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Chapter

Plant-Growth Promoting Endophytic Bacteria and Their Role for Maize Acclimatation to Abiotic Stress

*Víctor M. González-Mendoza, Mayra de la Torre
and Jorge Rocha*

Abstract

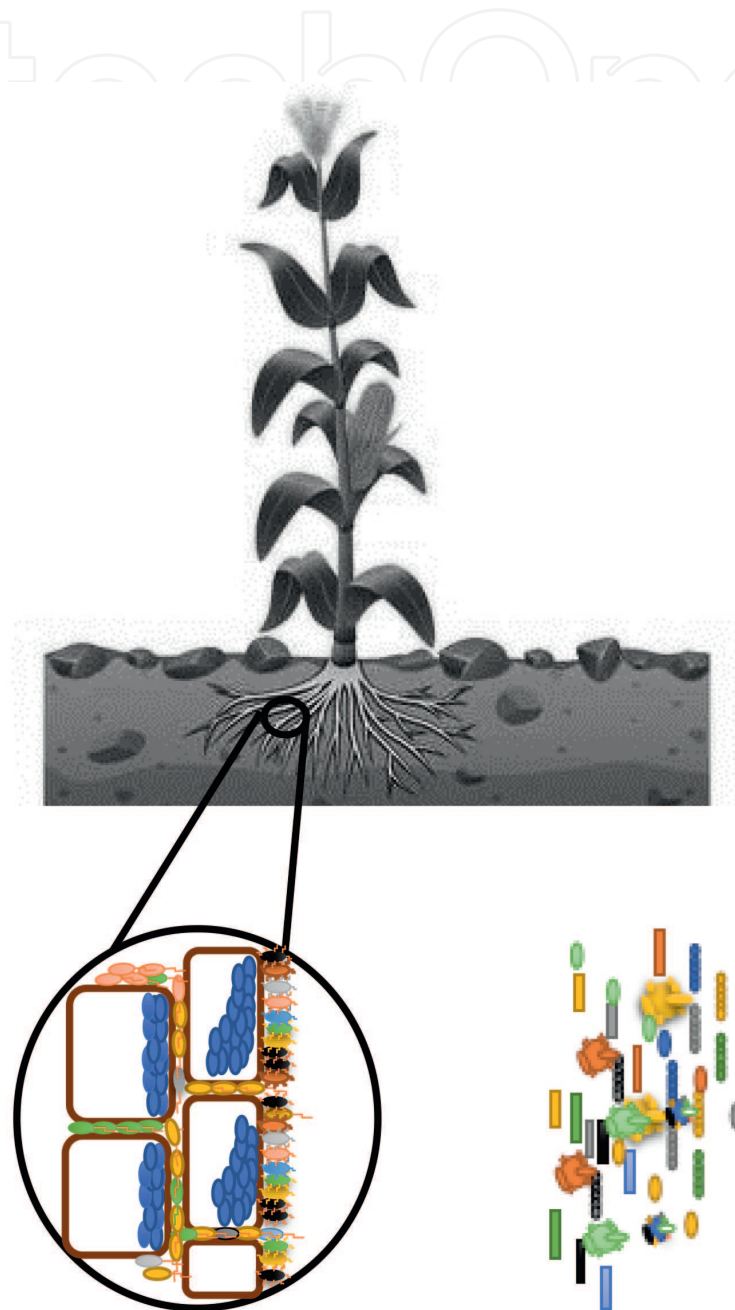
In order to grow, reproduce, and defend themselves, maize plants use various strategies to obtain adaptive advantages in varying conditions, for example, to tolerate abiotic stress (e.g., drought or heat due to climate change). One of these strategies is the establishment of interactions with plant-growth-promoting bacteria. Bacteria can be associated with plants in the rhizosphere, rhizoplane, or as endophytes. Recent evidence suggest that modern agricultural practices are detrimental to these beneficial plant-microbe interactions, and reservoirs like traditional agroecosystems called *milpas*, emerge as sources of microbiota associated with maize crops, with increased diversity and beneficial functions. Particularly, bacterial endophytes associated with native maize from *milpas* show promising features for their use as plant-growth-promoting inoculates, however, it is necessary to first understand the mechanisms known for beneficial functions of endophytes associated with maize and other plants. Here, we review the mechanisms of beneficial interactions between plants and endophytic bacteria, with emphasis on maize and with mentions of recent findings on maize landraces from *milpa* systems.

Keywords: plant associated-microbial communities, *milpa*, stress responses, amelioration, climate change

1. Introduction

Plants are constantly challenged with a plethora of stressful conditions and require several response mechanisms, including the interactions between the roots and soil microbes, which allow for nutrient availability, growth promotion, and disease suppression. Microbiota can be found associated to plants in different degrees and locations, which are divided into (1) endosphere (inter or intracellular tissues), (2) rhizoplane microbial (on the root surface and possibly attached to root hairs), and rhizosphere microbial (soil close to the root surface). The composition of each of these communities is influenced by the host genotype, soil source, cultivation practice, and so on [1–4] (**Figure 1**). Bacteria present in the endosphere have recently

been considered as potential agents for acclimation to abiotic stress response. One example is endophytic bacteria isolated from native maize from *milpa* traditional systems, which has been proposed as a bacteriome fraction that could be useful for obtaining products toward the bio-fertilization of maize crops [5]. *Milpas* are polyculture systems that include domesticated, semi-domesticated, and tolerated plant species that combine native maize landraces with almost any other crop, tree,



- | A) Endosphere | B) Rhizoplane | C) Rhizosphere |
|--------------------------|--|-----------------------|
| -Plant genotype | -Plant genotype | -Soil source |
| -Defense system | -Environmental factors | -Cultivation practice |
| -Intrinsically responses | -Extrinsically factor: carbon sources, phytochemicals, [O ₂], pH or nutrient depletion | |

Figure 1.

Localization of maize associated-microbial communities. (A) Endosphere; here, communities are affected by plant genotype, its defenses system, and intrinsic responses; (B) in the rhizoplane, extrinsic factors like carbon sources or phytochemicals, [O₂], pH, or nutrient depletion, affect microbial community composition; (C) in the rhizosphere, communities are strongly affected by soil source, cultivation practice, and others.

or shrub species. *Milpas* constitute a dynamic system with diverse genetic resources, used as the main crop of native maize (*Zea mays* L.) and as associated crops to beans (*Phaseolus* spp.), squashes (*Cucurbita* sp.), chili peppers (*Capsicum* sp.), tomatoes (*Solanum lycopersicum*), among others. Modern practices of agriculture affect bacterial diversity and functions, therefore, *milpas* have retained unique beneficial microorganisms that interact with native maize, which could have been lost in modern hybrid maize with monocultures, high-tillage, and large agrochemical input [6].

With the current worldwide agricultural practices trend, it is necessary to promote a reduction of agrochemical use and a reintroduction of ancestral agricultural practices and/or the use of microorganism-based bio-formulations that generate a beneficial interaction between plants and microbes and thereby influence plant growth. One option is the use of plant-growth-promoting endophytes, which could be regarded as a new approach to mitigate the detrimental effect of pests and/or diseases, low rainfall, and current climate change [5].

Endophytic bacterial species have been identified in a vast number of plants; notably, they are symbionts that usually do not cause negative effects on plant growth [1, 7, 8]. The endophyte community within the plant is very as dynamic but usually is enriched with specialized types of bacteria with features such as flagella, plant-polymer-degrading enzymes, type V and VI protein secretion systems, iron acquisition and storage, quorum sensing, detoxification of reactive oxygen species (ROS), degradation of aromatic compounds, among others [9]. Colonization of endophytic bacteria can be also classified into three main categories in accordance with lifestyle strategies as (1) obligate endophytes, unable to proliferate outside of plants and are likely transmitted via seed; (2) facultative endophytes, as free living in soil but will colonize plants once conditions are appropriate, and (3) passive endophytes, as do not actively seek to colonize the plant [7, 9, 10].

Recent work suggests that microorganisms from the bulk soil in *milpas* are selected by native maize roots. Native maize selectively recruits, including strains from phyla like Acidobacteria, Actinobacteria, and Bacteroidetes, with a higher relative abundance in comparison to soil adjacent to the roots [6]. Recently, Gastélum *et al.* reported a greater presence of endophytic microbial load in native maize vs. hybrid landraces, which include more bacterial strains with antagonistic activity against soil-borne bacteria, and overall harbor more diverse bacterial communities [5]. There are many factors influencing endophytes to colonize and penetrate the root tissue, as well as the resulting interaction. After colonization, the role of microbes could modulate plant growth and development by diverse mechanisms [11]. In order to grasp maize endophytic microbes from *milpas* for plant growth promotion, we first need to understand the mechanisms for growth promotion. Here, we will discuss how maize-related endophytes can potentially have used in the alleviation of abiotic stress and/or climate change.

2. Endophytic bacteria

Bacterial endophytes inhabit the tissues of plants for at least a part of their life cycle without harming or inhibiting the growth of the plant and establishing symbiotic associations than can result in great benefits for plant health. Endophytes are microorganisms that survive within healthy plant tissues and promote plant growth under stress. A large proportion of endophytic bacteria groups are shared between leaves and roots, suggesting that they are inoculated from the soil. These communities

are also dynamic, as they shift when the plants age [12]. Reinhold-Hurek et al. defined a community of least complexity where specific bacterial traits are required for internalization and establishment inside of this compartment, and host genotype likely has the strongest influence on community structure here, in comparison with other compartments such as the roots [9].

2.1 Plant-growth-promoting endophytes (PGPEs)

The PGPEs as well as PGPRs (plant-growth-promoting rhizobacteria) promote plant growth by regulating plant hormones, improving nutrition acquisition, siderophore production, and enhancing the antioxidant system [13]. Bacterial endophytes associated with plants can be classified into three groups, based on the ecological interaction: beneficial, deleterious, and neutral. Various genera of *Pseudomonas*, *Enterobacter*, *Bacillus*, *Klebsiella*, and *Burkholderia*, (which are normally considered pathogenic), are also present as PGPEs, promoting plant growth and development under both normal and stress conditions [14]. In most cases, these are indirect mechanisms, such as preventing the deleterious effects of other phytopathogenic microorganisms, and this function is achieved by antibiosis, induction of systemic resistance (ISR), and competitive exclusion [13–15]. There are several mechanisms for plant growth stimulation by PGPEs, such as nitrogen fixation; synthesis of auxin, 1-aminocyclopropane-1-carboxylate (ACC)-deaminase, siderophores production, and phosphate solubilization, and most of them are well documented [16]. In the case of endophytic bacteria isolated in native or hybrid genotypes of maize, genera, such as *Pantoea*, *Bacillus*, *Burkholderia*, *Klebsiella*, and others were found [6, 8]. There are mechanisms by PGPE to mitigate stress responses, and these are described in the following sections [17].

2.1.1 Nutrient fixation

PGPEs act as a direct enhancer to increase the accessibility and concentration of chemical elements by fixing or locking their nutritional supplies for plant growth and development [14]. To date, there are few nutrient-fixing bacteria reported as associated with maize.

2.1.2 Nitrogen fixation

Biological nitrogen fixation is a biological process that is carried out either by symbiotic or non-symbiotic interactions between microbes and plants. Symbiotic PGPRs, which are most frequently reported to fix atmospheric N₂ in soil, include strains of *Rhizobium* sp., *Azoarcus* sp., *Beijerinckia* sp., *Pantoea agglomerans*, and *Klebsiella pneumoniae* [10, 13]. Bio-fixation of atmospheric nitrogen is carried out by genera like *Azospirillum*, *Klebsiella*, *Burkholderia*, *Bacillus*, and *Pseudomonas* [18]. Someone of these species has been reported as endophytes in native maize.

2.1.3 Phosphate solubilization

Solubilization and mineralization of phosphorus by phosphate-solubilizing bacteria is an important trait that can be achieved by PGPR. Phosphate solubilizing PGPR includes genera, such as *Arthrobacter*, *Bacillus*, *Beijerinckia*, *Burkholderia*, *Enterobacter*, *Microbacterium*, *Pseudomonas*, *Erwinia*, *Rhizobium*, *Mesorhizobium*,

Flavobacterium, *Rhodococcus*, and *Serratia*, and some of these have been found associated to maize [19].

2.1.4 Potassium solubilization

Potassium solubilizing PGPR, such as *Acidithiobacillus* sp., *Bacillus edaphicus*, *Ferrooxidans* sp., *Bacillus mucilaginosus*, *Pseudomonas* sp., *Burkholderia* sp., and *Paenibacillus* sp., have been reported to release potassium in accessible form from potassium-bearing minerals in soils; some of them have been reported in interaction with maize [20].

2.1.5 Phytohormone production

One process employed by PGPRs is phytohormones production. Bacterial species, such as *Pantoea agglomerans*, *Rhodospirillum rubrum*, *Pseudomonas fluorescens*, *Bacillus subtilis*, *Paenibacillus polymyxa*, *Pseudomonas* sp., and *Azotobacter* sp., were found to carry out this mechanism and they have been tested in maize development [13].

2.1.6 Siderophore production

The production of siderophores by microbes is crucial for plant growth since these compounds chelate iron in the soil. This process is performed by a bacterium, such as *Pseudomonas* sp. and *Streptomyces* sp., and it is useful for generating soluble complexes that can be absorbed by plants, and some of these bacteria have been tested in maize [10].

2.1.7 Exopolysaccharide production (EPS)

EPS-producing PGPR, such as *Azotobacter vinelandii*, *Bacillus drentensis*, *Enterobacter cloacae*, *Agrobacterium* sp., *Xanthomonas* sp., and *Rhizobium* sp., play a vital role in maintaining water potential, aggregating soil particles, and ensuring an obligate contact between plant roots and rhizobacteria [21].

2.2 Acclimatation to abiotic stresses

It has been proposed that stress conditions cause the recruitment of particular microbial taxa from the soil. In this sense, environmental factors, such as drought, pH, and temperature have a significant impact on the microbiota associated to roots [15]. Advantages of bacterial endophytes on plant growth include protection from competing bacteria and fungi, a constant and reliable source of nutrition, and protection from exposure to a wide range of potentially deleterious environmental conditions, such as extreme temperature and the presence of inhibitory chemicals in the soil. Some of these responses are described below.

2.2.1 Chemical responses

Plant exudate compounds through their roots and these are key factors for the assembly of microbial communities in the rhizosphere. Some of these compounds are sugars, amino acids, organic acids, fatty acids, and secondary metabolites such as triterpenes [22]. On one hand, the composition of the root exudate profiles

changes in different plant species, genotypes, and developmental stages. Thus, it is suggested that variations in the composition of root-associated endophytic microbial are caused by changes in root exudation [15, 22]. On the other hand, endophytic bacteria also synthesize a varied array of secondary metabolites with unique chemical structures that have been exploited as biocontrol agents. Additionally, these bioactive compounds can be beneficial as they can stimulate plant growth and development. The composition of secondary metabolites produced by endophytic bacteria depends on the physiological status and species of plants and microorganisms. The bacterial genera include *Azotobacter*, *Serratia*, *Azospirillum*, *Bacillus*, *Caulobacter*, *Chromobacterium*, *Agrobacterium*, *Erwinia*, *Flavobacterium*, *Arthrobacter*, *Micrococcus*, *Pseudomonas*, and *Burkholderia*. These carry out mechanisms like nutrient fixation, neutralizing biotic and abiotic stress, and producing volatile organic compounds (VOCs) and enzymes to prevent diseases. However, the mode of action is different depending on PGPR-types and varies according to the type of host plant [23]. Our unpublished data report that some native maizes have been shown to induce the synthesis of anthocyanin and phenolic compounds in response to drought or waterlogging (unpublished data), cold, high salinity, or nutrient deficiency stresses. This response is a protective strategy to alleviate these adverse impacts [24]; (**Figure 2**). Studies have shown some specific changes in root exudation of primary and secondary metabolites as follows: (1) high sugar levels exuded in early plant developmental stages may attract a wide range of microbes that can consume sugar substrates, and (2) high levels of phenolics exuded in later plant developmental stages induce specialized pathways, where these compounds are used as specific substrates or signaling molecules in ways that vary across taxa [25].

2.2.2 Nutritional starvation responses

Plants exposed to nutrient limitations exhibit a wide range of responses that include changes to the quantity and composition of the compounds released by roots. In maize, N-deficit causes a reduced exudation of amino acids; P-deficiency

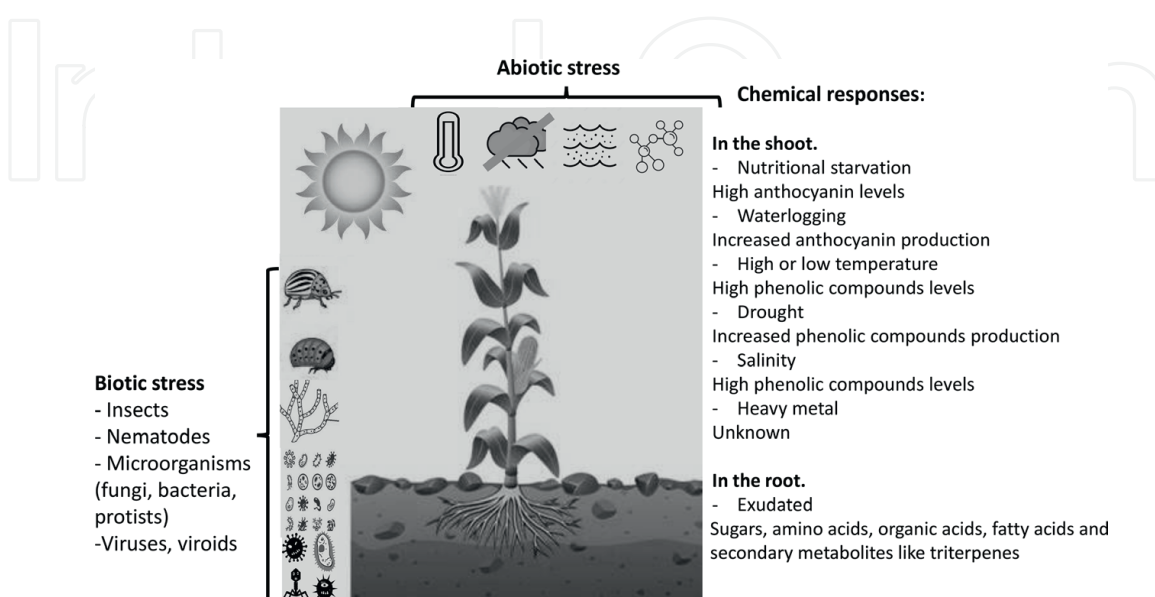


Figure 2.
Putative chemical response to abiotic stress.

stimulates the release of gamma-aminobutyric acid (GABA) and carbohydrates; whilst K-deficient plants release less sugars. Moreover, Fe deficiency causes increased release of glutamate, glucose, ribitol, and citrate [26]. Accordingly, plants exposed to different nutrient limitations show differences in the microbial structure composition. For example, P-deficient plants release compounds involved in bacterial chemotaxis and motility, whilst exudates released by Fe and K-deficient plants did not cause dramatic changes in bacterial composition [4, 26]. Interestingly, native maize landraces from *Los Tuxtlas*, Mexico show varying mycorrhizal dependency for P uptake, but there is still no data on bacterial composition [27].

2.2.3 High or low-temperature responses

Plants growing under high or low-temperature stress exhibit responses such as a decline in photochemical efficiency, stomatal conductance, and net CO₂ fixation. High temperatures cause changes in the plasma membrane, water content (transpiration), impaired photosynthesis activity, enzyme functioning, cell division, and plant growth. Some strategies to overcome this stress include the production and accumulation of enzymes and osmolytes. Temperature plays a significant role in the regulation of physiological and metabolic responses. Bacterial endophytes also possess effective mechanisms to protect the structure of proteins, membranes, and nucleic acid molecules, and in this way, they can survive under high temperatures or low temperatures. These phenomena have been studied in genera like *Pseudomonas cedrina*, *Brevundimonas terrae*, and *Arthrobacter nicotianae*, among others [14].

2.2.4 Waterlogging and water deficit responses

Waterlogging stress adversely impacts the physiology and photosynthetic capacity of the plant, and prolonged exposure generates severe damage to plant growth or productivity. Some strategies that are adopted by plants under water deficit response are reduction in transpiration loss through altering stomatal conductance and distribution, leaf rolling, root-to-shoot ratio dynamics, root length increment, accumulation of compatible solutes, enhancement in transpiration efficiency, osmotic and hormonal regulation, and delayed senescence [28]. In addition, bacterial endophytes can enhance plant tolerance through the maintenance of cell homeostasis and diminishing the adverse effects of oxidative stress [29].

2.2.5 Drought responses

Drought stress cause as responses a decline in turgor and water potentials, a suppression in photosynthesis, a decrease in the contents of the chlorophyll, and increased accumulation of proline in most plants [30]. Several studies suggest that the use of distinct endophytic bacteria could produce beneficial effects on their host plants if their co-inoculation does not generate antagonistic responses. They show mechanisms that involve the maintenance of the cell water homeostasis under drought conditions, allowing diminished water loss and increasing water inlet, carbon sequestration, nutrient cycling, resulting in health of crops, and rhizosphere ecosystem functioning [31, 32]. Many bacterial groups have been related to these mechanisms, for example, *Acinetobacter*, *Azospirillum*, *Azotobacter*, *Arthrobacter*, *Bacillus*, *Beijerinckia*, *Brevundimonas*, *Burkholderia*, *Clostridium*, *Delftia*, *Duganella*, *Erwinia*, *Enterobacter*, *Flavobacterium*, *Hydrogenophaga*, *Methylobacterium*, *Paenibacillus*,

Pantoea, *Proteus*, *Providencia*, *Pseudomonas*, *Psychrobacter*, *Rhizobium*, *Serratia*, *Stenotrophomonas*, *Streptococcus*, and *Streptomyces* [33, 34].

2.2.6 Salinity responses

Salinity stress induce a condition that prevents water uptake by the plant and relate to a decline in photosynthesis, growth, and uptake of other nutrients. Salinity adversely affects plant growth and development. Halophytic bacteria have several adaptations to mitigate salinity stress that include a reduced stomatal conductance of the host, lower water potential, uptake of inorganic ions, a salt discharge from roots, and accumulation of organic acids, among others [16]. Salinity can disrupt water uptake and ion equilibrium and lead to oxidative damage due to the production of ROS. Halophytic bacteria can keep these ROS at minimal levels due to the presence of an antioxidant system that consists of enzymes like catalase (CAT), peroxidase (POD), and superoxide dismutase (SOD). The salt-tolerant endophytes include genera like *Pseudomonas*, *Kocurias*, *Cronobacter*, *Gracilibacillus*, *Staphylococcus*, *Virgibacillus*, *Salinicoccus*, *Bacillus*, *Zhihengliuella*, *Brevibacterium*, *Oceanobacillus*, *Exiguobacterium*, *Arthrobacter*, and *Halomonas*. These bacterial groups possess an ACC deaminase activity with the potential to ameliorate plant salinity stress [16, 35, 36].

2.2.7 Heavy metal responses

Heavy metal stress is characterized by the inhibition of processes like photosynthesis, respiration, nitrogen and protein metabolism, and nutrient uptake [37]. There is a wide range of heavy metal-tolerant microorganisms and plant-associated microbes that involve various mechanisms such as efflux, impermeability to metals, volatilization, EPS sequestration, metal complexation, and enzymatic detoxification [14, 38]. The microorganisms with tolerance to heavy metals include genera such as *Rhizobacteria* and the phylum *Firmicutes* that promote plant growth and development during metal stress conditions. They carry out mechanisms to reduce ethylene concentration, production of plant growth regulators such as auxin indole-3-acetic acid (IAA), ACC deaminase, and disease suppression [14].

2.2.8 Pathogen responses

Biotic stress can be caused by different pathogens or plagues, such as bacteria, viruses, fungi, nematodes, protists, insects, and viroids. These result in a significant reduction in plant growth and development. Endophytic bacteria have been used as antagonists against plant pathogens and species like *Bacillus* spp. and *Pseudomonas* sp., produce a wide variety of compounds such as antibiotics, antifungal compounds, antivirals, and so on [39]. In plants, some defense mechanisms are activated by pathogenic or non-pathogenic invasion, that results in the activation of enzymes, such as chitinase, β -1, 3-glucanase, phenylalanine ammonia-lyase, polyphenol oxidase, peroxidase, lipoxygenase, SOD, CAT, and ascorbate peroxidase (APX). After these encounters, plants remain primed, which means that they are better prepared for future attacks by pathogens. PGPEs promote plant growth by producing metabolites that control phytopathogenic agents. These metabolites include β -1,3-glucanase, ACC-deaminase, and chitinase, which are generally involved in lysing cell

walls and neutralizing pathogens [40]. Finally, species from diverse genera, including *Pseudomonas*, *Bacillus*, *Arthrobacter*, *Stenotrophomonas*, and *Serratia* can produce VOCs that impact plant growth and development [13].

2.3 Abiotic stress amelioration by plant growth-promoting endophytes

The use of bacterial strains from rhizosphere, phyllosphere, or endosphere has been suggested to promote an amelioration of abiotic stress. Endophytes promote plant growth through nitrogen fixation, phytohormone production, nutrient acquisition, and by conferring tolerance to abiotic and biotic stresses. These mechanisms have been reported across many genera such as *Bacillus*, *Pantoea*, *Klebsiella*, *Burkholderia*, *Gluconobacter*, and *Pseudomonas*, among others [13, 41, 42]. Specifically, for maize endophytes, these functions have been associated with genera, such as *Massilia*, *Burkholderia*, *Ralstonia*, *Dyella*, *Chitinophaga*, and *Sphingobium*. However, the bacterial community structure significantly changes through different growth or development process. For example, *Massilia*, *Flavobacterium*, *Arenimonas*, and *Ohtaekwangia* were enrichment at early growth stages, whilst genera like *Burkholderia*, *Ralstonia*, *Dyella*, *Chitinophaga*, *Sphingobium*, *Bradyrhizobium*, and *Variovorax* were dominant at later stages [43]. In *milpa*, studies have reported the presence of genera such as *Flavitalea*, *Sphingomonas*, *Blastococcus*, *Luteitalea*, and *Vicinamibacter*, among others groups that are uncommon in hybrid maize [5]. Moreover, endophytes bacteria like *Bacillus*, *Enterobacter*, *Pseudomonas*, *Azotobacter*, *Arthrobacter*, *Streptomyces*, and *Isopterocola* were related to the alleviation of drought, heat, and salt stress in different crop plants, **Figure 3** [11, 44].

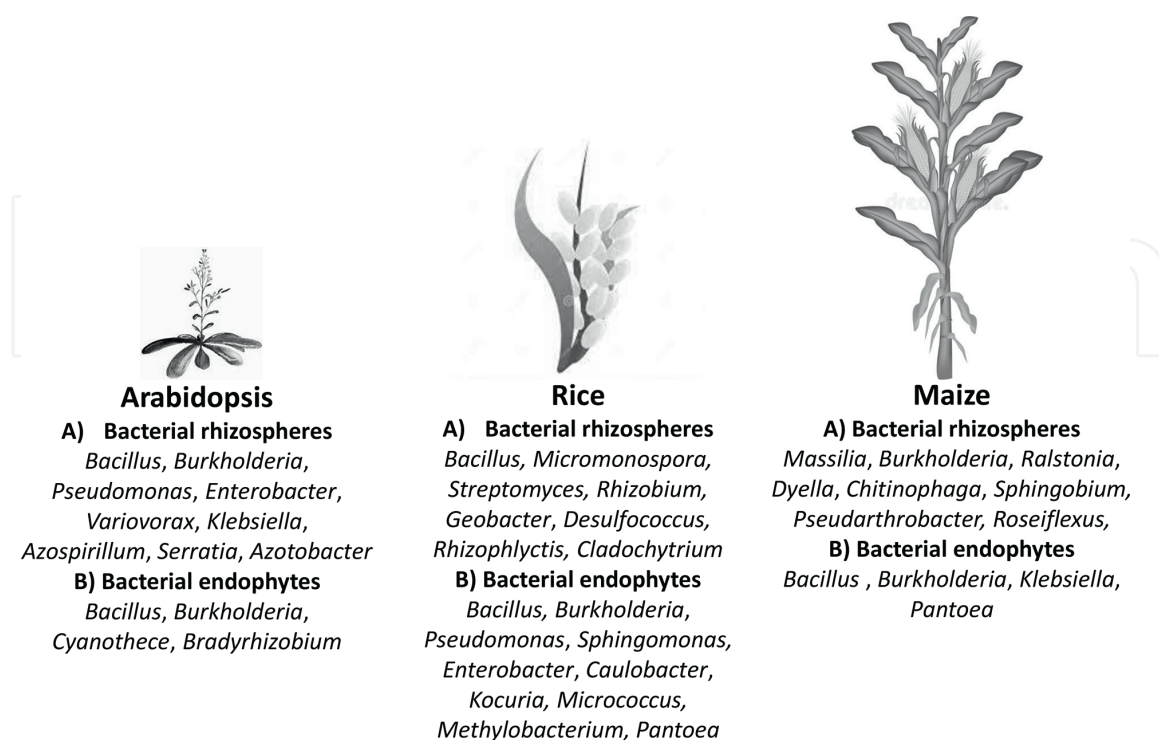


Figure 3. Potential bacterial endophytes from Arabidopsis, Rice, and maize.

Several studies have proposed that different rhizosphere bacterial types may serve as initial inoculum populations. It was shown that bacterial communities, such as epiphytic and endophytic, are highly similar in both leaves and roots, respectively, supporting the hypothesis that the communities are recruited from the soil [12]; (**Figure 3**). Firstly, rhizosphere microbial could be defined by exudates released from the host; this is because concentration gradients of carbon sources and phytochemicals function as attractants, while the modulation of oxygen and pH in the soil acts as limiter strategy, and finally, nutrient depletion works as selective mode [9] (**Figure 1**). Secondly, rhizoplane microbes could be recruited by favoring specific functions like attachment or adhesion. Swimming and other types of motility and chemotaxis are the first step to colonization. These depend on cell structures, such as flagella or pili, while colonization requires biofilm formation and adhesins. These are all important features for gaining access to the plant surface and to colonize in susceptible areas caused by wounds or mechanical injuries [42]; (**Figure 1**), Endophytic microbes are found in inter or intracellular spaces in the plant, and it is hypothesized that they require properties such as flagella and twitching motility that contribute to access and colonize at the host. On the other hand, lipopolysaccharide production (LPS), ROS detoxification, plant polymer degradation, quorum sensing, and type VI secretion system are important for the establishment inside the plant host [9, 42]. Finally, it has been reported that some mechanisms are central features in abiotic stress alleviation by plant growth-promoting endophytes. One important example is ACC deaminase activity to keep the stress ethylene concentration below growth inhibitory effects [16, 45–47].

3. Conclusions

The plant associated-microbial communities play important roles in nutrient competition, and in general, in plant health and crop yields. It is therefore important to clearly differentiate between the structure and diversity of bacterial communities found as endophytes vs. on the roots (rhizosphere). Important progress has been achieved in the study of beneficial microbes in maize, but recent studies show that there are unexpected differences between hybrid and native landraces, probably due to opposing farming systems between conventional modern crops and traditional *milpas* system with ancestral practices. It has been hypothesized that *milpa* practices favor the maintenance of specific microorganisms that could have been lost in modern hybrid maize with monocultures, high-tillage, and large agrochemical input techniques. Particularly, endophytic microbes appear to be important communities with unique diversity and functions in native maize. In order to understand *milpa* microbial diversity for developing sustainable solutions, it is first necessary to review our general knowledge on the role of endophytes for the health of plants in general, but specifically for maize. Today, it is increasingly recognized that these endophytic bacterial communities could be significant restore to plant health and they could have offered an opportunity to maximize crop productivity and mitigate the effects of climate change without huge impacts on the ecosystems.

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Author contributions

VMGM did the writing and drew the graphs. JR and MT revised this manuscript.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Author details

Víctor M. González-Mendoza¹, Mayra de la Torre² and Jorge Rocha^{3*}


1 Unidad Regional Hidalgo, CONACyT-Centro de Investigación en Alimentación y Desarrollo, Mexico

2 Department of Food Science, Centro de Investigación en Alimentación y Desarrollo A.C, Mexico

3 Unidad Regional Hidalgo, CONACyT-Centro de Investigación en Alimentación y Desarrollo, Mexico

*Address all correspondence to: jorge.rocha@ciad.mx

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