, Mendes R, Pizzirani-Kleiner AA, Azevedo JL (2005) Isolation and characterization of endophytic bacteria from soybean (Glycine max) grown in soil treated with glyphosate herbicide. Plant and Soil 273: 91-99.

106. Busse MD, Ratcliff AW, Shestak CJ, Powers RF (2001) Glyphosate toxicity and the effects of long-term vegetation control on soil microbial communities. Soil Biol Biochem 33: 1777-1789.

107. Dallmann CM, Scheneider L, Bohm GMB, Kuhn CR (2010) Impacto da aplicação de glifosato na microbiota do solo cultivado com soja geneticamente modificada. Revista Thema 7: 1-11.

108. Arantes SACM, Lovorenti A, Tornisielo VL (2007) Efeito da calagem e do glyphosate na atividade microbiana de diferentes classes de solos. Pesticidas: Revista de Ecotoxicologia e Meio Ambiente 17: 19-28.

109. Andréa MM de, Peres TB, Luchini LC, Bazarin S, Papini S, et al. (2003) Influence of repeated applications of glyphosate on its persistence and soil bioactivity. Pesqui Agropecu Bras 38: 1329-1335.

110. Tétard-Jones C, Edwards R (2016) Potential roles for microbial endophytes in herbicide tolerance in plants. Pest Manag Sci 72: 203-209.

111. Doty SL (2008) Enhancing phytoremediation through the use of transgenics and endophytes. New Phytologist 179: 318-333.

112. Compan t S, Duffy B, Nowak J, Clément C, Barka EA (2005) Use of plant growth-promoting bacteria for biocontrol of plant diseases: principles, mechanisms of action, and future prospects. Appl Environ Microbiol 71: 4951-4959.

113. Berg G, Hallmann J (2006) Control of plant pathogenic fungi with bacterial endophytes. In: Schulz BJE, Boyle CJC, Sieber TN (eds). Microbial root endophytes. Soil Biology 9: Springer, Berlin, Heidelberg.

114. Castillo U, Harper JK, Strobel GA, Sears J, Alesi K, et al. (2003) Kakadumycins, novel antibiotics from Streptomyces sp. NRRL 30566, an endophyte of Grevillea pteridifolia. FEMS Microbiol Lett 224: 183-190.

115. Ezra D, Castillo UF, Strobel GA, Hess WM, Porter H, et al. (2004) Coronamycins, peptide antibiotics produced by a verticillate Streptomyces sp. (MSU-2110) endophytic on Monstera sp. Microbiology 150: 785-793.

116. Ding L, Maier A, Fiebig HH, Linc WH, Hertweck C (2011) A family of multicyclic indolosesquiterpenes from a bacterial endophyte. Org Biomol Chem 9: 4029-4031.

117. Malinowski DP, Belesky DP (2000) Adaptations of endophyte-infected cool-season grasses to environmental stresses: mechanisms of drought and mineral stress tolerance. Crop Sci 40: 923-940.

118. Kaneko T, Minamisawa K, Isawa T, Nakatsukasa H, Mitsui H, et al. (2010) Complete genomic structure of the cultivated rice endophyte Azospirillum sp. B510. DNA Res 17: 37-50.

119. Bao Z, Sasaki K, Okubo T, Ikeda S, Anda M, et al. (2013) Impact of Azospirillum sp. B510 inoculation on rice-associated bacterial communities in a paddy field. Microbes Environ 28: 487-490.