



Review

Promising bacterial genera for agricultural practices: An insight on plant growth-promoting properties and microbial safety aspects



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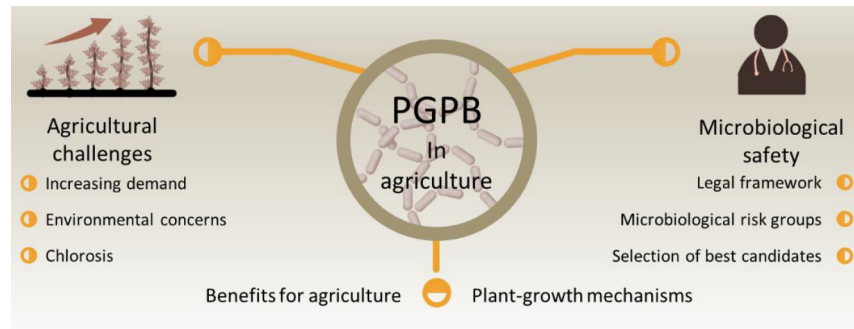
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HIGHLIGHTS

- The usefulness of bacteria for solving main agriculture problems is critically reviewed.
- Biosafety aspects linked with the use of PGPB in agriculture practices are discussed.
- An up to date overview of the main mechanisms associated with the use of PGPB is presented.
- The potentialities of several bacterial genera regarding their PGP properties are reviewed.
- Applied studies (field performance) of PGPB are presented.

GRAPHICAL ABSTRACT



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ABSTRACT

In order to address the ever-increasing problem of the world's population food needs, the optimization of farming crops yield, the combat of iron deficiency in plants (chlorosis) and the elimination/reduction of crop pathogens are of key challenges to solve. Traditional ways of solving these problems are either unpractical on a large scale (e.g. use of manure) or are not environmental friendly (e.g. application of iron-synthetic fertilizers or indiscriminate use of pesticides). Therefore, the search for greener substitutes, such as the application of siderophores of bacterial source or the use of plant-growth promoting bacteria (PGPB), is presented as a very promising alternative to enhance yield of crops and performance. However, the use of microorganisms is not a risk-free solution and the potential biohazards associated with the utilization of bacteria in agriculture should be considered. The present work gives a current overview of the main mechanisms associated with the use of bacteria in the promotion of plant growth. The potentiality of several bacterial genera (*Azotobacter*, *Azospirillum*, *Bacillus*, *Pantoea*, *Pseudomonas* and *Rhizobium*) regarding to siderophore production capacity and other plant growth-promoting properties are presented. In addition, the field performance of these bacteria genera as well as the biosafety aspects related with their use for agricultural proposes are reviewed and discussed.

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1. Introduction

World population is constantly increasing and currently there are around 7.7 billion people on planet Earth with current estimations placing a worldwide population of 10 billion by 2055 (Worldometers, 2018). This ever-increasing number puts Earth and its limited resources on stress. Arable fertile land is one of such resources (Alexander et al., 2017). As the population grows, more land is needed to supply enough food for all people. An alternative to avoid damaging progressively larger areas of wild land is to achieve increasing means of production.

A worldwide agricultural problem, with major implications in crop production, is the plant iron deficiency. Iron bioavailability is particularly low in calcareous soils (Hansen et al., 2006). Since it is estimated that calcareous soils cover about 30 % of world's cultivated soils, plant iron deficiency arises as a major agricultural worldwide problem (Barker and Stratton, 2015; Hansen et al., 2006). The most common practice to overcome this problem is the application of synthetic iron chelates (Nadal et al., 2012), mostly aminopolycarboxylate acids (APCAs), such as ethylenediaminetetraacetic acid (EDTA) or ethylenediaminedi(*o*-hydroxyphenylacetic) acid (EDDHA). Among APCAs, EDDHA/Fe(III) chelate is the most effective Fe fertilizer in neutral and alkaline soils (Alcañiz et al., 2017). In general, APCAs are strong chelating agents; however, they usually are not biodegradable (Bucheli-Witschel and Egli, 2001). Consequently, their accumulation in the environment is becoming a matter of great concern (Bucheli-Witschel and Egli, 2001).

The search for better, cheaper, and more environmental-friendly alternative processes for increase food production or to solve specific agricultural problems (such as iron induced-chlorosis) is of utter importance and a major challenge. Such alternatives should, desirably, replace non-green or unsustainable practices, such as the intensive use of agrochemicals in field fertilization (chemical fertilization) or in the fight against phytopathogens (use of pesticides). The use of natural compounds, produced for instance by plant-growth promoting bacteria (PGPB), can be regarded as an alternative proposal for a more

sustainable and environmental-friendly development of agricultural. Thus, it is not surprising the renewed and growing interest for PGPB (particularly in century XXI), which is translated into a huge number of published works (Fig. 1). Even, when the search in the Web of Science-Clarivate Analytics database is refined using the topics "siderophore production" and "bacteria" the same trend is observed (Fig. 1). Furthermore, the application of the *Azospirillum* genus has reached >3.5 million ha in South America in 2014, with a recorded average yield improvement of 10 % (Cassán and Diaz-Zorita, 2016). The use of different microbial agents by foliar application or by seed inoculation was also reported to have positive effects on major crops, such as rice, wheat, sugar beet, corn, and cotton (Tabassum et al., 2017). It is forecast that PGPB market share will reach USD 1.66 billion by 2022 (Timmusk et al., 2017). Market ready mixes of bacteria and/or fungi exists, such as mixes of *Bacillus amyloliquefaciens* with *Trichoderma virens* or the combination of *Trichoderma* with *Bradyrhizobium* (Backer et al., 2018), and more PGPB based products are available commercially, as listed by Mustafa et al. (2019).

Different authors have reviewed the properties and traits of some PGPB (Bhattacharyya and Jha, 2012; Hayat et al., 2010; Tabassum et al., 2017), with focus on siderophore production/use (Ahmed and Holmström, 2014a; Gupta et al., 2018; Saha et al., 2013), biofertilization (Gupta et al., 2018) or bio-pesticide properties (Glick, 2010; Olanrewaju et al., 2017; Saraf et al., 2014). However, to our knowledge, no review addressed the environmental and public safety of bacteria for agricultural purposes.

The present work aimed to perform a comprehensive review of the potential application of bacteria, in sustainable agriculture, crossing, at the same time, relevant information regarding their safety. Thus, the most promising PGPB genera, for agronomic practices, are presented, in respect to their siderophore production capacity. In addition, examples of studies using these bacteria in the promotion of plant growth and biosafety aspects linked with their use in an agronomic context are critically reviewed.

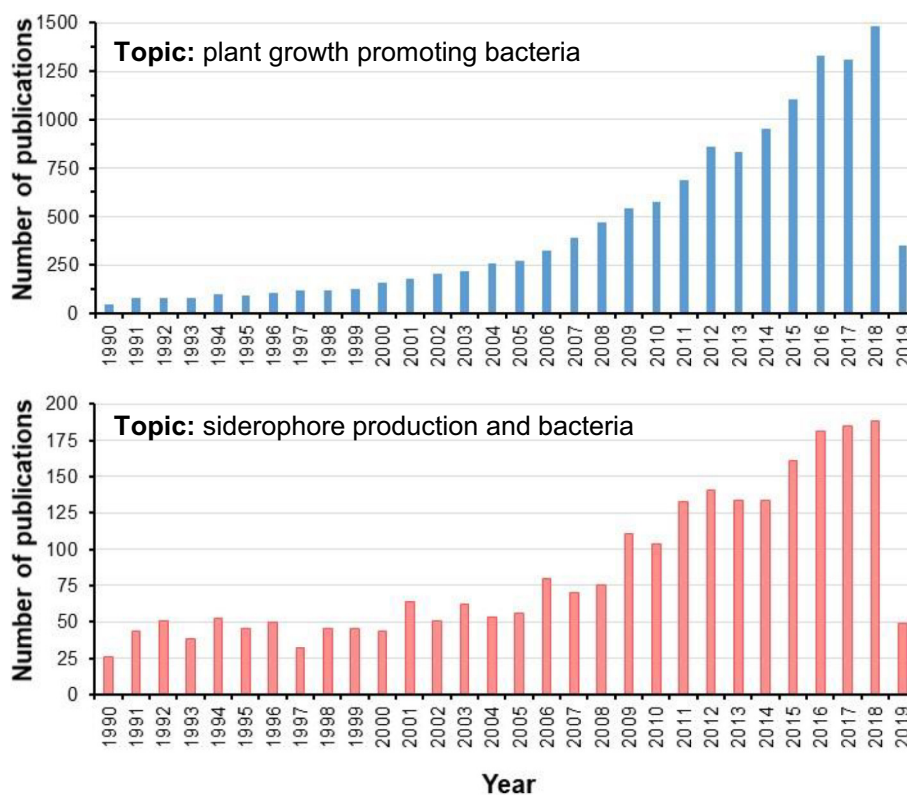


Fig. 1. Evolution of the works published with "plant growth promoting bacteria" or "siderophore production and bacteria" in the topic. Source: Web of Science-Clarivate Analytics, 2 April 2019; search from 1990 to 2019.

2. Agriculture challenges

2.1. Chlorosis in plants: an increasing issue

2.1.1. Iron function in plants

It is generally recognized that iron is an essential micronutrient required in many plant processes, among which photosynthesis (Barker and Stratton, 2015). Although not present in chlorophylls, Fe is necessary for their synthesis and for the correct functioning of the photosynthetic apparatus as it is present in the three main complexes of the photosynthetic system: photosystem I, cytochrome *b₆f* complex and photosystem II (Barker and Stratton, 2015; Briat et al., 2015; Broadley et al., 2012). In addition, non-heme Fe-S proteins (such as ferredoxin) and heme proteins, such as several enzymes (catalases and peroxidases) and cytochromes (which participate in the electron transport in photosynthesis, in chloroplasts, and in oxidative phosphorylation, in mitochondria) require the presence of iron to fulfill their functions in plant metabolism (Broadley et al., 2012). As a consequence, Fe is a key factor for proper plant biomass production and for high crop nutritional value (Briat et al., 2015). For a more detailed information about iron function in plants, the reader can consult the reviews performed by Broadley et al. (2012) and by Barker and Stratton (2015).

2.1.2. Iron deficiency in plants: chlorosis

The lack of iron in plants leads to a symptomatic array named iron deficiency induced chlorosis (IDIC), which is characterized by the appearance of yellow young leaves as a consequence of the inefficient chlorophyll production (Lucena, 2000). Plants under iron deficiency present chloroplasts with marked changes in their ultrastructure, being smaller under extreme iron deficiency (Broadley et al., 2012).

IDIC is a problem in agriculture as it can significantly reduce crop yields. Chlorotic plants will develop less, produce less biomass and yield less flowers and fruits, or even lead to complete crop failure (Guerinot and Yi, 1994). Some crops known to be susceptible to IDIC

are peach, kiwifruit, citrus and pear (Lucena, 2003), but some other valuable crops have also been described to suffer from IDIC, such as rice, soybean, cotton, peanut (Hansen et al., 2006), tomato (Chaney et al., 2008) and pea (Kabir et al., 2016). Furthermore, Fe shortage leads to loss of nutrient value on harvested crops. For example, on developing countries, the major Fe source are vegetables (Barton and Abadia, 2006). Thus, Fe deficiency may hinder the production of proteins (Broadley et al., 2012), reducing the nutritional value of food. Therefore, insufficient Fe in crops may have detrimental effects on animal and human health. This further reinforces the need to solve the issue of Fe nutrition of plants, especially in susceptible crops.

The low bioavailability of iron is a result of its chemical nature and its low solubility and dissolution kinetics. Although Fe is generally present in high quantities in soil, in well drained soils most of Fe is found as crystalline Fe (hydro)oxides, such as goethite and hematite (Colombo et al., 2014). Under aerated conditions and pH values above 7, these iron-minerals are highly insoluble and the free Fe concentration can be in the range of 10^{-10} mol L⁻¹ (García-Marco et al., 2006), which is a value much lower than the required for the normal plant development ($\sim 10^{-7}$ to 10^{-8} mol L⁻¹) (Lindsay and Schwab, 1982). This is further aggravated if iron-minerals present a low surface area, especially in well crystallized minerals. This limits the absorption of iron by plants, especially in alkaline calcareous soils. In plants, the effects of bicarbonate on iron transport may also limit the distribution and availability of iron on leaves (Mengel, 1994). The presence of nitrates can also interfere with the pH and redox balance. Nitrate uptake system of plants is normally mediated by a proton cotransport system, which can increase local rhizosphere pH. In strategy I plants, root reductases are speculated to reduce nitrate to nitrite in favor of Fe(III) to Fe(II), compromising Fe uptake by the root (Lucena, 2000). In strategy I plants (which corresponds to the most of non-graminaceous species), the reduction of Fe (III) to Fe(II) by a plasma membrane-bound reductase is an obligatory step prior to Fe intake via an iron regulated transporter (Barker and Stratton, 2015). Finally, heavy metals in soil can also disrupt the Fe

Table 1
Factors affecting iron availability and uptake by plants.

Causes of low iron availability	Causes for low iron uptake by plants
High pH, due to carbonates in soil (pH > 7 is critical)	Bicarbonate buffering
Types of minerals	Presence of nitrates affects pH and redox state
Low iron mineral surface	Presence and competition of heavy metals

uptake system on roots (Bashmakova et al., 2015). The main factors that influence the iron availability and uptake by plants are summarized in Table 1.

2.1.3. The use of iron fertilizers

2.1.3.1. Drawbacks of the use of inorganic and organic (synthetic) compounds. The challenge to overcome IDIC in agriculture and to increase crop yield has been of great importance and interest. The first response to the problem was the use of inorganic iron fertilizers, such as FeSO₄ (Shenker and Chen, 2005). However, the supply of iron in this manner is inconsequential because iron readily precipitates due to the buffering capacity of carbonate/bicarbonates present in some soils (Lucena, 2003). Thus, organic chelating agents are more adequate for this purpose. While some organic acids, such as malic, citric and oxalic acids (Fig. 2), are suitable for foliar application or hydroponics (a method of growing plants using mineral nutrient aqueous solution instead of soil) where chlorosis is not severe, they are ineffective in providing Fe to plants in alkaline calcareous soils (Lucena, 2003). Another approach consists in the use of synthetic organic chelating agents, namely APCAs, which have high iron complex stability and are more adequate for soil application (Bucheli-Witschel and Egli, 2001). APCAs are compounds containing one or more nitrogen atoms to which carboxyl groups are linked (Fig. 2). Examples of synthetic APCAs are: diethylenetriaminepentaacetic acid (DTPA), EDDHA, ethylenediaminedi(*o*-hydroxy-*p*-methylphenylacetic) acid (EDDHMA), ethylenediaminedi(2-hydroxy-5-sulfophenylacetic) acid (EDDHSA), ethylenediaminedi(5-carboxy-2-hydroxyphenylacetic) acid (EDDCHA), EDTA and N-(hydroxyethyl)ethylenediaminetriacetic acid (HEDTA) (Fig. 2). The use of these compounds is regulated in the EU (European Union, 2003).

However, several issues arise from the use of such synthetic chelates in the agriculture. Firstly, the synthesis of EDDHA, which is one of the most commonly used synthetic chelating agents, originates a mixture of regioisomers: *o,o*-EDDHA, *o,p*-EDDHA, and *p,p*-EDDHA. The last two isomers have lower complexing capability and, therefore, reduces the value and efficiency of EDDHA as a iron fertilizer (Hernández-Apaolaza et al., 2006). Similar issues related to impurities in EDDHMA, EDDHSA and EDDCHA production were also found (Alvarez-Fernández et al., 2002). EDTA, although widely used in agriculture, has shown lower performances compared to EDDHA due to its lower chelating stability constants (Ferreira et al., 2019; López-Rayó et al., 2019). New APCA agents, such as *N,N'*-bis(2-hydroxy-5-methylphenyl) ethylenediamine-*N,N'*-diacetic acid (HJB) (López-Rayó et al., 2009) or *N,N'*-bis(2-hydroxybenzyl)ethylenediamine-*N,N'*-diacetic acid (HBED) (Nadal et al., 2012) have been developed to cope with the issue of racemic mixtures of EDDHA and related chelating agents, since their syntheses yields purer compounds than the previous ones.

Another important problem associated with the extensive use of APCAs is related to their environmental impact. Synthetic APCAs are not biodegradable or poorly biodegradable (Bucheli-Witschel and Egli, 2001). For example, EDTA has been described as poorly biodegradable (Oviedo and Rodríguez, 2003), and its persistence and translocation in soil has been described (Bloem et al., 2017). As consequence of the limited biodegradability of APCAs, questions regarding its possible toxic effects on aquatic organisms and in mammals, as a result of the mobilization of heavy metals, have been raised (Bucheli-Witschel and Egli, 2001).

2.1.3.2. Use of chelating compounds of biological origin as alternative. It is important to underline that a chelating agent must have some degree of persistence in soil in order to fulfill their function: efficient supply of iron for correcting chlorosis in plants. However, regarding to the biodegradability of the chelating agent, a balance should be achieved in order to avoid either an inefficient supply of iron (in the case of a fast biodegradability) or a possible toxic effect due to the leaching of metals (if not biodegradable).

In this context, new alternatives to synthetic APCAs should be sought in an attempt to find better candidates for being used as biodegradable iron fertilizers in agricultural practices. As possible candidates can be the APCAs of biological origin (natural occurring APCAs), such as ethylenediaminedisuccinate (EDDS), produced by *Amycolatopsis orientalis* or rhizobactin, produced by *Rhizobium meliloti* (Fig. 2) (Bucheli-Witschel and Egli, 2001). The latter compound is classified as siderophore (please see siderophore definition in Section 3.3.2.1), which present a better biodegradability comparing with the most synthetic APCAs (Fazary et al., 2016).

2.2. Pathogenic impairment on crops

As reported above, high crop yields are critical to meet the ever-increasing demand on food. However, plant pathogens have a major impact on crop efficiency, quality and yield around the world. For example, it was estimated that >484 M bushels of soybeans were lost due to diseases in twenty eight U.S. states, during 2009 (Koenning and Wrather, 2010). *Zymoseptoria tritici*, a species of filamentous fungus, was responsible for wheat crop yield reductions with severe epidemics resulting in losses of up to 50%; this pathogen was also responsible for the use of circa of 70% of the fungicides in the European Union (EU) (Fones and Gurr, 2015). Since their introduction in the 19th century, chemical fungicides, have been the main mean to fight and control fungi related plant diseases, with the consequent benefits to world's population feeding. Their use increased and by 2014 the world consumption of fungicides was of circa 14.7 billion US dollars (Maienfisch and Stevenson, 2015). However, the pressure on the discontinuation of fungicides is growing mainly due to: 1) considerable resistance to fungicides (Possiede et al., 2009); 2) fungicides and pesticides are generally considered concerning contaminants of water and soil causing environmental and health issues (Kaonga et al., 2017). These facts resulted on the decrease of the number of fungicides used in some countries (Zhang, 2018). For example, in Japan, recently, the trend of fungicide use has been declining (Kaonga et al., 2017). However, new developing economies may lead to a new surge in fungicide usage (Zhang, 2018).

Therefore, in addition to the need for further regulations on production, distribution and education for the use of pesticides, there is a need to: 1) develop of new, low toxic and highly efficient alternatives to combat plant pathogens; 2) minimize chemical pesticides and optimize the use of bio-pesticides. These points are of interest of this review and will be further addressed in following sections.

3. Plant-growth promoting bacteria

3.1. Definitions

Plant growth promoting bacteria (PGPB), consists in a large group of microorganisms that can be found in the rhizosphere (plant growth promoting rhizobacteria, PGPR), on the root surface or associated to it (Basu et al., 2017; Kloepper and Schroth, 1978). These bacteria live and interact with plants and improve plant growth (Basu et al., 2017; Chauhan et al., 2015; Gupta et al., 2018). Bacteria are indispensable part of this ecosystem and their presence is beneficial for plant growth (Bhattacharyya and Jha, 2012; Chauhan et al., 2015). Sometimes, plant roots, stimulate colonization of bacteria on the rhizosphere by exuding ions, free oxygen, water, enzymes, mucilage and a diverse carbon-containing primary and secondary metabolites, which can be used by

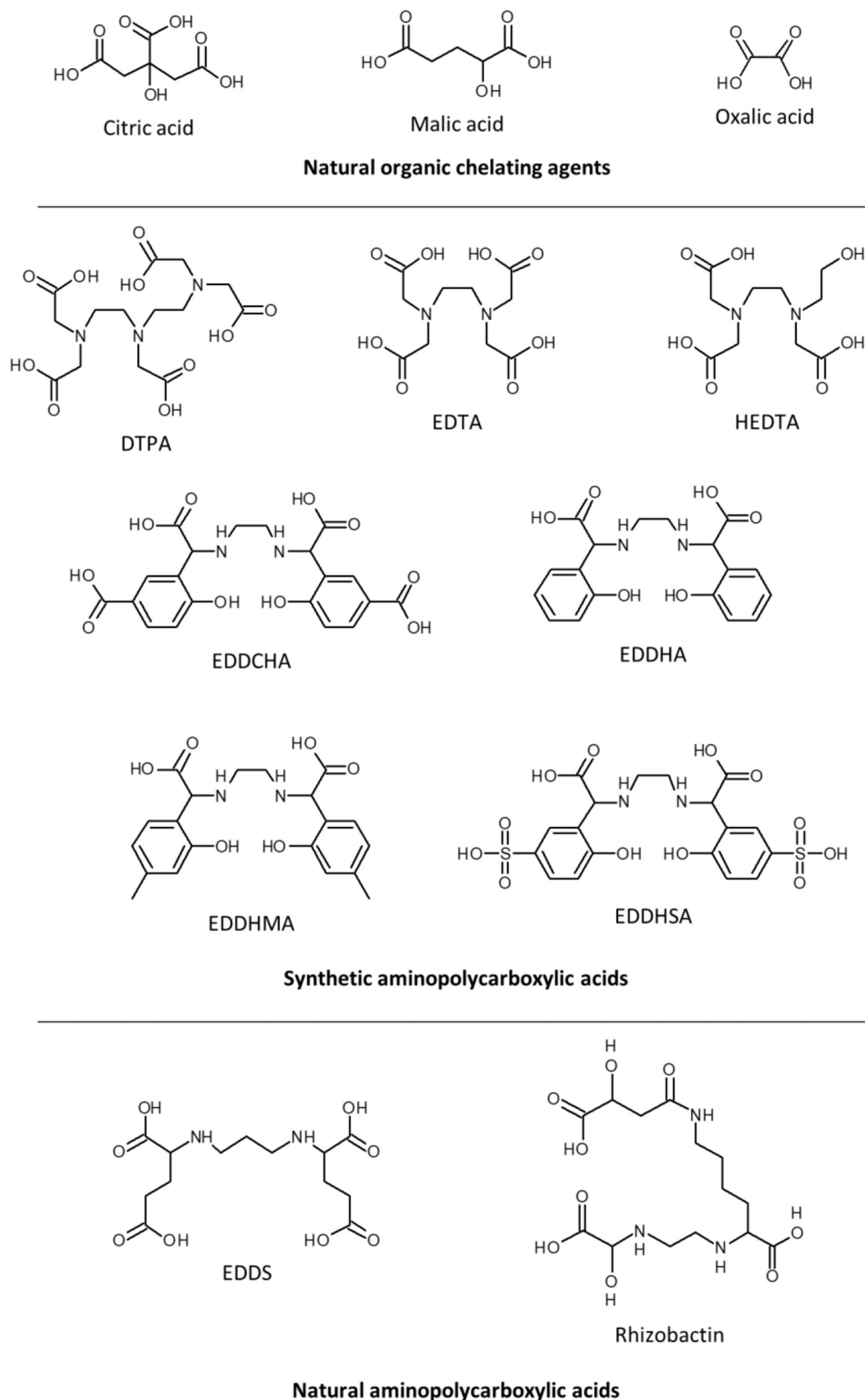


Fig. 2. Examples of natural and synthetic chelating agents used to correct iron chlorosis.

bacteria (Dutta and Podile, 2010); therefore, the bacterial population may be as much as one thousand times more dense in the rhizosphere than in the bulk soil (Glick, 2014).

PGPR can be classified as: 1) extracellular-PGPR, which corresponds to bacteria mostly found on the rhizosphere or rhizoplane (surface of plant root that is in contact with soil) and more rarely on the spaces between root cortex and 2) intracellular-PGPR, which is related to bacteria found inside specialized nodules in roots (Jorquera et al., 2010). In more recent years, the PGPR classification was refined to include only species that satisfy two of the following three conditions: aggressive colonization, plant growth stimulation and biocontrol of pathogenic organisms (Bhattacharyya and Jha, 2012).

3.2. Mechanisms of action

The PGPB can exert their positive input on plant growth by different mechanisms, which can be classified by different ways. One possibility consists on the classification of the bacteria according to its function: biofertilizer, biostimulator or biocontrol (Fig. 3). Biofertilizers are mixtures of living microorganisms that when applied to seeds, plants or soil, promote the increase of nutrient supply, such as NH_4 , SO_4^{2-} or PO_4^{3-} . A biostimulator is a microorganism with the ability to produce phytohormones, such as auxins (plant growth regulators with morphogen-like characteristics, like indole acetic acid, IAA) and cytokinins (substance that promote cell division). A biocontrol microorganism is that which promotes plant growth by controlling pathogenic populations, for instance, by producing antibiotics, hydrogen cyanide (HCN) or enzymes with the ability to hydrolyze the fungal cell wall (Bhattacharyya and Jha, 2012). The dissociation of HCN originate cyanide ion, which is a potent inhibitor of many metalloenzymes, particularly copper-containing cytochrome c oxidases (Blumer and Haas,

2000). Therefore, the production of HCN by PGPB can originate an important reduction of phytopathogens and harmful rhizobacteria with the corresponding enhancement of plant health (Haas and Défago, 2005).

The mechanisms of action of PGPB can also be classified as being direct or indirect. Direct mechanisms consist on the supply of nutrients to the plant (either by nitrogen fixation or phosphate solubilization), increasing iron bioavailability (through siderophore production) as well as by production of phytohormones, like IAA (Fig. 3). Indirect mechanisms include antibiotic production, removal of phytotoxic substances, competition with pathogenic organism and stimulation of mycorrhizae (symbiotic association between fungus and plant roots) growth (Bhattacharyya and Jha, 2012).

3.3. Benefits of PGPB

3.3.1. Macronutrients

Plants need an array of elements/nutrients in greater quantity than others, namely carbon, which they obtain from the atmosphere. Plants also obtain other important macronutrients from the soil such as potassium, nitrogen, phosphorus or sulfur (Fig. 3). Regarding soil macronutrients, PGPB should, by definition, be capable of supplying host plants with additional nutrients or facilitate the acquisition of existing ones. Some bacteria are able to fix N_2 (conversion of atmospheric nitrogen to ammonium) and supplying nitrogen to plants. Genera, such as *Azotobacter* (Kraepiel et al., 2009), *Azospirillum* (Steenhoudt and Vanderleyden, 2000), *Azorhizobium* and *Rhizobium* (Cocking, 2003), among others, are known to help plant growth by nitrogen fixation (Fig. 3). Within nitrogen-fixing bacteria some are free-living, i.e., do not require host to perform the process (such as: *Azotobacter* spp., *Agrobacterium* spp. and *Azospirillum lipoferum*) while others are

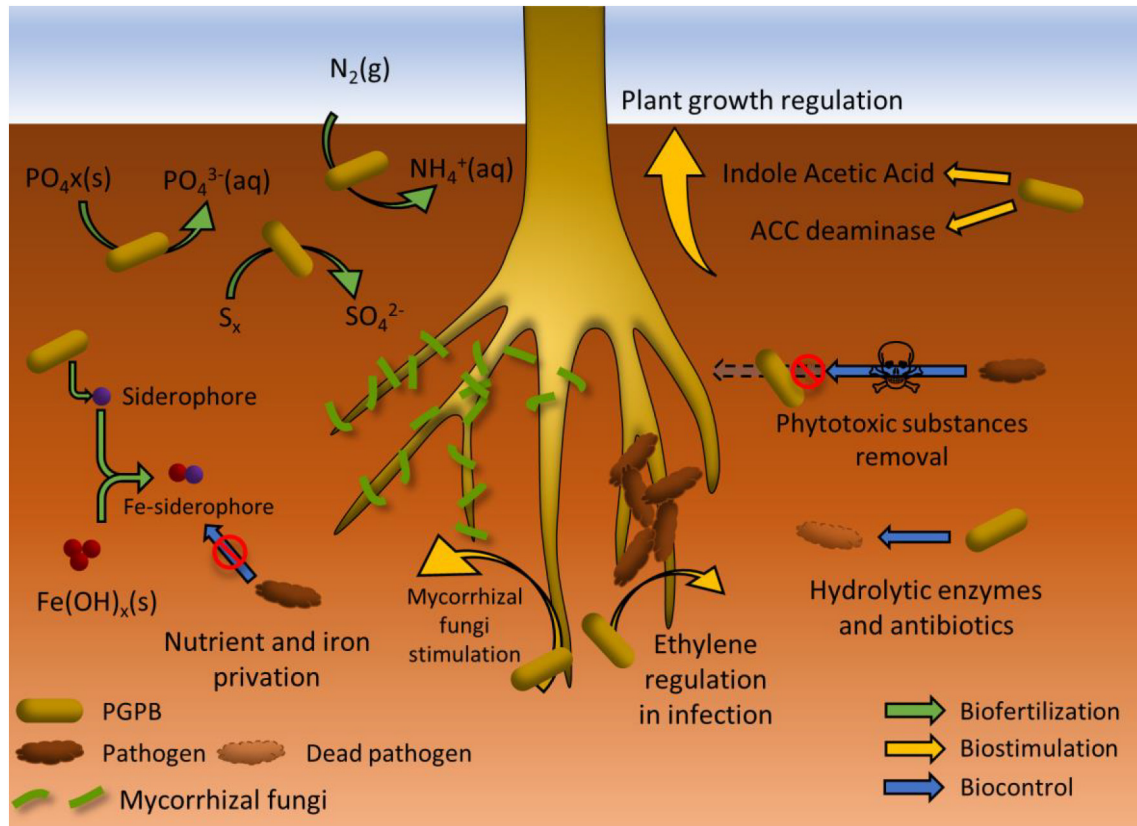


Fig. 3. Mechanisms of action of plant growth promoting bacteria in the rhizosphere. Biofertilization mechanisms (green arrows) are those which act at the nutrition level. Biostimulation mechanisms (yellow arrows) act on the plant's regulatory system, by action of phytohormones and signaling components. Biocontrol mechanisms (blue arrows) rely on the control of pathogenic microbial populations. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

symbiotic and only fix nitrogen in association with certain plants, such as leguminous (for example: *Rhizobium* spp. and *Azorhizobium* spp.) (Madigan and Martinko, 2006). PGPB comprises various rhizobia bacteria (such as *Rhizobium* and *Bradyrhizobium*) that grow free-living in the soil and infect the root cells of specific plants (legumes, such as soybeans) and leads to the formation of root nodules (Olanrewaju et al., 2017). Inside the plant cells, the rhizobia are transformed into swollen, misshapen forms named bacteroids; then, single or several bacteroids become enclosed by portions of the plant cell membrane to form the symbiosome (Madigan and Martinko, 2006). Only after the formation of the symbiosome, the bacteroids transform atmospheric nitrogen, through the enzyme nitrogenase, into ammonia. In return, plant supply organic acids (for bacteroids to produce energy) and provides an appropriate micro-environment for the action of nitrogenases, thus establishing a symbiotic relationship between plant and bacterium (Madigan and Martinko, 2006; Olanrewaju et al., 2017).

Phosphorus is found in soil, as phosphates, but usually it is found in insoluble forms and, thus, not bioavailable for plants. Some bacteria have the ability of dissolving inorganic phosphates helping plants to cope their phosphorus needs (Fig. 3). Such bacteria comprise genera, such as *Azotobacter* (Kannapiran and Ramkumar, 2011), *Burkholderia*, *Enterobacter*, *Serratia* (Mamta et al., 2010) and *Pantoea* (Sulbarán et al., 2009). A major mechanism for phosphorus uptake in over 80 % of plant species is through the symbiotic association between plant roots and fungi, known as mycorrhizae (Drinkwater et al., 2017). In plant-mycorrhizal association, the fungi colonizes plant roots and obtain organic molecules from root secretions and get mineral nutrients, such as phosphate, obtained from the soil (Madigan and Martinko, 2006). The capacity of some PGPB, such as *Streptomyces* spp. or *Rhizobium* spp. to stimulate mycorrhizal fungi (Mycorrhiza Helper Bacteria) further contributes for a better phosphorous supply to plants (Baba et al., 2015; Franco-Correa et al., 2010).

Reduced inorganic sulfur compounds can be oxidized to sulfate by some bacteria genera like *Aquaspirillum*, *Bacillus*, *Pseudomonas*, *Thiobacillus* or *Xanthobacter* (Friedrich et al., 2001). This sulfate can be further absorbed by plants and promote their growth (Fig. 3).

Potassium is found in soils mainly in non-exchangeable mineral sources. Some *Bacillus* spp. are capable of dissolving potassium bearing minerals, constituting a supply of K to plants. These potassium solubilizing microorganisms and their mechanisms have been recently reviewed (Sattar et al., 2019).

3.3.2. Siderophores

3.3.2.1. Definition and function. Siderophores (from the greek *sideros* meaning iron and *phores* meaning bearer) are low weight molecules (between 500 and 1500 Da) that possess a great affinity and selectivity to bind and complex Fe(III) (Ahmed and Holmström, 2014a).

Siderophores are produced by microorganisms, such as bacteria and fungi, as well as by some graminaceous plants, as part of a strategy to obtain iron from the environment (Sah and Singh, 2015). As discussed above (iron deficiency in plants: chlorosis; Section 2.1.2), Fe(III) is very bio unavailable; in physiological conditions, the dissolved iron levels can be as low as 10^{-10} mol·L⁻¹ (Kraemer, 2004). Microorganisms need an optimal Fe concentration of about 10^{-5} to 10^{-7} mol·L⁻¹ (Saha et al., 2016) while for plants, some estimate place optimal Fe concentration at 10^{-9} to 10^{-4} mol·L⁻¹ (Guerinot and Yi, 1994) while other authors estimate a value of 10^{-7} to 10^{-8} mol·L⁻¹ (Lindsay and Schwab, 1982) for proper plant development.

3.3.2.2. Composition and structure. More than five hundred siderophores have been reported; among them, more than two hundred seventy have been structurally characterized (Barry and Challis, 2009). Despite this great variety, some common moieties are found among siderophores. These compounds usually have negatively charged oxygen atoms with high electron charge displaced [the higher the negative

charge, the higher the affinity for Fe(III)]. In order to favor the more thermodynamically stable high-spin Fe(III) complexes, the most common geometry is octahedral with a six donor atoms arrangement and minimal ligand repulsion (Hider and Kong, 2010).

The most common moieties are oxygen bidentate, namely, catecholate, hydroxamate and carboxylate (Table 2). Others moieties exist, such as oxygen and nitrogen/oxygen-based, but are less frequent among microorganisms (Saha et al., 2016).

Besides the type of donor groups, side chains and complexation energies, other factors are equally important to define the stability strength of the complex. Among them, the denticity (number of donor groups in a single ligand that bind to the central atom) of the chelating agent is of paramount importance, as higher denticity results in a higher stability of the chelate formed (Hider and Kong, 2010). Then, in nature, it is expectable that the most common siderophores are hexadentate (six donor atoms) and can be found in linear or cyclic fashions (Hider and Kong, 2010). The pH is also a determinant factor on the kind of siderophores found. Usually, hydroxamates are more commonly found in neutral to acid environments while catecholates are more commonly found in neutral to alkaline environments (Saha et al., 2013).




Several bacterial genera were described to produce siderophores, such as *Azotobacter* (Baars et al., 2016; McRose et al., 2017; Romero-Perdomo et al., 2017), *Azospirillum* (Banik et al., 2016), *Bacillus* (Kesaulya et al., 2018; Pourbabaee et al., 2018), *Dickeya* (Sandy and Butler, 2011), *Klebsiella* (Bailey et al., 2018; Zhang et al., 2017), *Nocardia* (Hoshino et al., 2011), *Pantoea* (Burbank et al., 2015; Soutar and Stavrinides, 2018), *Paenibacillus* (Liu et al., 2017), *Pseudomonas* (Baune et al., 2017; Deori et al., 2018; Pourbabaee et al., 2018), *Serratia* (Coulthurst, 2014) and *Streptomyces* (Gáll et al., 2016; Goudjal et al., 2016; Schütze et al., 2014).

3.3.2.3. Stability and environmental fate. In the environment, the majority of siderophore producers are confined to plant rhizosphere (Chauhan et al., 2015). For this reason, the siderophore concentration is maximum in the rhizosphere zone, where concentrations as high as $0.1 \mu\text{mol}\cdot\text{L}^{-1}$ and $1 \text{mmol}\cdot\text{L}^{-1}$ for bacterial siderophore and plant phytosiderophore, respectively, were reported (Harrington et al., 2015). Conversely, siderophore concentration drops dramatically from rhizosphere to bulk soil, where siderophore concentrations can be as low as $10 \text{nmol}\cdot\text{L}^{-1}$ (Ahmed and Holmström, 2014b). However, these values may be underestimated due to sorption phenomena and inadequate extraction and detection protocols for siderophore quantification (Harrington et al., 2015). In fact, in soil, siderophores may adsorb to clay minerals (oxyhydr)oxides and organic matter (Powell et al., 1982). For example, the desferrioxamine B-Fe(III) complex has been shown to adsorb strongly with montmorillonite (Siebner-Freibach et al., 2006). However, this may be a positive aspect since the adsorbed Fe(III) complexes may be released over a greater period of time for plant usage (Ahmed and Holmström, 2014b). Similarly, it was demonstrated that desferrioxamine B adsorbs to iron-containing kaolinite and facilitates the dissolution of iron present on the clay-mineral (Rosenberg and Maurice, 2003).

In the environment, other fate for siderophores is its abiotic degradation, which may take place through hydrolyses and/or oxidation processes. The siderophores with hydroxamate moieties may suffer hydrolyses and generate hydroxylamine groups; this process is followed by the reduction of Fe(III) to Fe(II) (Simanova et al., 2010). Laboratory studies have shown that hydrolyze products from coprogen (tri-hydroxamate siderophore) were also effective iron-carriers to cucumber and maize plants (Hördt et al., 2000). All these facts evidence a possible strategy for siderophore utilization where the presence of “sacrificial” moieties may help on the reduction, dissolution and transport of iron to (micro)organisms (Harrington et al., 2015).

The exposure to sunlight has also influence on the mechanisms of siderophore degradation and mineral dissolution. The type of siderophore as well as the presence of chelated Fe, can induce different

Table 2
Main moieties found in siderophores.

Functional moiety	Structure
Catecholate, catechol	
Hydroxamate, hydroxamic	
Carboxylate (If R ₁ = OH; α-hydroxy-carboxylate)	

behaviours. For example, hydroxycarboxylates, when complexed with iron are photo-reactive, while catecholates are only photo-reactive when not complexed; hydroxamates are not photo-reactive in both circumstances (Barbeau et al., 2003). The exposure to light also improves the rate of dissolution of some minerals by siderophores. Desferrioxamine B and aerobactin have been shown to dissolve lepidocrocite (an iron oxide-hydroxide mineral) faster when under UV-light exposure (Borer et al., 2009). Some other non-siderophore compounds carboxylates-containing, such as oxalate and malonate (and their α-hydroxycarboxylate versions), have been shown to be photo-reactive when adsorbed into some iron minerals, such as hematite (Fe₂O₃) or lepidocrocite, with possible dissolution of the minerals (Borer and Hug, 2014). Therefore, on its many forms, siderophore degradation, may have a positive influence on the iron uptake by organisms. This is due to the promotion of dissolution rates of mineral phases, iron reduction and transport to cells, while part of a dynamic environment of varied strategies for iron sequestration by organisms. As for their biotic fate, siderophores interact unavertable with (micro)organisms, being taken in by bacteria and plants (Bucheli-Witschel and Egli, 2001). It was also described the capacity of some bacteria to use siderophore as carbon and nitrogen source (Pierwola et al., 2004; Villa et al., 2014).

3.3.3. Phytohormones and ACC deaminase

The plant growth is controlled by phytohormones, namely auxins and ethylene, which control and model several aspects on plant, such as cell expansion and division, cell elongation and differentiation, and a variety of physiological responses (Jiang et al., 2017).

Among auxins, the most common is indole-3-acetic acid (IAA), which is known to be produced not only by plants but also by fungi and bacteria (Duca et al., 2014). Given its importance to the plant, there are several redundant tryptophan dependent metabolic pathways: the indole-3-pyruvic acid, indole-3-acetamide and indole-3-acetonitrile based pathways. These metabolic pathways have been described and reviewed elsewhere (Duca et al., 2014). Besides plants, some bacteria genera are also capable of producing IAA, such as *Agrobacterium* (Rashid et al., 2012; Sitbon et al., 1992), *Azospirillum* (Perrig et al., 2007), *Azotobacter* (Ahmad et al., 2008; Farajzadeh et al., 2012; Torres-Rubio et al., 2000), *Bacillus* (Ahmad et al., 2008; Mehta et al., 2010), *Enterobacter* (Shailesh et al., 2011; Viruel et al., 2011), *Nocardia* (Khamna et al., 2009), *Pantoea* (Shailesh et al., 2011; Viruel et al., 2011), *Rhizobium* (Shailesh et al., 2011; Tan et al., 2014), *Serratia* (Mamta et al., 2010), and *Streptomyces* (Gopalakrishnan et al., 2014). The IAA produced is part of the signaling and communication system between plants and bacteria present in the rhizosphere (Spaepen et al., 2007).

The correlation between IAA concentration and plant growth is not linear. Plants have an optimal endogenous IAA levels for their best development (Duca et al., 2014). Excess quantities of IAA may cause pathogenic effects on plants, such as the inhibition of root growth (Duca et al., 2014). Therefore, the use of IAA for plant stimulation has to be carefully regulated to avoid inhibitory effects from over dosage. In this context, plants possess neutralization mechanisms to control IAA

excess, like inactivation of IAA by conjugation with sugars, amino acids or peptides (Sitbon et al., 1992).

Other important plant growth regulator is ethylene, which controls the growth of root, leaves, flowers and fruits (Dubois et al., 2018) as well as the interaction with microorganisms on roots (Gamalero et al., 2008). Ethylene is derived from 1-aminocyclopropane-1-carboxylate (ACC) and is produced in plants as response to multiple stresses (Dubois et al., 2018). Thus, different stresses, such as metals and chemicals, mechanical damage, water and temperature extremes, induce ethylene biosynthesis through the induction of ACC synthase (Dubois et al., 2018). When in excess, ethylene may be toxic to the plant causing defoliation and other harmful cellular effects (Desbrosses et al., 2009).

ACC deaminase (ACCD) is an enzyme produced by some bacteria, such as *Azotobacter* (Dubey et al., 2012; Farajzadeh et al., 2012), *Bacillus* (Belimov et al., 2001) and *Pseudomonas* (Kamran et al., 2016; Sandhya et al., 2010) and is considered as a key trait for PGPB strains (Glick, 2014). ACCD is beneficial for plants as it decreased ACC levels by cleaving it into ammonia and α-ketobutyrate. This helps to regulate ethylene adverse effects by reducing its levels. Therefore, PGPB capable of producing ACCD are beneficial for plants grown in stress conditions such as drought (Sandhya et al., 2010), salt (Mayak et al., 2004) and heavy metals (Belimov et al., 2001) by regulating plant's ACC levels and, thus, of ethylene to non-toxic levels.

3.3.4. Pathogen antagonism

As an indirect method of plant growth promotion, antagonistic properties to plant pathogens are a valuable asset, as they can severely reduce or eliminate the incidence of plant diseases caused by fungi and bacteria. PGPB can achieve these effects by several mechanisms: production of hydrolytic enzymes; competition for nutrients; modulate ethylene levels caused by pathogenic infection; production of siderophores and antibiotics (Fig. 3) (Beneduzi et al., 2012). Several genera have been described as having antagonistic behavior to one or more plant pathogen, such as *Bacillus* (Heidarzadeh and Baghaee-Ravari, 2015), *Azospirillum* (Tortora et al., 2011), *Pseudomonas*, *Coniothyrium*, *Pythium* (Woo and Lorito, 2007), *Serratia*, *Burkholderia* and *Staphylococcus* (Opelt et al., 2007). The use of these microorganisms has shown good results on improving plant growth over time when colonization of rhizosphere is successful (Backer et al., 2018; Mustafa et al., 2019; Tabassum et al., 2017).

3.4. Microbiological safety

3.4.1. The need of using safe microorganisms

One of the main problems when working with microorganism is their safety. In fact, the spread of microorganisms is a cause of concern, particularly when they are pathogenic to humans and/or to other organisms, such as animals and plants. Such considerations should also be taken into account when it is intended to use microorganisms for agricultural practices.

The use of microorganisms for agronomic proposes can fall in one of the two categories: 1) production of a compound (for instance, a fertilizer), that can be used in agriculture, by microbial fermentation or 2) bio-inoculants: the microorganisms (individual strains or microbial consortia) are added directly to the soil or as a seed coating when re-seeding (Owen et al., 2015). In the first scenario, the organisms are confined to the place of production. However, production conditions and appropriate safety measures should be considered in order to reduce risks. The process, which includes the microbial cultivation and downstream processing (microbial harvesting, recovering and product processing), equipment and facilities should be designed in order to avoid or minimize the release of biological agents into work place. In addition, proper treatment and disposal of biological wastes should be taken into account as well as the training of the operators and the implementation of collective and individual protection measures. Even when working

with biological agents with lowest risk, i.e., no or low individual and community risk, unlikely to cause human disease (group 1 biological agents; please see below), the procedures of good occupational safety and hygiene should be considered (European Union, 2000). According to EU directive (2000/54/EC), activities in which workers are (or are potentially) exposed to biological agents as a consequence of their work, the replacement of biological agents (that pose a risk to human health) for other microorganisms which pose no risk is mandatory, whenever possible (European Union, 2000). In the second case (bio-inoculants) the biological agent goes beyond the controlled area of the place of production. In this kind of application, it is very likely that the microorganisms will be set loose on the environment and may disrupt the natural microbial communities. For these reasons, the use of non-pathogenic microorganisms (to humans, animals and plants) is not only advisable but also desirable and even mandatory.

3.4.2. Biosafety classification

Organisms can be classified according to four risk-to-humans groups, as described in the Directive 2000/54/EC (European Union, 2000). Those biological agents unlikely to cause human disease are classified in group 1. If capable of causing disease and be a hazard to the workers, but no risk of spreading to the community, is classified in group 2; if can cause severe human disease or can spread to the community, is classified in group 3. In both these cases (2 and 3) there is usually effective prophylaxis or treatment available. If the biological agent causes severe human disease and is a serious hazard to workers and may present a high risk of spreading to the community and there is usually no effective prophylaxis or treatment available, then it is classified as group 4.

Besides the classification of biological agents taking into account the possible risks to humans, remarks can also be made on possible pathogenicity on vertebrates, invertebrates and plants (Committee on Biological Agents, 2015). The technical rules for biological Agents (TRBA)-466 (Committee on Biological Agents, 2015) are a well-suited tool for assessing the appropriateness of a given bacterium regarding its safety use in agricultural practices. For further crosscheck on risk groups of a given bacterium, the reader can consult the American Biological Safety Association site (<https://my.absa.org/Riskgroups>), which hosts most risk classifications for pathogenic species (although non-pathogenic species are not found there) or the Canadian Pathogen Safety Data Sheets (Public Health Agency of Canada, 2018).

Due to the reasons presented above, for agricultural purposes is desirable the use of microorganisms characterized as Risk 1; this requirement is absolutely necessary when biological agents are used directly applied in the soils.

4. Promising bacterial genera for agricultural practices

A thorough review of the literature was conducted for the bacteria genera with plant growth promotion (PGP) properties belonging mostly to risk 1, which also have no or low phytotoxicity. In the following subsections, alphabetically, several genera of bacteria were reviewed taking into consideration the PGP attributes discussed above (namely, siderophore production, plant nutrient provision, biostimulation and biocontrol properties) and biosafety level (risk groups evaluation). It is also worthy to note that particular traits described in some genera may not be present in all species of the genera; similarly, some characteristics described may not be present in all strains belonging to a given species. For an exact information regarding the presence of a

Table 3
Main characteristics of promising bacterial genera for agricultural practices.

Genus	General characteristics		Siderophore		Other agronomic characteristics		
	Gram	Morphology	Name	Type	Biofertilization	Biostimulation	Biocontrol
<i>Azospirillum</i>	Negative	Rod or spiral	Spirilobactin 2,3 - DHB 3,5- DHB-threonine 3,5 - DHB-lysine	Catechol Catechol Catechol Catechol	Nitrogen fixation Phosphate solubilization	IAA ACCD GA Kinetin Abscisic acid Zeatin	HCN production EPA: <i>Colletotrichum acutatum</i>
<i>Azotobacter</i>	Negative	Spherical or ovoid	2,3 - DHB Aminochelin Azotochelin Protochelin Azotobactin Vibrioferrin 3,4 - DHB	Catechol Catechol Catechol Catechol Mixed Mixed Chatecol	Nitrogen fixation Phosphate solubilization	IAA ACCD	HCN production EPA: <i>Fusarium oxysporum</i> <i>Rhizoctonia solani</i> <i>Macrophomina phaseolina</i>
<i>Bacillus</i>	Positive	Rod	Schizokinen N- schizokinen N-schizokinen-A Itoic acid Bacillobactin Petrobactin	Hydroxamate Hydroxamate Hydroxamate Catechol Catechol Mixed	Phosphate solubilization Ammonia production	IAA ACCD GA	HCN production EPA: <i>Macrophomina phaseolina</i> <i>Ralstonia solanacearum</i> <i>Rhizoctonia solani</i> <i>Fusarium oxysporum</i>
<i>Pantoea</i>	Negative	Rod	Enterobactin-like Desferrioxamine-like Pyoverdine-like Pyochelin-like	Catechol Hydroxamate Mixed Mixed	Nitrogen fixation Phosphate solubilization	IAA ACCD GA Cytokines Abscisic acid	EPA: <i>Pseudomonas syringae</i> <i>Erwinia amylovora</i>
<i>Pseudomonas</i>	Negative	Straight or slightly curved rods	Pyochelin Pseudobactin(s) Pyoverdine(s) Pyocyanin Ferribactin 7-hydroxytropolone	Other Mixed Mixed Other Mixed Other	Nitrogen fixation Ammonia production Phosphate solubilization	IAA ACCD	HCN production EPA: <i>Erwinia amylovora</i> <i>Fusarium oxysporum</i> <i>Fusarium udum</i> <i>Pythium ultimum</i>
<i>Rhizobium</i>	Negative	Rod	Agrobactin Vicibactin Schizokinen 2,3 - DHB-threonine Rhizobactin	Catechol Hydroxamate Hydroxamate Catechol Catechol	Nitrogen fixation Phosphate solubilization	IAA ACCD	EPA: <i>Fusarium oxysporum</i> <i>Rhizoctonia solani</i> <i>Sclerotium rolfsii</i> <i>Macrophomina phaseolina</i>

ACCD: 1-aminocyclopropane-1-carboxylate deaminase; DHB: dihydroxybenzoic acid; EPA: example of pathogen antagonism; GA: gibberellic acid; IAA = indole-3-acetic acid.

specific characteristic in given genera, species or strain, the reader can consult the respective bibliographic references quoted.

4.1.1. *Azospirillum*

4.1.1.1. General genus description. The members of the genus *Azospirillum* are free living, but usually found colonizing plant roots, normally Gram negative, typically rod or spiral-shaped bacteria (Table 3). The species *Azospirillum brasilense* and *Azospirillum lipoferum* were first described (Lin et al., 2015). Subsequently, different species have been isolated and added to *Azospirillum* genus, such as *Azospirillum amazonense* (Cecagno et al., 2015) and *Azospirillum melinis* (Peng et al., 2006). *Azospirillum* genus is currently one of the most used PGPB as a result of its known properties for promoting the growth of several cereals, as it is the case of maize (Cassán and Diaz-Zorita, 2016).

4.1.1.2. Siderophore production. *Azospirillum* species are capable of producing siderophores. A catechol-type siderophore, named spirilobactin, was identified in iron-depleted medium of *Azospirillum brasilense* (Bachhawat and Ghosh, 1987). A strain of *Azospirillum lipoferum*, was described to produce 2,3-dihydroxybenzoic acid (2,3-DHBA) and 3,5-DHBA conjugated with threonine and lysine (Shah et al., 1992), which are also responsible for siderophore-mediated Mo intake by *Azospirillum lipoferum* (Saxena et al., 1989). Others *Azospirillum* spp. have been described to produce siderophores (Banik et al., 2016; Sahoo et al., 2014).

4.1.1.3. Other PGP properties. *Azospirillum* spp. were reported to produce phytohormones, such as: IAA (Sahoo et al., 2014), kinetin (a type of cytokinin) (Tien et al., 1979), abscisic acid, zeatin (Perrig et al., 2007; Sahoo et al., 2014), ACCD, gibberellic acid (GA) (Sahoo et al., 2014). *Azospirillum* spp. are also able to fix nitrogen (Bellone et al., 2011; Gadagi et al., 2004), solubilize phosphate (Rodriguez et al., 2004) as well as producing HCN (Sahoo et al., 2014) and of having antagonistic properties toward some plant pathogens, such as *Colletotrichum acutatum* (Tortora et al., 2011).

4.1.1.4. Applied studies. Field studies with *Azospirillum* species yield, in a general way, good results (Fukami et al., 2016). For this reason, this genus has been received an increased attention. Banik et al. (2016) used new *Azospirillum* strains for improvement of rice production. Inoculation studies with *Azospirillum* spp. were conducted on wheat (Bashan et al., 1990; Noreen and Noreen, 2014), rice (García de Salamone et al., 2012) and soybean (Bashan et al., 1990). More recently, the interest in *Azospirillum* strains has increased due to positive results for plant growth enhancing in soils under osmotic stress (Fasciglione et al., 2015; García et al., 2017; Gonzalez et al., 2015).

4.1.1.5. Microbiological safety. All *Azospirillum* species belong to risk group 1 (Committee on Biological Agents, 2015). In addition, no adverse effects are predicted to plants, invertebrates or other non-human vertebrates, making *Azospirillum* a presumably safe and eco-friendly genus to use (Committee on Biological Agents, 2015). In fact, some studies have shown that the inoculation of soybean with *Azospirillum brasilense* did not affect native rhizobia population while increasing grain yield (Bellone et al., 2011).

4.1.2. *Azotobacter*

4.1.2.1. General genus description. The *Azotobacter* genus is characterized by spherical or ovoid Gram-negative bacteria (Table 3), usually motile, that can be found in soils, mostly in neutral or alkaline soils but also in aqueous medium and associated with plants (Voets and Dedeken, 1966). *Azotobacter* strains are also known to form resistant cysts during dormant phases or when exposed to some reagents (Diaz-Barrera and Soto, 2010). This genus is of great importance to the environment due

to their great nitrogen fixation capacity, which is achieved as a consequence of the high metabolic rate of the three nitrogenases (McRose et al., 2017).

4.1.2.2. Siderophore production. *Azotobacter vinelandii* has the ability to produce several siderophores (Fig. 4). Azotobactin, initially called yellow-green fluorescent peptide, was isolated by Bulen and LeComte (1962). Latter, Corbin & Bulen isolated 2,3-DHBA and azotochelin, produced by *Azotobacter vinelandii* under iron stress (Corbin and Bulen, 1969). In the meanwhile, the structure of azotobactin was characterized by Fukasawa et al. (1972); Fekete et al. (1983) concluded that all these three compounds are produced in iron depleted media and act as siderophores. Page and Tigerstrom (1988) isolated the mono-catechol amino-chelin and, finally, in 1995, protochelin was isolated and characterized. This siderophore is a tri-catecholate, which is believed to be resultant of the condensation of amino-chelin and azotochelin (Cornish and Page, 1995). The medium conditions for all siderophore production by *Azotobacter vinelandii* have been determined. In medium containing Fe(III) concentrations higher than $7 \mu\text{mol} \cdot \text{L}^{-1}$, only 2,3-DHBA is produced; when iron concentrations are below $7 \mu\text{mol} \cdot \text{L}^{-1}$, azotochelin and amino-chelin are produced. If iron concentration in medium is under $3 \mu\text{mol} \cdot \text{L}^{-1}$, azotobactin is produced; finally, if iron is limited and Mo concentration is high ($>100 \mu\text{mol} \cdot \text{L}^{-1}$), protochelin is produced (Duhme et al., 1998). More recently, in a broad genetic study on *Azotobacter vinelandii*, vibrioferrin was hinted, opening the possibility that one more siderophore is produced by *Azotobacter vinelandii* (Baars et al., 2016). Vibrioferrin was later described to be regulated by vanadium and molybdenum levels of culture medium (McRose et al., 2017).

In *Azotobacter chroococcum* strains, hydroxamate type siderophore production was described (Suneja et al., 1994), being dependent on the iron levels of the medium (Page, 1987). It was found an inverse relationship between nitrogen fixation and the (uncharacterized) siderophore production in *Azotobacter chroococcum* (Suneja et al., 1996). It was also found that ammonium citrate decreases the production of hydroxamate siderophores on *Azotobacter chroococcum* while boosting the production of catechol siderophores (Suneja et al., 1996).

Other *Azotobacter* species also produce siderophores (some of which were not yet characterized). For instance, *Azotobacter paspali* (reclassified as *Azorhizophilus paspali*) produces 3,4-dihydroxybenzoic acid (Collinson et al., 1987), *Azotobacter salinestris* produces hydroxamate type siderophores (Page and Shivprasad, 1995) and *Azotobacter beijerinckii* produces an unidentified siderophore type (Kannapiran and Ramkumar, 2011).

4.1.2.3. Other PGP properties. Some *Azotobacter* spp. have the capacity to fix nitrogen, solubilize phosphate, produce HCN, IAA (Ponmurugan et al., 2012) and ACCD (Sahoo et al., 2013). *Azotobacter* spp. were also reported as possible biocontrol agents against *Fusarium oxysporum* (Chauhan et al., 2012), *Rhizoctonia solani* (Fatima et al., 2009) or *Macrophomina phaseolina* (Dubey et al., 2012).

4.1.2.4. Applied studies. Due to their plant-growth promoting traits, *Azotobacter* spp. have been applied into plants to evaluate their capabilities to improve crop yields; examples are: cotton (Chauhan et al., 2012; Romero-Perdomo et al., 2017), sesame (Dubey et al., 2012), maize (Shirinbayan et al., 2019), wheat (Mahato and Kafle, 2018), rice (Sahoo et al., 2013), tomato (Chauhan et al., 2012), or maize (Shirinbayan et al., 2019). Growth improvement was measured through the increase to disease resistance (Chauhan et al., 2012; Dubey et al., 2012), plant biomass (Mahato and Kafle, 2018; Romero-Perdomo et al., 2017; Shirinbayan et al., 2019), nitrogen and Fe concentration (Shirinbayan et al., 2019), grain yield (Dubey et al., 2012; Mahato and Kafle, 2018) and drought resistance (Shirinbayan et al., 2019).

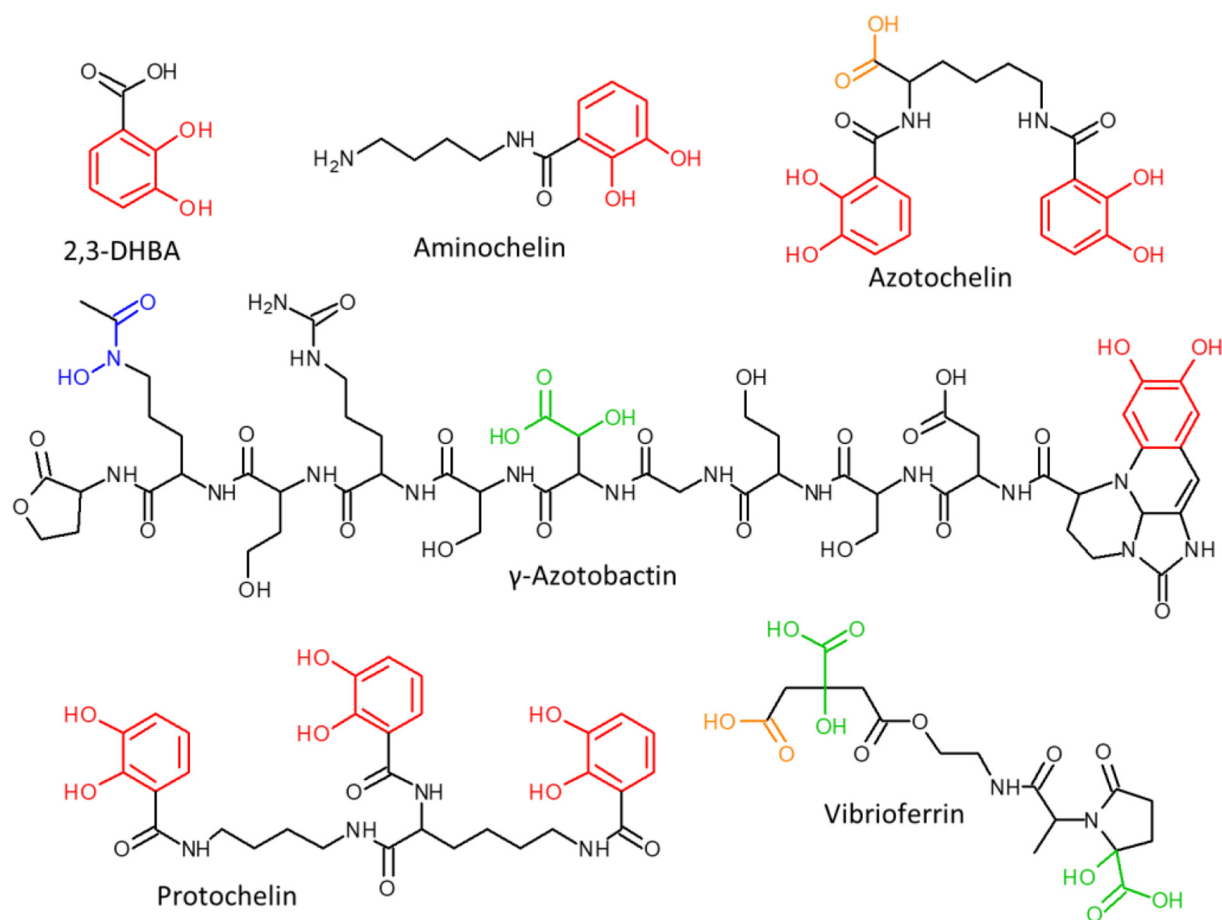


Fig. 4. Siderophores produced by *Azotobacter vinelandii*. Red: catechol moieties; orange: carboxylate moieties; green: α -hydroxycarboxylate moieties; blue: hydroxamate moieties. 2,3-DHBA: 2,3-dihydroxybenzoic acid. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4.1.2.5. Microbiological safety. All the seven species registered on TRBA 466 are classified as risk group 1 (Committee on Biological Agents, 2015). Therefore, *Azotobacter* is a safe genus to be manipulated by humans. In addition, no indicated pathogen to plants or other organisms was described (Committee on Biological Agents, 2015). Piromy et al. (2013) have studied the effects of some PGPB inoculants (including *Azotobacter* spp.) in the microbial diversity and have concluded that the diversity indices were not different between the PGPB-inoculated and un-inoculated.

4.1.3. *Bacillus*

4.1.3.1. General genus description. *Bacillus* genus is constituted by rod shaped, Gram-positive bacteria (Table 3), which can be either obligate aerobes or facultative aerobes, catalase positive and endospores producer (Turnbull, 1996). It is an omnipresent genus in nature, being found either in soil or water and even in extreme conditions, such as extremely alkaline (*Bacillus alcalophilus*) (Ntougias et al., 2006) or hot environments (*Bacillus thermophilus*) (Yang et al., 2013). Other known species from the genus are *Bacillus subtilis*, a model species broadly studied and described (Graumann, 2012), *Bacillus anthracis*, anthrax agent (Sheff, 2003), *Bacillus thuringiensis*, which is used as a natural insecticide (Sanchis and Bourguet, 2008) and *Bacillus megaterium*, which is among the biggest known bacteria; more recently, it became popular due to its recombinant protein production capacity (Bunk et al., 2010).

4.1.3.2. Siderophore production. It was described the ability of *Bacillus megaterium* to produce schizokinen, a di-hydroxamate, α -hydroxycarboxylate siderophore (Fig. 5) (Byers et al., 1967). Later on,

the ability of this bacterium to produce a deprotonated siderophore version (N-schizokinen) and respective amine versions (N-schizokinen-A) (Hu and Boyer, 1995) was also described. In this particular species, siderophore production is strongly correlated with carbon source in medium as well as with shaking and aeration conditions (Santos et al., 2014).

For *Bacillus subtilis*, the production of 2,3-dihydroxybenzoylglycine, also known as itoic acid (Fig. 5), was described by Ito and Neilands (1958) in iron depleted conditions. Subsequently, the trimeric ester, named bacillibactin (Fig. 5) was described (May et al., 2001). The genes responsible for bacillibactin production have also been found in *Bacillus amyloliquefaciens* (Dunlap et al., 2013; Niazi et al., 2014). The production of bacillibactin was also reported in *Bacillus anthracis*, *Bacillus cereus* and *Bacillus thuringiensis* (Wilson et al., 2006). Petrobactin (Fig. 5), a di-catecholate and α -hydroxycarboxylate siderophore, is synthesized by *Bacillus anthracis* (Koppisch et al., 2005) as well as by some strains of *Bacillus thuringiensis* (Koppisch et al., 2008), and probably by *Bacillus cereus* (Wilson et al., 2006).

4.1.3.3. Other PGP properties. Concerning to plant growth promotion characteristics, several works report different traits in *Bacillus* genus. The production of ACCD, IAA (Kumar et al., 2014), GA (Lenin and Jayanthi, 2012), ammonia (Ahmad et al., 2008) and the capacity to solubilize inorganic phosphates (Pourbabaee et al., 2018) by different *Bacillus* has been reported. In addition the production of HCN (Pourbabaee et al., 2018) and biocontrol potential of *Bacillus* spp. against *Macrophomina phaseolina* (Kesaulya et al., 2018), *Ralstonia solanacearum* (Huang et al., 2016) or *Rhizoctonia solani* and *Fusarium oxysporum* (Kumar et al., 2014) was described.

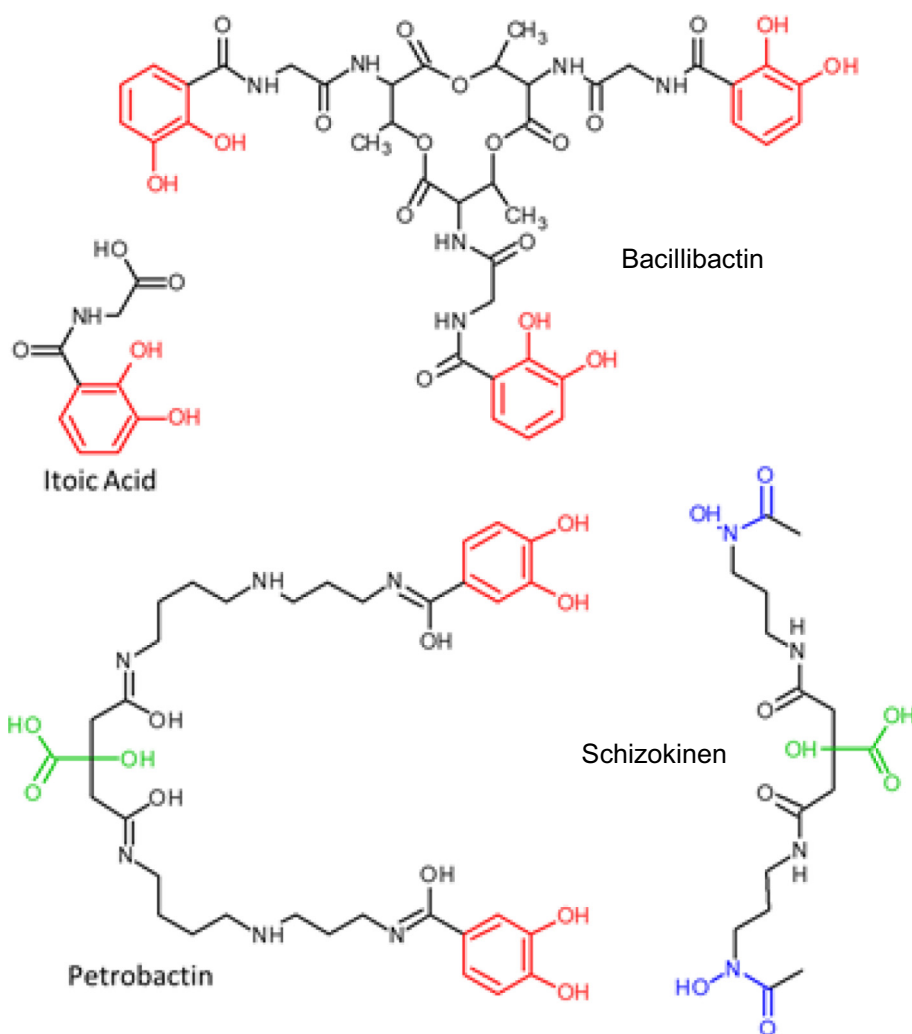


Fig. 5. Examples of siderophores produced by *Bacillus* genus. Red: catechol moieties; green: α -hydroxycarboxylate moieties; blue: hydroxamate moieties. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4.1.3.4. Applied studies. Some authors applied *Bacillus* spp. to plants in order to test their effects on the plant/crop yield. For example, *Bacillus* spp. were applied to banana (Kesaulya et al., 2018), sunflower (Pourbabaee et al., 2018), bean (Sabaté et al., 2017), tobacco (Wu et al., 2016) and tomato (Akram et al., 2015; Heidarzadeh and Baghaee-Ravari, 2015) with positive outcomes, such as: increase of biomass (Akram et al., 2015; Pourbabaee et al., 2018; Sabaté et al., 2017), Fe and chlorophyll concentration (Pourbabaee et al., 2018) and resistance to pathogens (Kesaulya et al., 2018; Sabaté et al., 2017; Wu et al., 2016).

4.1.3.5. Microbiological safety. According to the TRBA 466, only three *Bacillus* species are not classified in risk group 1: *Bacillus anthracis* (risk group 3), *Bacillus cereus* and *Bacillus weihenstephanensis* (risk group 2) (Committee on Biological Agents, 2015). The most commonly found species (*Bacillus subtilis*, *Bacillus megaterium*, *Bacillus amyloliquefaciens* and *Bacillus pumilus*), belong to risk group 1. *Bacillus thuringiensis* is pathogenic to invertebrates and *Bacillus cereus* is a toxin producer but safe in technical conditions (Committee on Biological Agents, 2015).

Regarding the impact of *Bacillus* spp. inoculation on local rhizosphere populations, contradictory results have been reported. Felici et al. (2008) reported no changes on the rhizosphere communities after inoculation with *Bacillus subtilis*, whereas Probanza et al. (2002) have concluded that the introduction of two *Bacillus* (*Bacillus licheniformis* CECT 5106 and *Bacillus pumilus* CECT 5105) inoculants

caused an alteration in the microbial rhizosphere composition. However, some changes in the microbial rhizosphere composition can be positive; for example, the application of *Bacillus amyloliquefaciens* ZM 9 affected positively the rhizosphere composition of tobacco plants by reducing pathogen populations (Wu et al., 2016).

4.1.4. *Pantoea*

4.1.4.1. General genus description. The *Pantoea* genus, which has *Pantoea agglomerans* as type species, was recently separated from the *Enterobacter* genus. It is a motile Gram-negative rod shaped bacteria (Table 3), forming yellow mucoid colonies (Walterson and Stavrínides, 2015). Given to its versatility, ubiquity and genetic tractability, make it an ideal genus for the development of commercially relevant medical, agricultural and environmental bio products (Walterson and Stavrínides, 2015). Since the creation of the genus with *Pantoea agglomerans*, new species have strengthened the ranks of *Pantoea* genus, such as *Pantoea allii* (Brady et al., 2011), *Pantoea vagans*, *Pantoea eucalypti*, *Pantoea deleyi* and *Pantoea anthophila* (Brady et al., 2009).

4.1.4.2. Siderophore production. The production of siderophores was described for several *Pantoea* species, such as *Pantoea agglomerans*, *Pantoea eucalyptii* (Viruel et al., 2011), *Pantoea allii* (Pereira and Castro, 2014), *Pantoea ananatis* (Kim et al., 2012; Loaces et al., 2011), as well as for other *Pantoea* species (Loaces et al., 2011). However, little

is known about these siderophores. The strain *Pantoea vagans* C9-1 is known to produce an enterobactin-like (catechol) siderophore and a desferrioxamine-like siderophore (Feistner and Ishimaru, 1996); the production of the latter compound is dependent on plasmatic transcription. Therefore, this characteristic is susceptible to be lost on some mutants (Smits et al., 2010). *Pantoea stewartii* subsp. *stewartii* produces a siderophore under iron-limiting conditions, which biosynthesis and export of proteins are encoded by the *iucABCD-iutA* operon; this operon is homologous to the aerobactin biosynthetic gene cluster found in a number of enteric pathogens (Burbank et al., 2015). It was also described that the strain *Pantoea eucalypti* M91 is capable of producing pyoverdine-like and pyochelin-like siderophores under alkaline growth conditions (Campestre et al., 2016). More recently, in a phylogenetic and comparative genomic study, desferrioxamine-like, enterobactin-like, and aerobactin-like siderophore biosynthetic gene clusters were found in several *Pantoea* strains (Soutar and Stavrinides, 2018). Judging from these findings, *Pantoea* strains are potentially capable of producing multiple and different types of siderophores.

4.1.4.3. Other PGP properties. The production of phytohormones, such as IAA, abscisic acid and GA (Feng et al., 2006) and cytokines (Omer et al., 2004) by different *Pantoea* spp. was reported. The production of ACCD was also described for *Pantoea* spp. strains (Trifi et al., 2017). In addition, nutrient based promoting traits, such as phosphate solubilization or nitrogen fixation (Kim et al., 2012) were described. The biocontrol potential of *Pantoea* spp. against *Pseudomonas syringae* (Xie et al., 2017) or *Erwinia amylovora* (Ait Bahadou et al., 2018) has also been reported.

4.1.4.4. Applied studies. The use of *Pantoea* spp. isolates for agronomic practices was tested in pot or field studies. Thus, the increased mass in plant bean (Gopalakrishnan et al., 2017), and in canola (Trifi et al., 2017), biocontrol action in mulberry seedlings (Xie et al., 2017), Fe intake in *Lotus japonicus* (Campestre et al., 2016), root development in olive trees (Montero-Calasanz et al., 2013), and increased crop yield and biomass in tomato, cucumber or pepper (Kim et al., 2012) was described.

4.1.4.5. Microbiological safety. Regarding safety aspects of working with *Pantoea* strains, from the twenty seven species listed on the TRBA-466, only four are not listed as risk group 1: *Pantoea agglomerans*, *Pantoea breunneri*, *Pantoea eucrina* and *Pantoea septica* (Committee on Biological Agents, 2015). Eleven species have been known as plant pathogens strains (Committee on Biological Agents, 2015). Despite this, the use of *Pantoea* strains, namely *Pantoea agglomerans*, at commercial level, as adjuncts to agricultural practice, has been reported (Glick, 2012). *Pantoea allii*, *Pantoea ananatis* and *Pantoea vagans*, which also have plant-growth properties, as reported above, are risk 1 species and can be possible species alternatives.

4.1.5. *Pseudomonas*

4.1.5.1. General genus description. The *Pseudomonas* genus is of medical and biotechnologically importance. It consists in aerobic, straight or slightly curved rods, Gram-negative bacteria (Table 3). *Pseudomonas* strains are found in biofilms or in planktonic forms with one or more polar flagella. Due to their high metabolic versatility, these bacteria are able of using most carbon sources (Özen and Ussery, 2012). The *Pseudomonas* genus is widely spread in the environment and some biotechnological important bacteria are inhabitants of a wide range of niches, such as soil and water environments, in addition to plant and animal associations (Özen and Ussery, 2012).

The *Pseudomonas* genus is one of the main PGPB genus that has received wide attention from the scientific community, being recognized for their biocontrol (Beneduzi et al., 2012) and agricultural potential (Bhattacharyya and Jha, 2012; Hayat et al., 2010).

4.1.5.2. Siderophore production. Several siderophores produced by *Pseudomonas* genus have been identified. Liu and Shokrani (1978) coined the term pyochelin to designate the large quantity of siderophores produced by *Pseudomonas aeruginosa* capable of harvesting iron from transferrin. The structural characterization of pyochelin (A) (Fig. 6) was latter made by Cox and co-workers (Cox et al., 1981; Cox and Graham, 1979). Meyer and Abdallah (1978) isolated and characterized the yellow-green, fluorescent, water-soluble pigment, produced by *Pseudomonas fluorescens*, suggesting that it was a siderophore. Kloepper et al. (1980) described the production of a siderophore in *Pseudomonas* strain B10. Later on, their colleagues characterized the structure of both pseudobactin (Fig. 6) and pseudobactin A (different in the quinoline derivatives) produced by *Pseudomonas* strain B10 (Teintze et al., 1981; Teintze and Leong, 1981). Pyoverdines are a large family of siderophores composed by a chromophore and a peptide chain (Fig. 6). The composition of this chain varies greatly from one pyoverdine to another and between different fluorescent *Pseudomonas* species (Ringel and Brüser, 2018). For example, three different pyoverdines, named, pyoverdine, pyoverdine₀ and pyoverdine A (as well as ferribactin), were isolated from *Pseudomonas fluorescens* (Philson and Llinas, 1982). The production of pyoverdines by *Pseudomonas aeruginosa*, such as pyoverdine Pa, (Wendenbaum et al., 1983) and pyoverdine C, D and E (Briskot et al., 1986), as well as a blue pigment named pyocyanin (Cox, 1986), was also reported. Other *Pseudomonas*, such as *Pseudomonas syringae*, also produce pyoverdine type siderophores (Torres et al., 1986). Other example is *Pseudomonas chlororaphis* ATCC 9446 that produces pyoverdines and ferribactins similar to those produced by *Pseudomonas fluorescens* ATCC 13525 (Hohlneicher et al., 1995). Others authors described the production of hydroxamate siderophores by *Pseudomonas fluorescens* NCIM 5096 and *Pseudomonas putida* NCIM 2847 (Sayyed et al., 2005). The production of pyoverdine siderophores by *Pseudomonas aureofaciens* was also reported (Beiderbeck et al., 1999). In fact, given the wide production of siderophores by *Pseudomonas* spp., it has been proposed the use of siderophore typing as a form of identification of fluorescent and non-fluorescent *Pseudomonas* (Meyer et al., 2002, 1997). The importance, synthesis and variability of pyoverdines in *Pseudomonas* was also consequently reviewed (Visca et al., 2007). Some *Pseudomonas* have been described to produce non-fluorescent iron chelating compounds, such as 7-hydroxytropolone, which is produced in large quantities by *Pseudomonas donghuensis* (Jiang et al., 2016).

4.1.5.3. Other PGP properties. Other PGP characteristics had been extensively reported. The production of IAA and ACCD (Berta et al., 2014; Bona et al., 2015, 2017) by *Pseudomonas* spp. has been reported. In addition, HCN (Subramanian and Satyan, 2014) and ammonia production (Rashid et al., 2012; Subramanian and Satyan, 2014) as well as phosphate solubilization (Subramanian and Satyan, 2014) and nitrogen fixation (Pham et al., 2017) by *Pseudomonas* spp. was described. Antagonistic behavior on several plant pathogens, such as *Erwinia amylovora* (Ait Bahadou et al., 2018), *Fusarium oxysporum* (Deori et al., 2018) *Pythium ultimum* and *Fusarium udum* (Sulochana et al., 2014) was also described.

4.1.5.4. Applied studies. Given the described properties of *Pseudomonas* spp., this genus has been tested for their potential as agronomic inoculants. These studies have been conducted in crops such as sunflower (Pourbabaee et al., 2018), tomato (Nagata, 2017), chickpea (Gopalakrishnan et al., 2017; Sulochana et al., 2014), green gram (Kumar et al., 2015), wheat (Rasouli-Sadaghiani et al., 2014), rice (García de Salamone et al., 2012) or olive (Montero-Calasanz et al., 2013). Thus, it was reported the increase of Fe concentration (Nagata, 2017; Pourbabaee et al., 2018; Rasouli-Sadaghiani et al., 2014), (dry) plant mass (García de Salamone et al., 2012; Pourbabaee et al., 2018; Sulochana et al., 2014), resilience to drought (Pourbabaee et al., 2018), grain yield (García de Salamone et al., 2012; Gopalakrishnan et al.,

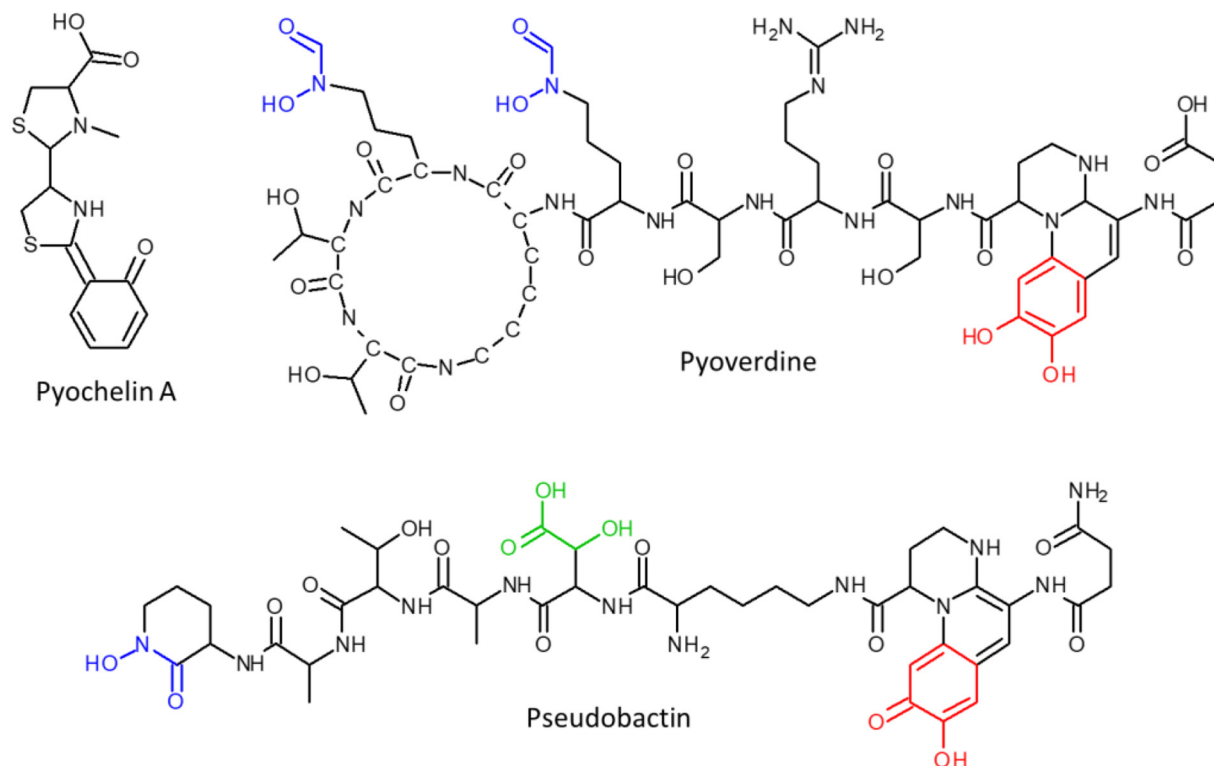


Fig. 6. Examples of siderophores produced by *Pseudomonas* genus. Red: catechol moieties; green: α -hydroxycarboxylate moieties; blue: hydroxamate moieties. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2017), shoot length (Sulochana et al., 2014) or root length (Montero-Calasanz et al., 2013).

4.1.5.5. Microbiological safety. Regarding *Pseudomonas* spp. safety, a total of two hundred fifty five species (subspecies included) belonging to the group risk 1 were isolated (Committee on Biological Agents, 2015). However, some of the most mentioned species, as PGPB, are not risk 1, or, have other notes of pathogenicity in invertebrates/plants. For example, both *Pseudomonas aeruginosa* and *Pseudomonas putida* are risk 2 level, with known human and vertebrate pathogenic properties. However, there are some species that are not pathogenic and are suitable for safe application, with PGP traits. For instance, *Pseudomonas fluorescens* (a risk group 1 with only a remark for invertebrates) when inoculated in plants roots was reported as innocuous for the rhizosphere (De La Fuente et al., 2002). Also, the inoculation of *Pseudomonas fluorescens* in rice seems not impact, significantly, culturable microbial communities in rhizosphere (García de Salamone et al., 2012).

4.1.6. Rhizobium

4.1.6.1. General genus description. The *Rhizobium* genus includes Gram-negative rod shape bacteria (Table 3), usually mobile and able to use simple carbohydrates, predominantly aerobic chemoorganotrophs. Some species have shown to fix nitrogen while most of them do not fix it when they present as free living (Somasegaran and Hoben, 1994). Although not mandatory, they are also commonly found in the nodules of plant's roots; in this case, they are found as nitrogen fixators, forming symbiotic relations with the host plant (Lodwig et al., 2003). *Rhizobium leguminosarum* is the representative species of this ever-growing genus (Parte, 2018), which has >90 species registered on microorganisms banks, such as Deutsche Sammlung von Mikroorganismen und Zellkulturen.

Being symbionts with plants, it is predictable that *Rhizobium* species have traits that help the plants growth, as part of its symbiotic relation. In fact, not only *Rhizobium* species fixate nitrogen when in symbiosis

with plants but they also produce other compounds, such as siderophores, phytohormones and other growth regulators.

4.1.6.2. Siderophore production. Several siderophores have been described to be produced by *Rhizobium* spp. *Rhizobium radiobacter* (then known as *Agrobacterium tumefaciens* and later as *Agrobacterium radiobacter*) was shown to produce a tri-catecholate siderophore named agrobactin (Fig. 7) (Eng-Wilmot and Van der Helm, 1980; Ong et al., 1979). Some strains of *Rhizobium radiobacter* were also able to produce hydroxamate type siderophores (Leong and Neilands, 1982). Smith and Neilands (1984) reported that *Rhizobium meliloti* produces a non-catecholate and a non-hydroxamate siderophore named rhizobactin (Fig. 2); later on, these authors have been working on its structure and described it as a di α -hydroxy-carboxylate siderophore (Smith et al., 1985). *Rhizobium meliloti* 1021 strain (also known as *Sinorhizobium meliloti* or *Ensifer meliloti*) was found to produce a variant of rhizobactin, named rhizobactin 1021 (Persmark et al., 1993). *Rhizobium leguminosarum* IARI 102 produced 2,3-DHBA conjugated with threonine (2,3-DHBA-Thr) (Fig. 7), under iron starved conditions. On the other hand, the *Rhizobium leguminosarum* IARI 917 strain was described to produce the schizokinen siderophore (Fig. 5) (Storey et al., 2006). *Rhizobium leguminosarum* ATCC 14479 was described to produce vicibactin (Fig. 7), a try-hydroxamate, and two other iron-binding siderophore-like compounds (Wright et al., 2013). It can then be concluded that *Rhizobium* genus has the ability to produce several siderophores, which can be tapped for possible uses in agricultural, medical and engineering purposes.

4.1.6.3. Other PGP properties. The production of ACCD and IAA has been described in *Rhizobium* spp. (Hernández et al., 2017). *Rhizobium* spp. has also the ability to solubilize phosphate (Kumar et al., 2015; Xing et al., 2016) and to fix atmospheric nitrogen when in root nodules (Datta et al., 2015). The antagonistic activity against different plant pathogens, such as *Fusarium oxysporum* (Arfaoui et al., 2006), *Rhizoctonia solani*, *Sclerotium rolfsii* (Sai Prasad et al., 2014) *Macrophomina*

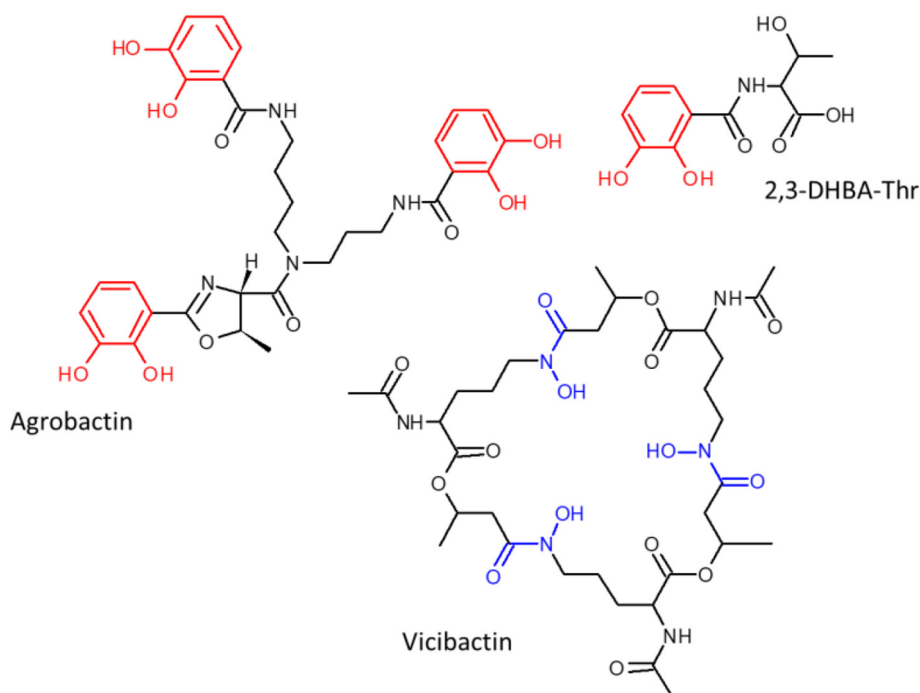


Fig. 7. Different siderophores produced by *Rhizobium* genus. Red: catechol moieties; orange: carboxylate moieties; green: α -hydroxycarboxylate moieties; blue: hydroxamate moieties. 2,3-DHBA-Thr: 2,3-dihydroxybenzoic threonine. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

phaseolina and *Aspergillus niger* (Sharma and Das, 2010) was also documented.

4.1.6.4. Applied studies. The development of crops such as bean (de Souza et al., 2016), green gram (Kumar et al., 2015), rice (Bhattacharjee et al., 2012), groundnut (Arora et al., 2001), crambe (de Aquino et al., 2018), lettuce or carrot (Flores-Félix et al., 2013) have been tested with the inoculation of different *Rhizobium* spp. The inoculation has resulted in different positive outcomes, such as increase of shoot mass (Bhattacharjee et al., 2012; de Souza et al., 2016; Flores-Félix et al., 2013), nitrogen plant content (Baba et al., 2015; Bhattacharjee et al., 2012; Flores-Félix et al., 2013) and root development (de Aquino et al., 2018) or reduced effects of pathogenic agents (Arora et al., 2001; Siddiqui et al., 2007).

4.1.6.5. Microbiological safety. *Rhizobium* genus has about sixty-three species identified in the TRBA-466 list, belonging all of them to risk group 1 bacteria (Committee on Biological Agents, 2015). Some species, such as *Rhizobium radiobacter*, have strains with plant phytopathogenicity. *Rhizobium* inoculation studies have shown that this genus does not have a negative impact on the native community; instead, it contributes to an increase of the bacterial community (Ambrosini et al., 2016). Therefore, considering the proven capabilities to promote plant growth without causing any harm to human health and rhizosphere communities, the bacteria belonging to *Rhizobium* genus can be seen as an alternative for agronomic application.

5. Concluding remarks

As the world's population continues to increase, as well as the quality of life in some developing countries, the demand for food of quality equally increases. The limited space available for farming means that the usable space must be worked with the best efficiency possible. On the other hand, agriculture presents some problems, such as the development of chlorotic plants due to the iron limitation, which is particularly severe under calcareous soils, or the loss of crops due diseases caused by phytopathogenic microorganisms. Both cases contribute to the reduction of crops yield. In addition, the intensive agriculture

practice carried out in the last decades, with the use of chemical fertilizers and herbicides, caused an increase of soil and water pollution. The climate changes and the intensification of areas of infertile and unproductive soil create new challenges, which require to transform the traditional farming practices into a more precise agriculture. This can be obtained with the aid of a multi-disciplinary approach using new scientific advances obtained in areas, such as biotechnology and nanotechnology.

In the present review, it was presented one of the possible solutions for the development of more sustainable agro-ecosystems: the use of bacteria to improve the quality and quantity of harvest crops. More specifically, it was discussed the suitability of some bacteria genera (*Azospirillum*, *Azotobacter*, *Bacillus*, *Pantoea*, *Pseudomonas* and *Rhizobium*) as source of biological iron-fertilizers (siderophores) and other compounds that promotes the plant growth and prevent the action of infectious agents that cause plant diseases. Additionally, the application of bacteria in different crops improvement was presented and the bio-safety aspects associated with the use of microorganisms in agronomic conditions were also addressed. In Table 3, it was summarized the main characteristics of promising bacterial genera for agriculture practices. Within these bacterial genera, particular strains may be more specialized in a given trait, while others, presented a wide properties spectra. But all genera have in common the presence of strains belonging to group 1 of biological agents, which makes them safe to be used for agricultural practices.

Although, in recent years, there has been an increased interest in the exploitation of the benefits associated with the use PGPB in terms of biofertilization and biocontrol (as can be seen from the rise of the number of publications in this field, Fig. 1), more studies need to be directed toward the use of safety PGPB as inoculants or as producers of compounds (such as siderophores) with the goal to improve crop productivity and reduce environmental impacts. Thus, the development of new inoculants (using safety bacteria), the increase of inoculum efficiency and the use of PGPB treated with nanoparticles may provide a new way to reduce the aggressive impact of agrochemicals (fertilizers and pesticides), decrease the production costs and boost the yield of crops. The design of new siderophore-based formulations for correcting iron-

induced chlorosis, eco-friendly (biodegradable), able to complex iron in environments with low bioavailability (such as calcareous soils) and with the ability to deliver efficiently iron to plants remains an important research area.

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Declaration of interest

The authors declare that they have no conflict of interest.

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