

Beneficial Functions of Soil Microbiome for Sustainable Agriculture

Funciones Benéficas del Microbioma del Suelo para la Agricultura Sustentable

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Abstract

Plant-associated microbes are key factors for the health of crops; in this sense, microbial inoculants represent a promising strategy for maintaining productivity in modern agricultural production systems, while sustainably adapting to adverse climatic factors, reducing pollution and decreasing use of toxic substances for the environment. Genomic and metagenomics tools have allowed a better understanding of how intensive agriculture has negative effects on the diversity and function of the plant microbiome, and in turn, how the management of microbial communities can mitigate some negative effects of crop modernization. Here we review the beneficial roles of plant-associated bacteria, and the symbiotic interactions between the microbiome and various economically important crops; we also discuss how this knowledge can provide strategies towards a more sustainable agricultural production.

Soil microbiome, Sustainable agriculture, Functional microorganisms

Resumen

Los microorganismos asociados a las plantas son factores clave para la salud de los cultivos; en este sentido, los inoculantes microbianos representan una estrategia prometedora para mantener la productividad en los sistemas de producción agrícola modernos, adaptándose de manera sostenible a factores climáticos adversos, reduciendo la contaminación y disminuyendo el uso de sustancias tóxicas para el medio ambiente. Las herramientas genómicas y de metagenómica han permitido una mejor comprensión de cómo la agricultura intensiva tiene efectos negativos en la diversidad y función del microbioma de las plantas, y, a su vez, cómo el manejo de las comunidades microbianas puede mitigar algunos efectos negativos de la modernización de los cultivos. En este trabajo, revisamos los roles benéficos de las bacterias asociadas a las plantas y las interacciones simbióticas entre el microbioma y diversos cultivos de importancia económica; también discutimos cómo este conocimiento puede proporcionar estrategias para lograr una producción agrícola más sustentable.

Microbioma del suelo, Sustentabilidad agrícola, Microorganismos funcionales

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Introduction

Modern agricultural production systems are focused on growing high-yielding plant varieties in monoculture systems, or sometimes, simple rotations. These require a large amount of toxic agrochemicals such as pesticides and fertilizers, and they use highly industrialized, intensive soil management. These practices are not sustainable since they cause soil eutrophication, ecosystems pollution, high water consumption, deforestation, greenhouse gas emissions and loss of biodiversity (Wagg *et al.*, 2019). Under this production systems, soil and water are exploited excessively. In second half of the XX century, this production model was considered ecologically adequate, but factors such as climate change and water scarcity have become more prominent.

Therefore, agricultural production has focused on developing more sustainable systems. (Baveye *et al.*, 2018). New production strategies have been implemented such as precision agriculture, that is controlled by sophisticated technologies such as IoT (Internet of Things), deep and machine Learning, AI, among others (Coulibaly *et al.*, 2022; Akhter *et al.*, 2022; Saranya *et al.*, 2023). These systems also incorporate genetically modified organisms (Woźniak-Gientka *et al.*, 2023; Tyczewska *et al.*, 2023; Mohammadi *et al.*, 2023) and development of new resistant hybrid varieties (Duarte-Aké *et al.*, 2023; Paudel *et al.*, 2023; Mourtala *et al.*, 2023; Zhang *et al.*, 2023). However, these methods need advanced technologies and sophisticated infrastructure, which are not accessible in many countries. Likewise, some countries have strict regulations on the use of GMOs.

A more accesible and sustainable alternative is the management of the soil microbiome. The soil microbiome represents 25% of the total biodiversity of the planet. The functioning of the ecosystem and soil productivity is highly dependent in the microbial communities since they control biogeochemical cycles, especially the carbon cycle. In recent decades, a large number of articles have been published demonstrating the beneficial effects of PGPB (Plant Growth Promoting Bacteria) on the health and development of plants, and in crop productivity, using various cultivation methods such as green houses, pots, or in open field.

It has been shown that PGPB facilitate the nutrient flow, increase the production of hormones, volatile or regulatory compounds in important crop plants such as Corn, (Jochum *et al.*, 2019; Bomfim *et al.*, 2020; Song *et al.*, 2023), Wheat, (Safdarian *et al.*, 2020; da Silva *et al.*, 2022; Almutairi *et al.*, 2023; Karimzad *et al.*, 2023), Rice, (Xiao *et al.*, 2020; Cavite *et al.*, 2021; Pan *et al.*, 2023), Sunflowers, (Furnkranz *et al.*, 2009; Rojas-Tapia *et al.*, 2012), Legumes (Chiappero *et al.*, 2019; de la Osa *et al.*, 2021; Sapre *et al.*, 2022) and Arabidopsis, (Chen *et al.*, 2022; do Amaral *et al.*, 2023). PGPB also facilitates the absorption capacity of toxic substances such as heavy metals, and mediate the resistance of crops to adverse abiotic factors such as high salinity in soils or drought, among others (Li *et al.*, 2017; Bhise *et al.*, 2019; Becze *et al.*, 2021; Tirry *et al.*, 2021; Chatterjee & Niinemets, 2022; Sapre *et al.*, 2022; Wu *et al.*, 2023; Yue *et al.*, 2023; Cardoso *et al.*, 2023).

Throughout history, agricultural production systems have been in constant adaptation (Anderson *et al.*, 2020); in present times, the main challenge is to maintain performance in food production but using more sustainable practices (Malhi *et al.*, 2021). In this sense, it is essential to incorporate technological advances but also to consider the contribution of the microbiome in agricultural production. This work reviews some of the most notable functions of the microbiome that can be used in more sustainable agricultural production systems.

Microbial diversity contributes functional structure in the soil

The formation of a functional structure involves several biological processes in which bacteria and fungi generate organic substances such as mucilage, hyphae, polysaccharides, proteins, lipids, etc. These compounds can interact with biotic factors such as carbonates, metal oxides and other components present in the soils, all of which stimulate the nutrients flow between soil and plants (Yang *et al.*, 2020).

In recent years, this interaction has been studied with growing interest in the rhizosphere and rhizoplane. This process depends on various factors such as the amount of hair roots, the physical structure of the surrounding soil and mucilage secreted by beneficial bacteria or by roots such as auxin (Xu *et al.*, 2021). As a result, more stable organo-mineral aggregates are generated.

This structure can be formed when conditions of moderate drought occurs, since it has not been observed in flooded soils. Likewise, this structure favors tolerance to drought and acidity of the plants, improves the accumulation of phosphorus, contains a higher nitrogen content than bulk soil.

Microbial diversity also benefits from this structure, since alpha diversity increases in the endosphere and it can improve the assembly of bacterial communities in crops such as rice (Xu *et al.*, 2021; Yudina *et al.*, 2023). These interactions are favored when exopolysaccharide-producing microorganisms are present such as *Bacillus* and *Azospirillum*.

These bacteria improve both soil aggregation and the water status of the leaves when plants grow in drought conditions because volatile organic compounds such as esters are released. Ethers, aldehydes, naphthyl derivatives, ketones, alkalis, and benzene derivatives facilitate interactions between microbes and induce the secretion of root exudates in rice, maize, and cotton (Aslam *et al.*, 2022).

Microbes improve nutrient flow from the soil to the plant

The flow of energy and nutrients in agroecosystems is crucial because it is directly related to environmental issues such as global warming, soil eutrophication, and the generation of pollutants (Bhattacharyya *et al.*, 2022). The soil microbiome mediates biogeochemical cycles that regulate these processes. For example, in the regulation of terrestrial carbon flow, some autotrophic bacteria along with plants can absorb atmospheric CO₂ (Mukhtar *et al.*, 2023).

In the soil, the contribution of CO₂ emissions is 9-fold higher than emissions from anthropogenic causes and is mainly due to the decomposition of organic matter and autotrophic respiration (Dutta & Dutta, 2016; Jansson *et al.*, 2020). On the other hand, some methanotrophic bacteria consume part of the CH₄ generated by the decomposition of organic matter, reducing the harmful effects of this gas on the environment, as this bacteria consume up to 60% of the CH₄ produced on the planet (Leng *et al.*, 2015; Dutta & Dutta, 2016).

Therefore, the balance between the generation of these greenhouse gases by the soil and the capacity of bacteria to assimilate them can be leveraged to mitigate the environmental impact caused by agricultural production.

In the nitrogen cycle, soil bacteria also play a prominent role since the amount of N₂O generated by the soil can be up to 65% of the total. For this, the processes of nitrification and denitrification are crucial for regulating this cycle. Nitrogen fixation is mainly carried out by diazotrophic bacteria and archaea (Kuypers *et al.*, 2018). Various studies have supplemented fertilizers and biofertilizers with bacteria in intensive corn and wheat crops, revealing differences in the expression of genes related to nitrogen fixation such as *nifH* (encoding nitrogenase reductase), *amoA* (encoding ammonia monooxygenase), *nirK* and *nirS* (encoding nitrite reductase), and *nosZ* (encoding nitrous oxide reductase) (Grzyb *et al.*, 2021).

This supplementation improves soil denitrification and enhances plant growth. Additionally, it increases the abundance of PGPB associated with the decomposition of organic matter, such as Chloroflexi and Bacteroidetes, reducing nitrogen losses in the soil by 54% (Chen *et al.*, 2019).

On the other hand, atmospheric ammonia (NH₃) emissions related to the use of agrochemicals can be significantly decreased (by 44%) when using organic fertilizers. If these fertilizers are inoculated with *B. subtilis*, the reduction can reach up to 71%. This reduction is mainly addressed by considering the composition of the soil microbiota, where some genera are associated with processes such as ammonization, ammoxidation, and nitrosation (Di Benedetto *et al.*, 2017; Sun *et al.*, 2020). Regarding bacterial communities, differences were also found in relation to the type of fertilizer used, with a higher richness and evenness index for organic fertilizer with and without inoculation compared to compound fertilizer. Importantly, some plant growth-related bacterial genera such as *Bacillus*, *Nitrospira*, and *Rhodoplanes* were enriched when using organic fertilizer inoculated with *B. subtilis* (Sun *et al.*, 2020).

Microbes contribute to plant growth

Plant growth promoting bacteria (PGPB) is a very important group in the soil microbiome. Plants can recruit different phyla of bacteria from the soil, such as *Actinobacteria*, *Bacteroidetes*, *Firmicutes*, and *Proteobacteria*, belonging to various genera like *Achromobacter*, *Arthrobacter*, *Azospirillum*, *Azotobacter*, *Bacillus*, *Burkholderia*, *Exiguobacterium*, *Flavobacterium*, *Gluconacetobacter*, *Herbaspirillum*, *Methylobacterium*, *Paenibacillus*, *Pseudomonas*, *Rhizobium*, *Serratia*, and *Staphylococcus*, as well as fungi like *Trichoderma*, *Laccaria*, and *Piriformospora* that promote plant growth (Kour *et al.*, 2019). These interactions are facilitated by root exudates such as sugars, organic acids, amino acids, phenolic compounds, saponins, among other substances. In turn, bacteria can regulate and stimulate plant growth by producing phytohormones such as auxins, gibberellins, abscisic acid, ethylene, cytokinins, and also participate in nutrient exchange with the soil.

Hence these interactions modulate the plant response to stress induced by nutrient limitation, drought, flooding, extreme temperatures, high soil salinity, and contamination (Zuluaga *et al.*, 2021; Chai *et al.*, 2022). For example, in the wheat domestication process, these metabolites promote plant biodiversity, improve survival, provide protection against pathogens, and enhance the complexity of soil bacterial consortia (Yue *et al.*, 2023).

These benefits are also observed in fungi such as *Piriformospora indica*, which promotes growth and stress resistance to drought in corn. There is a significant increase in the expression of genes related to 17 metabolic processes, including signal perception, stress response, redox regulation, transport, and distribution of proteins in different cellular organelles. Processes related to the production of phytohormones such as abscisic acid, cytokinins, ethylene, gibberellins, jasmonic acid, and brassinosteroids are particularly noteworthy. These hormones play crucial roles in the response to drought in different plant species (Zhang *et al.*, 2018).

Inoculations with strains of the *Bacillus* genus also have a positive effect on various crops such as *Triticum aestivum* L., *Bromopsis inermis* L., *Pisum sativum* L., and *Zea mays* L., *Arabidopsis*, and soybean crops, showed increased plant resistance to drought, stimulation in growth, reduction of oxidative stress, improvement in the quantity of fresh shoots and roots, chlorophyll content in leaves, increased production of biologically active metabolites, and enhanced response to auxin (Khan *et al.*, 2020; García-Cárdenas *et al.*, 2023; Kuramshina & Khairullin, 2023).

Microbes mediate control of pests and pathogens

Microbes can stimulate defense mechanisms in plants by competing with other microorganisms for space or nutrients, and also inducing systemic resistance in plants through the production of antibiotics, lytic enzymes, or volatile compounds. These mechanisms are primarily regulated by the production of phytohormones, which are generated by the stimulation of secondary metabolites produced by microorganisms in the soil (Rolfe *et al.*, 2019).

From a genetic perspective, in microbial communities, some secondary metabolites exuded in the roots of crops modulate the composition of bacterial and fungal communities associated with the rhizosphere, promoting plant growth, defense, and increased resistance to plant pathogens such as bacteria, viruses, protozoa, insects, and herbivores (Hu *et al.*, 2018; Vannier *et al.*, 2019). These effects are significant because plants can alter the composition of soil bacteria by secreting bioactive molecules into the rhizosphere, such as sugars, amino acids, carboxylic acids, as well as various secondary metabolites.

These molecules have diverse effects on the plant, serving as signaling molecules, attractants, stimulants, inhibitors, or repellents. Consequently, the accumulation of pathogens in the soil can suppress plant growth, while the accumulation of beneficial microbes, such as nitrogen-fixing bacteria or mycorrhizal fungi, can enhance plant development (Hu *et al.*, 2018).

One of these molecules is benzoxazinoids, which trigger changes in the root-associated microbiome structure, leading to an increase in jasmonic acid and salicylic acid signaling pathways in the leaves. This, in turn, activates jasmonic acid-dependent defenses that suppress the growth of pathogens in plants (Yuan *et al.*, 2019). Therefore, it is likely that microbes and their metabolites are transmitted and influence the beneficial bacterial assembly for the next plant generation (Hu *et al.*, 2018; Yuan *et al.*, 2019).

Microbes aid in pollutant degradation

Plants can recruit microorganisms in the root system for the degradation of toxic contaminants such as chemicals, pharmaceuticals, heavy metals, and nanoparticles that are introduced into the soil through pesticides, organic fertilizers, contaminated irrigation water, and microplastics (Rolli *et al.*, 2021). Many of these phytoremediation processes actually take place in the rhizosphere, where the plant creates a microhabitat in the surrounding areas of the roots. In this microhabitat, oxygen, metabolites, and exudates are produced, facilitating the degradation of derivatives of aromatic compounds, polycyclic aromatics, long-chain hydrocarbons, and microplastics (Simmer & Schnoor, 2022).

Regarding soils contaminated with heavy metals, it was observed that *Bacillus cereus* strains enhance the growth capacity and phytoextraction of heavy metals by *Brassica nigra* (Aktar *et al.*, 2021). On the other hand, Rizvi *et al.* (2019) analyzed wheat varieties contaminated with Ni (100 $\mu\text{mol mL}^{-1}$) and Pb (200 $\mu\text{mol mL}^{-1}$) grown in a culture media. These metals induced structural alterations in roots and leaves, along with a decrease in the amount of proline and malondialdehyde. However, when the seeds were inoculated with *B. subtilis*, the activity of antioxidant enzymes such as catalase, superoxide dismutase, and glutathione S reductase increased.

This caused a lower accumulation of metals in plant tissues (roots, seeds, and shoots), allowing the plants to better survive even in soils contaminated with heavy metals.

In a different study, the growth of corn in soils contaminated with multiple heavy metals such as Pb, Ni, Zn, Cu, and Cd was analyzed, under abiotic stress caused by increasing the crop temperature to 45 °C, and the effect of growth-promoting bacteria on corn development was examined. For this purpose, a strain of *B. cereus* was isolated and identified from soils contaminated with heavy metals, and corn seeds were inoculated. The results showed a significant increase in biomass, chlorophyll, carotenoids, and protein content, as well as enhanced antioxidant enzyme activity, compared to the non-inoculated controls (Bruno *et al.*, 2021).

Conclusions

Sustainable progress of agricultural practices needs to take into account the role that microorganisms play in crop adaptation to various adverse environmental factors, enhancing crop resistance to pests and diseases, increasing plantation biodiversity, and their importance in nutrient flow between soil and crops. Parallel to technological and scientific advances in the development of precision agricultural production processes, it is evident that agricultural production is still highly dependent on natural factors. This is reflected in a significant increase in the number of organic farmers in recent years.

The benefits of some Plant Growth-Promoting Bacteria (PGPB) are still being studied and are not fully understood, and genomic and metagenomic tools are being explored to understand the function and assembly of synthetic communities more deeply to enhance these benefits. This calls for the integration of precision agricultural systems with the beneficial effects of bacteria, which can enhance the mitigation of adverse environmental impacts related to agricultural production, making it sustainable while maintaining competitive yields.

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