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Mini Review

# Ecosystem functions of microbial consortia in sustainable agriculture

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## Abstract

Knowledge of the agricultural soil microbiota, of the microbial consortia that comprise it, and the promotion of agricultural practices that maintain and encourage them, is a promising way to improve soil quality for sustainable agriculture and to provide food security. Although numerous studies have demonstrated the positive effects of beneficial soil microorganisms on crop yields and quality, the use of microbial consortia in agriculture remains low. Microbial consortia have more properties than an individual microbial inoculum, due to the synergy of the microorganisms that make them up. This review describes the main characteristics, ecosystem functions, crop benefits and biotechnological applications of microbial consortia composed of arbuscular mycorrhizal fungi, plant growth promoting bacteria and actinobacteria, to promote the restoration of agricultural soils and, consequently, the quality and health of agricultural crops. The aim is to provide knowledge that will contribute to the development of sustainable and sufficiently productive agriculture, which will adapt in a good way to the pace of the growing human population and to climate change.

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**Key words:** *Microbial consortia, Arbuscular mycorrhizas, Plant growth-promoting rhizobacteria, actinobacteria, Ecosystem functions, Agriculture, Sustainability, Resilience, Multifunctionality, Soil microorganism, Soil biodiversity.*

**Abbreviations:** greenhouse gases (GHG), arbuscular mycorrhizal fungi (AMF), plant growth promoting bacteria (PGPR), gibberellins (gibberellic acid, GA3), auxins (indolacetic acid, AIA), abscisic acid (ABA), enzyme 1-aminocyclopropane 1-carboxylate deaminase (ACC).

## Introduction

Currently, conventional agriculture is presented as a major threat to soil biodiversity [1]. The excessive use of agrochemicals, the excessive tillage, the decrease of organic matter, the soil pollution among others have generated the alteration of the microbial functional diversity and the worldwide soil degradation , threatening the food chain and safety [2-4]. Nevertheless, there is still a great potential in soils which requires to adopt strategies that protect them from harmful agricultural practices [5].

Although there are multiple strategies for addressing sustainable agriculture and feeding people by reducing environmental impacts, it has been widely reported that promoting agricultural practices that increase biodiversity and the composition of soil microorganisms, such as organic or agro-ecological agriculture, represents an important alternative for obtaining good quality food and improvements in environmental, economic and social aspects [6-8].

Increased microbial biodiversity stabilizes the functioning of agro-ecosystems and increases the resilience to climate change [9]. Since ancient times microorganisms have been present in association with plants and animals giving them multiple benefits in a dynamic equilibrium, which has been attributed to multiple communication systems. Among them the chemical messages at rhizosphere level [10-12]. These communication systems are fundamental in the agricultural ecosystem, since they regulate all biogeochemical processes in the soil maintaining its fertility and health. These processes include the decomposition, nutrient cycling, and maintenance of organic

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matter, regulation of pathogens, degradation of contaminants, reduction of greenhouse gases (GHG), which directly affect both crop productivity and the environmental quality [13-15].

In order to benefit from the enormous potential of the soil microbiome, it is necessary to know the distribution and composition of microbial communities in different territories and on different time scales, such as seasonal variations [16]. This information also allows predicting the changes that can be generated in a global climate change scenario. In addition, not knowing the effects of the loss of diversity in specific places and times, it can generate a great impact on ecosystem sustainability and therefore on human well-being [17-19]. The greater the diversity of microorganisms in the soil, the greater the functionality of that soil [20, 21], which is turn means food with higher nutraceutical quality proportional to the soil nutrition and health.

Recently, increasing attention has been given to crops rich in nutrients, minerals, antioxidants, or other metabolites, as they represent higher food quality and reduce the risk of chronic diseases [22-24]. In this context, new crops practices have emerged that allow obtained high yields of biomass with high concentration of beneficial metabolites. The development of biofertilizers made up with beneficial microbial species has emerged [25], as well as the development of microbial consortia of different soil microorganisms [26].

Thus, it is necessary to understand the processes that determine the composition and abundance of soil microorganism communities in order to obtain their multiple benefits in the agricultural systems and indirectly in human health. This review aims at describing the main characteristics, ecosystem functions, crop benefits and biotechnological applications of microbial consortia composed of arbuscular mycorrhizal fungi, plant growth promoting bacteria and actinobacteria to promote sustainable agriculture and thus the quality and health of agricultural crops.

## Discussion

1. Arbuscular mycorrhizal fungi (AMF)

At the ecological level, mycorrhizal network theory allows the analysis of interactions between plant fungal soil partners as complex multi-species of underground networks [27]. Among the microorganisms present in the soil, arbuscular mycorrhizal fungi (AMF) are fundamental to soil ecology and agriculture [28]. They form a symbiotic composite association with 93% of terrestrial plant families, including multiple agricultural crops. They are the oldest known and most prevalent associations in nature [29,30].

AMF belong to the subphylum *Glomeromycotina* containing *Archaeosporales, Diversisporales, Glomerales*, and *Paraglomerales* [31], and their symbiosis with plants consists of receiving carbohydrates and lipids from the plant and having specific structures such as arbuscula and vesicles that allow the exchange of nutrients with plants at the level of the root bark [32,33]. These have several functions and benefits for plants that are mainly related to increased nutrient uptake, promoting phosphorus, iron and zinc uptake by crops through direct plant root pathways [34,35], positively affecting crop growth, yield and reproductive success, thus reducing fertilizer needs in agricultural systems [36,37].

The establishment of mycorrhizae alters the biological and physicochemical properties of the rhizosphere, leading to the formation of the so-called mycorrhizosphere, where they improve the soil structure, the relationship of water in the soil [38], and have an important effect on the induction of systemic resistance to biotic stresses [39].

Conventional agriculture, with its intensive practices, generates a decrease in the diversity of arbuscular mycorrhizae, which means that fewer species of slow colonization potential and rapid sporulation prevail. This leads to a considerable decline in ecosystem functions of arbuscular mycorrhizae [40, 41]. All the benefits that arbuscular mycorrhizae provide to crops can be used in sustainable agriculture to reduce environmental impact and obtain food of higher nutritional quality that benefits humans [42,43]. Within these alternatives, organic agriculture is the most widely reported [44-48].

AMF can be an excellent alternative as biofertilizer in agriculture, as shown by multiple laboratory and field studies [25,49]. In highly degraded soils, an external inoculum could be beneficial, taking into account some considerations such as the type of species and the characteristics of the agricultural system[50,51], considering that to overcome situations of biotic or abiotic stress a mixture of species is better than a single type of mycorrhiza [52], but in many agricultural systems native species communities could be promoted that are equally effective without including the ecological risks of an aggressive strain that could displace naturally beneficial species [53].

## 2. Plant growth promoting bacteria (PGPR)

Plant growth promoting rhizobacteria, or PGPR, are a diverse group of bacteria that colonize the plant rhizosphere showing a positive impact on the environment. The most widely reported bacterial species are of the genera *Bacillus, Pseudomonas, Lactobacillus, Acetobacter, Azospirillum, Paenibacillus, Serratia, Burkholderia, Herbaspirillum and Rhodococcus* [54]. The interactions between the plant and PGPR are synergistic leading to relevant benefits for both the plant crops and the plant microbiome.

On the one hand, the plant promotes PGPR establishment through the production of storage substances such as carbohydrates, organic acids and minerals, as well as the production of root exudates, which are used by PGPR for nutrition [55, 56] or as a tool to establish symbiotic interactions such as the mycorrhizal or dinitrogen-fixing nodulation [10]. The establishment can be endophytic, leading to the colonization of the inner plant structures, including seeds, or to the colonization of the plant intercellular spaces; the establishment can involve also the free living bacterial cells in the rhizosphere [57, 58]. Once established, PGPR show a benefit for plant growth (in terms of yields per hectare of land), crop quality traits, and plant health through direct or indirect mechanisms regulated for biotic and abiotic stress [54, 58]. Direct mechanisms promote plant growth by releasing substances stimulating aerial biomass production, root development, and stem elongation. This is achieved through the release or solubilization of phosphates and other nutrients such as potassium (K), zinc (Zn) and silicon (Si), the uptake of biologically fixed di-nitrogen ($N_2$), the chelation of iron (Fe) and other micronutrients such as Zn, B, Ca, Mg, Cu [54, 59, 60], and the increase of available lithospheric oxygen [61]. In addition, PGPR usually synthesize phytohormones such as gibberellins (gibberellic acid, GA3), auxins (indolacetic acid, AIA), cytokinins, ethylene, and abscisic acid (ABA) [54,60], which model plant growth and plant cell division. These substances can induce the production of the enzyme 1-aminocyclopropane 1-carboxylate deaminase (ACC), which reduces the level of ethylene in the roots of the crops, thus improving the root length and density [62].

Indirect mechanisms of plant health induction involve modification of the rhizosphere environment and its ecology, inducing systemic resistance and stimulating the innate resilience of the plant (basal genetic resistance) [63]. Among them, PGPR release substances such as siderophores, antibiotics, pigments, organic acids (malic, acetic, citric, oxalic, lactic, formic, gluconic and 2-keto-gluconic), water-soluble vitamins (niacin, thiamine and biotin molecules or antioxidants) and volatile organic compounds (monoterpene alcohols) [64]. These substances activate the protection mechanisms of plants against herbivores, insects and pathogenic microorganisms and promote the synthesis of physical and chemical barriers against abiotic stress. In turn, they allow PGPR to be more competitive in niche colonization since they can interfere with the *quorum* detection signal and inhibit the formation of biofilms by pathogenic bacteria [65].

PGPR also promote the synthesis of hydrolytic enzymes (such as glucanases and chitinases) that produce abnormal morphological changes in the fungal mycelium, such as the fracture and lysis of the spikes [66], preventing the development of pathogenic fungi. *Pseudomonas frederiksbergensi*, *Bacillus spp*. and *Planomicrobium sp.* have been shown to be effective in improving tolerance to cold and saline stress, which has been linked *e.g*. to the activity of antioxidant molecules [57, 67-71]; the production of volatile terpenoids by *Pseudomonas spp.* and *Bacillus spp.* have increased the protective barriers against soil-borne pathogens in *Mentha piperita* and *V. vinifera* plants [64, 72].

The application of PGPR over time led to relevant benefits in agroforestry management. In this context, species of Azospirillum, Pseudomonas and Paenibacillus  have been used for their beneficial effects on the growth and yield of different cereal crops, such as wheat and rice [56, 73]. Specifically, *Pseudomonas sp.,* and *Paenibacillus sp*. have shown a high capacity to make $Fe^{3+}$ available to plants [73]. *Bacillus sp.* and *Pseudomonas sp.* strains have proven to be excellent biofertilizer inoculants, having direct and indirect effects on insect pests associated with agricultural crops and also for the biological control of nematodes [74, 75]; the bacterium *Pseudomonas frederiksbergensis* OS261 has been used as a biostimulant under water and salt stress conditions [70].

In forest nurseries, strains of *Bacillus, Pseudomonas* and *Azospirillum* have allowed an increase of germination and stimulation in the rooting of cuttings, biocontrol of bacterial wilt and the survival of plants after transplanting, which has been associated with better root development and consequently to an increase in the uptake of nutrients [60].

Another application for legume crops is the production of root nodules with high capacity to fix nitrogen in soybean (*Glycine max L.*). Species of the *Pantoea, Serratia, Acinetobacter, Bacillus, Agrobacterium* and *Burkholderia, Pseudomonas* and *Ochrobactrum* have been used [66], some of them showing ancillary inhibitory activity against pathogens. However, species such as *B. cepacia* may also be involved in infection in humans and their use in agriculture is restricted [76]. Therefore, it is important to have a thorough understanding of the safety traits for human health of these microorganisms not having a long history of use before their field application. In the European Union, a recent legislative provision, i.e. the so-called Fertilizer Act [77] covers these borderline aspects and makes a clear distinction of what can marketed as a biofertilizer or as a plant protection product. The placement on the market of latter category falls under another regulation of the European Parliament and Council [78].

## 3. Actinobacteria

Actinobacteria (formerly known as actinomycetes) are the largest group of prokaryotes and comprise six classes, six orders and fourteen suborders within which there are both cultivable and non-cultivable species. Bacterial that are present in terrestrial environments, can be easily recognized as they generate the characteristic earthy odor that produces an organic compound known as geosmin ($C_{12}H_{22}O$).

Actinobacteria can colonize plant roots endophytically or adhere to epidermal or subcortical root cells. In this context, endophytic bacteria have been described to enter the host plant through root hairs, stomas, wounds, and sprouting hydathodes [79], while in free-living bacteria, structures such as flagella, fimbria, exopolysaccharides, and lipopolysaccharides may facilitate the bacterial attachment to the plant roots [79].

Actinobacteria are classified as Gram-positive, can be either aerobic or anaerobic, and exhibit various morphological, physiological, and pigmentation traits characteristic of actinobacterial taxa [80-

83]. The pigments are commonly known as melanoid polymers and are similar to humic substances present in soil [82, 84]. These pigments are not necessary for the growth of bacteria but have a significant contribution to improved survival.

In addition to morphological identification, the identification of actinobacteria has now been facilitated by the use of molecular tools. The genomic organization of actinobacteria has reported more than 20 sequenced species, which is still a small number. In general, they differ from other bacteria by having a large genome ranging from 1 to 12 Mb in size that is characterized by a high content of G + C, even higher than 70% and contain large plasmids [82]. Specifically, it is possible to use 16S rRNA sequence analysis and other preserved sequences to identify some actinobacterial genera [81, 85, 86]. The most referenced actinobacterial genera are *Microbispora, Microbacterium, Micrococcus, Micromonospora, Nocardia, Rhodococcus, Streptomyces, Streptosporangium, Streptoverticillium, Arthrobacter, Actinomyces, Corynebacterium* and *Frankia*. These have been studied principally due to their great capacity to generate diverse bio-active molecules [84].

Actinobacteria have a wide economic and scientific interest, mainly focused on the study of their application in human health and agriculture [87]. On the one hand, these bacteria are able to synthesize a wide and diverse range of secondary metabolites (more than 10,000 compounds reported) with antimicrobial, antitumor and anti-inflammatory activity [84, 88], and to promote plant growth under abiotic and biotic stress conditions, due to the synthesis of plant growth regulators (phytohormones) and organic acids [80]. In addition, Actinobacteria can fix atmospheric nitrogen, solubilize minerals such as phosphorus [89], produce siderophores [80] to overcome limited nitrogen, iron, and phosphorus conditions, respectively [79], and some species can produce antibiotics *in situ* contributing to maintain the plant health.

Actinobacteria also have the ability to synthesis volatile organic compounds that diffuse into the air and soil through the pores acting as chemical agents of communication between species, suppression of plant pathogens, formation of biofilms, indicators during differentiation, formation of mycelium and sporulation and modification of pH in the environment [90]. In addition, these can synthesize antimicrobial signaling peptides and quorum sensing regulators, which protect the organism from damage and facilitate interactions with the environment [87].

These bacteria play an important role in the decomposition of plant biomass, playing a vital role in ecologies and processes such as the carbon cycle [91]. Actinobacteria have a large reservoir of lytic enzymes such as proteases, exo- and endo-glucanases, amylases, lipases, pectinases and xylanases that degrade the components of the plant cell wall facilitating the entry of the cells into the root [79, 80, 87, 92]. They also synthesize lytic enzymes such as chitinases, dextranases, cutinases, peroxidases, laccases, which degrade the cell wall of pathogens and are responsible for their inhibition and growth [93].

More importantly, these bacteria have the capacity to persist in the soil at high cell density with a high rate of viability, which has led to the study of different applications in agriculture. They act either by suppressing the growth of phytopathogens and promoting growth of important crop plants, i.e. corn, tomato and banana [94] or the ability to fix nitrogen in non-leguminous plants [80]. Nitrogen-fixing bacteria include members of the Frankia family, *Corynebacterium* sp., and *Pseudonocardia dioxanivorans.* Some of them are used as alternative nitrogen fertilizers [80]. Commercial products based on actinobacteria have been generated, mainly from species of the genus *Streptomyces* [95] that protect plants against foliar and soil-borne diseases. These organisms can be used as insecticides, herbicides, antifungals and biocontrol agents, as well as plant growth promoters [82].

## 4. The microbial consortia

Soil microbes are key ecosystem services provider and drive multifunctional processes, encompassing the interaction of different microbial communities, and the interaction of these with the other soil biota components, i.e. the micro- and mesofauna. Within this complex interconnected network, microorganisms are responsible for maintaining the energy fluxes supporting the entire ecosystem, through the recirculation of available resources [96]. However other organisms form ecological groups in the same environment and share a high multifunctionality in the ecosystem [16, 97]. Soil microfauna is fundamental to the functionality of the ecosystem and any changes in these key organisms can produce changes at the vegetational, biome and microbial level [20].

The most relevant groups of microorganisms in the soil are arbuscular mycorrhizal fungi and plant growth promoting bacteria. These microorganisms together increase nitrogen fixation and uptake, solubilize phosphorus, convert ammonium (which can be chemically bound to clay particles) into the soluble, easily assimilable nitrate, protect from other pathogenic microorganisms, and even remediate contaminated soils [98, 99].

Arbuscular mycorrhizae, besides being related to plants, are also related to the PGPR in the rhizosphere and to the endobacteria, affecting their activity and generating a synergy in functionality [100,102]. The interactions between AM fungi and soil bacteria influence the expression of fungal genes. The interactions include the adhesion of bacteria to the surface of fungal spores, conidia and hyphae, the injection of molecules into the fungal spores, the degradation of the fungal cell wall and the production of volatile substances [102].

The consortia (fungi and bacteria) have multiple applications to sustainable agriculture that have been reported to allow greater nutrient uptake and biocontrol of pathogens, depending on agricultural practices that allow their maintenance [103]. Likewise, different communities of soil fungi have been detected to affect the soil formation or stabilization at the macro- and microaggregate scale through different mechanisms of physical, biochemical, and biological processes [104,105].

The biotechnological applications of consortia such as the application of biofertilizers or biostimulants is justified in agricultural soils of the Mediterranean climate that have a percentage of less than 3.5% of organic matter, where microorganisms can no longer perform their functions [106]. Considering that in these cases the soil microbiota must be restored with fundamental taxonomic groups or initiators such as arbuscular mycorrhizal fungi [107], the application of microbial consortia is the preferred approach. These inoculants will have less ecological impact on the ecosystem and therefore on the environment and health [7]. Although further studies at micro- and meso-cosm level, followed by field research, will allow to assess the ability of selected AMF and bacteria to interact with native microorganisms and maintain their beneficial activities[108], the agricultural use of microbial consortia containing bacteria, fungi and AMF is in its exponential phase [109], based on a range of evidences including wheat [110, 111], Mediterranean vegetables [112], lettuce [113], vegetables [114] , basil [115], tomato [116], and maize [117].

Despite the demonstrated benefits produced by soil microorganisms, there is ample space for gaining further insight, especially on arbuscular mycorrhizal fungi, which are crucial for many ecosystem services, such as nutrient cycling and food production. An example is the case of Latin America [118]. In Latin America [119] and Africa there is a need to focus on soil health and biodiversity among farmers, major agribusinesses, and policy makers, complementing the current productivity paradigm with sustainability and conservation objectives. Therefore, it is vital to describe the development of rhizosphere microbiome in all relevant crops, as microbial communities are deeply affected by agricultural management [120,121]. The databases of association between higher plants and mycorrhizal fungi are critical for addressing biogeographic and evolutionary issues [17]. In addition, soil biota is a key factor for the application of appropriate microbial inoculants in the field, but the genotype/genotype interactions between the microbial strain(s) and the crop cultivar(s), *e.g.* maize, often requires prior screening to obtain the desired results [119]. And this is due to the lack of knowledge or neglect of the plant microbiome when selecting the germoplasm for higher productivity [1].

It has been observed that microbial communities are highly sensitive to changes in environmental properties, for example, the geographical location where the type of soil and its pH play a fundamental role in the distribution of species In the same way, the climatic conditions and the type of vegetation determine in a dynamic interrelationship the biodiversity of the microbial communities in the different ecosystems[123, 124].

Likewise, the specific inoculants of a single group of commercially produced microorganisms represent a small genetic group of fungi and/or bacteria selected to be both generalists and aggressive colonizers [7]. These traits have the potential to affect local communities of microorganisms, which may not be resistant to the introduction of other exogenous species [125]. The role of potentially invasive species in soil ecosystems has received little attention, despite knowledge of the role of soil biodiversity in ecosystem processes.

Currently, the knowledge of the identity of the species that make up a microbial community can be achieved through metagenomics. In order to be able to associate the functionality of certain taxa with the characteristics of crop productivity and resilience it is necessary to carry on studies including the isolation and cultivation of the species [26]. In Latin America and Africa there are still many knowledge gaps, where microbial communities are not known or are unidentified taxa [39,119]. This represents a problem when predicting changes at the ecosystem level that may be generated in the future, which is relevant in decision making when designing public policies [17]. To protect the functionalities of terrestrial ecosystems in a productive eco-compatible modern agriculture, it is necessary to include soil microbiota and soil biota in environmental protection and impact assessment policies [16, 20].

Climate change with its consequent events such as droughts, temperature increase and $CO_2$ increase, generates environmental changes that affect the microbial community and therefore the whole ecosystem. In agriculture, this generates a great challenge since there is a great impact on the productivity and resilience of agricultural systems [6, 7]. Currently, different strategies are being developed to abort this issue, one of them being the Climatic Smart Agriculture, which seeks to develop a sustainable food system, to increase crop productivity and quality, to reduce the impacts of climate change, through the adaptation and building of crop resilience, conserving and increasing carbon stocks in soils and reducing GHGs [21].

Some examples for smart agriculture are the reported associations of the bacteria *Rahnella aquatilis* which improves organic phosphorus solubilization when associated with the mycorrhizal fungus *Rhizophagus irregularis*. The rhizospheric yeast fungi *Cryptococcus flavus* or *Candida railenensis* and the arbuscular mycorrhizal fungus *Rhizophagus irregularis* whose association promotes root growth in corn plants [126]; the *Brettanomyces naardensis* yeast with fungi that reduce the incidence of the pathogen *Macrophomina phaseolina* in sunflower plants; in addition, this association significantly improves growth parameters such as plant height, dry weight and number of leaves [127]. It has also been reported that consortia between filamentous fungi and PGPR stimulate the growth and yield of substances produced by plants as essential oils [128].

## Conclusions

The biotechnological application of microorganisms either through the selection and inoculation of specific microbial strains or just by promoting the activity of naturally occurring microbes, holds a great potential for sustainable agriculture, as these innovative agronomic practices have the capacity to replace conventional agricultural practices. Beneficial microbes are multifunctional, with effects ranging from protection from pathogens to reduction of drought, stimulation of nutrient uptake, and can reproduce and be self-sufficient. In addition, microbe management can promote systems that are resilient to climate change.

When thinking about the formulation of microbial consortia we should consider functional taxa of various species that are effective and compatible with other soil organisms where they will be applied according to their geographical and climatic conditions. It is expected that future research related to sustainable agriculture will focus on the importance of soil (micro)biota, focusing on both the morphology of cultivable microorganisms and the metagenomics of all species found in the soil, in order to formulate distribution maps that will allow us to make informed decisions on the effect of agricultural practices on (micro)biomes.

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## Conflict of Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this short review.

## References

1. Porter SS, Sachs JL (2020) Agriculture and the Disruption of Plant–Microbial Symbiosis. Trends in Ecology & Evolution 35(5): 426-439. https://doi.org/10.1016/j.tree.2020.01.006
2. Hartman K, van der Heijden MG, Wittwer RA, Banerjee S, Walser JC, et al. (2018) Cropping practices manipulate abundance patterns of root and soil microbiome members paving the way to smart farming. Microbiome 6: 1–14. https://doi.org/10.1186/s40168-017-0389-9
3. Springmann M, Clark M, Mason-D'Croz D, Wiebe K, Bodirsky BL, et al. (2018) Options for keeping the food system within environmental limits. Nature 562: 519–525. https://doi.org/10.1038/s41586-018-0594-0
4. Stavi I, Lal R (2015) Achieving Zero Net Land Degradation: Challenges and opportunities. Journal of Arid Environments 112: 44–51. https://doi.org/10.1016/j.jaridenv.2014.01.016
5. Sá JC, Lal R, Cerri CC, Lorenz K, Hungria M, et al. (2017) Low-carbon agriculture in South America to mitigate global climate change and advance food security. Environment International 98: 102–112. https://doi.org/10.1016/j.envint.2016.10.020
6. Altieri MA (2018) Agroecology the science of sustainable agriculture. (2nd Edition), CRC Press, Boca Raton, Florida, USA, pp. 448. https://doi.org/10.1201/9780429495465
7. Bender SF, Wagg C, van der Heijden MG (2016) An underground revolution: Biodiversity and soil ecological engineering for agricultural sustainability. Trends in Ecology and Evolution 31: 440–452. https://doi.org/10.1016/j.tree.2016.02.016
8. Eyhorn F, Muller A, Reganold JP, Frison E, Herren HR, et al. (2019) Sustainability in global agriculture driven by organic farming. Nature Sustainability 2: 253–255. https://doi.org/10.1038/s41893-019-0266-6
9. Isbell F, Craven D, Connolly J, Loreau M, Schmid B, et al. (2015) Biodiversity increases the resistance of ecosystem productivity to climate extremes. Nature 526: 574–577. https://doi.org/10.1038/nature15374
10. Oldroyd GE (2013) Speak, friend, and enter: Signalling systems that promote beneficial symbiotic associations in plants. Nature Reviews Microbiology 11: 252–263. https://doi.org/10.1038/nrmicro2990

11. Bassler BL, Losick R (2006) Bacterially Speaking. Cell 125(2): 237-246. https://doi.org/10.1016/j.cell.2006.04.001
12. Brameyer S, Bode H, Heermann R (2015) Languages and dialects: bacterial communication beyond homoserine lactones. Trends in Microbiology 23(9): 521-523. https://doi.org/10.1016/j.tim.2015.07.002
13. Bardgett RD, Van Der Putten WH (2014) Belowground biodiversity and ecosystem functioning. Nature 515: 505–511. https://doi.org/10.1038/nature13855
14. Mendes R, Garbeva P, Raaijmakers JM (2013) The rhizosphere microbiome: Significance of plant beneficial, plant pathogenic, and human pathogenic microorganisms. FEMS Microbiology Reviews 37: 634–663. https://doi.org/10.1111/1574-6976.12028
15. Philippot L, Raaijmakers JM, Lemanceau P, Van Der Putten WH (2013) Going back to the roots: The microbial ecology of the rhizosphere. Nature Reviews Microbiology 11: 789–799. https://doi.org/10.1038/nrmicro3109
16. Delgado-Baquerizo M, Maestre FT, Reich PB, Jeffries TC, Gaitan JJ, et al. (2016) Microbial diversity drives multifunctionality in terrestrial ecosystems. Nature Communications 7:1–8. https://doi.org/10.1038/ncomms10541
17. Chu H, Gao GF, Ma Y, Fan K, Delgado-Baquerizo M (2020) Soil microbial biogeography in a changing world: Recent advances and future perspectives. American Society for Microbiology 5:1–12. https://doi.org/10.1128/mSystems.00803-19
18. Kuzyakov Y, Blagodatskaya E (2015) Microbial hotspots and hot moments in soil: Concept and review. Soil Biology and Biochemistry 83:184–199. https://doi.org/10.1016/j.soilbio.2015.01.025
19. Wagg C, Bender SF, Widmer F, Van Der Heijden, MG (2014) Soil biodiversity and soil community composition determine ecosystem multifunctionality. Proceedings of the National Academy of Sciences of the United States of America 111: 5266–5270. https://doi.org/10.1073/pnas.1320054111

20. Delgado-Baquerizo M, Reich PB, Trivedi C, Eldridge DJ, Abades S, et al. (2020) Multiple elements of soil biodiversity drive ecosystem functions across biomes. Nature Ecology and Evolution 4: 210–220. https://doi.org/10.1038/s41559-019-1084-y
21. Das S, Ho A, Kim PJ (2019) Editorial: role of microbes in climate smart agriculture. Frontiers in Microbiology 10: 1–3. https://doi.org/10.3389/fmicb.2019.02756
22. Rillig MC, Lehmann A, Lehmann J, Camenzind T, Rauh C (2018) Soil biodiversity effects from field to fork. Trends in Plant Science 23: 17–24. https://doi.org/10.1016/j.tplants.2017.10.003
23. Ochoa-Hueso R (2017) Global change and the soil microbiome: A human-health perspective. Frontiers in Ecology and Evolution 5: 71. https://doi.org/10.3389/fevo.2017.00071
24. Wall DH, Nielsen UN, Six J (2015) Soil biodiversity and human health. Nature 528: 69–76. https://doi.org/10.1038/nature15744
25. Berruti A, Lumini E, Balestrini R, Bianciotto V (2016) Arbuscular mycorrhizal fungi as natural biofertilizers: Let’s benefit from past successes. Frontiers in Microbiology 6:1–13. https://doi.org/10.3389/fmicb.2015.01559
26. Kong Z, Hart M, Liu H (2018) Paving the way from the lab to the field: Using synthetic microbial consortia to produce high-quality crops. Frontiers in Plant Science 9: 1–5. https://doi.org/10.3389/fpls.2018.01467
27. van der Heijden MG, Martin FM, Selosse MA, Sanders IR (2015) Mycorrhizal ecology and evolution: the past, the present, and the future. New Phytologist 205:1406–1423. https://doi.org/10.1111/nph.13288
28. Thirkell TJ, Charters MD, Elliott AJ, Sait SM, Field KJ (2017) Are mycorrhizal fungi our sustainable saviours? Considerations for achieving food security. Journal of Ecology 105: 921–929. https://doi.org/10.1111/1365-2745.12788
29. Brundrett MC, Tedersoo L (2018) Evolutionary history of mycorrhizal symbioses and global host plant diversity. New Phytologist 220:1108–1115. https://doi.org/10.1111/nph.14976
30. Smith SE, Read DJ (2008) Mycorrhizal Symbiosis. (2nd Edition), Academic Press, Elsevier, London, UK, pp. 800. https://doi.org/10.1016/B978-0-12-370526-6.X5001-6

31. Spatafora JW, Chang Y, Benny GL, Lazarus K, Smith ME, et al. (2016) A phylum-level phylogenetic classification of *zygomycete* fungi based on genome-scale data. Mycologia 108: 1028–1046. https://doi.org/10.3852/16-042
32. Rich MK, Nouri E, Courty PE, Reinhardt D (2017) Diet of Arbuscular Mycorrhizal Fungi: Bread and Butter? Trends in Plant Science 22: 652–660. https://doi.org/10.1016/j.tplants.2017.05.008
33. Parniske M (2008) Arbuscular mycorrhiza: The mother of plant root endosymbioses. Nature Reviews Microbiology 6: 763–775. https://doi.org/10.1038/nrmicro1987
34. Smith SE, Jakobsen I, Grønlund M, Smith FA (2011) Roles of arbuscular mycorrhizas in plant phosphorus nutrition: Interactions between pathways of phosphorus uptake in arbuscular mycorrhizal roots have important implications for understanding and manipulating plant phosphorus acquisition. Plant Physiology 156: 1050–1057. https://doi.org/10.1104/pp.111.174581
35. Coccina A, Cavagnaro TR, Pellegrino E, Ercoli L, McLaughlin MJ, et al. (2019) The mycorrhizal pathway of zinc uptake contributes to zinc accumulation in barley and wheat grain. BMC Plant Biology 19: 133. https://doi.org/10.1186/s12870-019-1741-y
36. Azcón-Aguilar C, Barea J (2015) Nutrient cycling in the mycorrhizosphere. Journal of Soil Science and Plant Nutrition 25: 372–396. https://doi.org/10.4067/S0718-95162015005000035
37. Cavagnaro TR, Bender SF, Asghari HR, van der Heijden MG (2015) The role of arbuscular mycorrhizas in reducing soil nutrient loss. Trends in Plant Science 20: 283–290. https://doi.org/10.1016/j.tplants.2015.03.004
38. Augé RM, (2004) Arbuscular mycorrhizae and soil/plant water relations. Canadian Journal of Soil Science 84: 373–381. https://doi.org/10.4141/S04-002
39. Cameron DD, Neal AL, van Wees SC, Ton J (2013) Mycorrhiza-induced resistance: More than the sum of its parts? In Trends in Plant Science 18(10): 539–545. https://doi.org/10.1016/j.tplants.2013.06.004

40. Oehl F, Sieverding E, Ineichen K, Mäder P, Boller T, et al. (2003) Impact of land use intensity on the species diversity of arbuscular mycorrhizal fungi in agroecosystems of Central Europe. Applied and Environmental Microbiology 69: 2816–2824. https://doi.org/10.1128/AEM.69.5.2816-2824.2003
41. Oehl F, Sieverding E, Mäder P, Dubois D, Ineichen K, et al. (2004) Impact of long-term conventional and organic farming on the diversity of arbuscular mycorrhizal fungi. Oecologia 138: 574–583. https://doi.org/10.1007/s00442-003-1458-2
42. Turrini A, Avio L, Giovannetti M, Agnolucci M (2018) Functional complementarity of arbuscular mycorrhizal fungi and associated microbiota: the challenge of translational research. Frontiers in Plant Science 9:10–13. https://doi.org/10.3389/fpls.2018.01407
43. Gianinazzi S, Gollotte A, Binet MN, van Tuinen D, Redecker D, et al. (2010) Agroecology: the key role of arbuscular mycorrhizas in ecosystem services. Mycorrhiza 20: 519–530. https://doi.org/10.1007/s00572-010-0333-3
44. Silva-Flores P, Aguilar A, Diban M, Mujica M, (2019) Chapter 14 Mycorrhizas in the South American Mediterranean-type ecosystem: Chilean matorral. In: Pagano M., Lugo M. (eds) Mycorrhizal Fungi in South America (1st edition). Fungal Biology, Springer, Cham, Switzerland, pp. 374. https://doi.org/10.1007/978-3-030-15228-4_14
45. Säle V, Aguilera P, Laczko E, Mäder P, Berner A, et al. (2015) Impact of conservation tillage and organic farming on the diversity of arbuscular mycorrhizal fungi. Soil Biology and Biochemistry 84: 38–52. https://doi.org/10.1016/j.soilbio.2015.02.005
46. Bedini S, Avio L, Sbrana C, Turrini A, Migliorini P, et al. (2013) Mycorrhizal activity and diversity in a long-term organic Mediterranean agroecosystem. Biology and Fertility of Soils 49(7): 781–790. https://doi.org/10.1007/s00374-012-0770-6
47. Verbruggen E, Röling WF, Gamper HA, Kowalchuk GA, Verhoef HA, et al. (2010) Positive effects of organic farming on below-ground mutualists: Large-scale comparison of mycorrhizal fungal communities in agricultural soils. New Phytologist 186: 968–979. https://doi.org/10.1111/j.1469-8137.2010.03230.x

48. Gosling P, Hodge A, Goodlass G, Bending GD (2006) Arbuscular mycorrhizal fungi and organic farming. Agriculture, Ecosystems and Environment 113: 17–35. https://doi.org/10.1016/j.agee.2005.09.009
49. Pellegrino E, Bedini S (2014) Enhancing ecosystem services in sustainable agriculture: Biofertilization and biofortification of chickpea (*Cicer arietinum* L.) by arbuscular mycorrhizal fungi. Soil Biology and Biochemistry 68: 429–439. https://doi.org/10.1016/j.soilbio.2013.09.030
50. Rouphael Y, Franken P, Schneider C, Schwarz D, Giovannetti M, et al. (2015) Arbuscular mycorrhizal fungi act as biostimulants in horticultural crops. Scientia Horticulturae 196: 91–108. https://doi.org/10.1016/j.scienta.2015.09.002
51. Verbruggen E, van der Heijden MG, Rillig MC, Kiers ET (2013) Mycorrhizal fungal establishment in agricultural soils: Factors determining inoculation success. New Phytologist 197(4): 1104–1109. https://doi.org/10.1111/j.1469-8137.2012.04348.x
52. Crossay T, Majorel C, Redecker D, Gensous S, Medevielle V, et al. (2019) Is a mixture of arbuscular mycorrhizal fungi better for plant growth than single-species inoculants?. Mycorrhiza 29: 325–339. https://doi.org/10.1007/s00572-019-00898-y
53. Hart MM, Antunes PM, Chaudhary VB, Abbott LK (2018) Fungal inoculants in the field: Is the reward greater than the risk?. Functional Ecology 32: 126–135. https://doi.org/10.1111/1365-2435.12976
54. Backer R, Rokem JS, Ilangumaran G, Lamont J, Praslickova D, et al. (2018) Plant growth-promoting rhizobacteria: Context, mechanisms of action, and roadmap to commercialization of biostimulants for sustainable agriculture. Frontiers in Plant Science 871: 1–17. https://doi.org/10.3389/fpls.2018.01473
55. Hassan MK, McInroy JA, Kloepper, JW (2019) The interactions of rhizodeposits with plant growth-promoting rhizobacteria in the rhizosphere: A review. Agriculture 9(7): 142. https://doi.org/10.3390/agriculture9070142

56. Braga LF, Oliveira FA, do Couto EA, Santos KF, Ferreira EP, et al. (2018) Polyphasic characterization of bacteria obtained from upland rice cultivated in Cerrado soil. Brazilian Journal of Microbiology 49: 20–28. https://doi.org/10.1016/j.bjm.2017.04.004
57. Abbas R, Rasul S, Aslam K, Baber M, Shahid M, et al. (2019) Halotolerant PGPR: A hope for cultivation of saline soils. Journal of King Saud University – Science 31: 1195–1201. https://doi.org/10.1016/j.jksus.2019.02.019
58. Akram MS, Shahid M, Tariq M, Azeem M, Javed MT, et al. (2016) Deciphering *Staphylococcus sciuri* SAT-17 mediated anti-oxidative defense mechanisms and growth modulations in salt stressed maize (*zea mays* l.). Frontiers in Microbiology 7: 1–14. https://doi.org/10.3389/fmicb.2016.00867
59. Rijavec T, Lapanje A (2016) Hydrogen cyanide in the rhizosphere: Not suppressing plant pathogens, but rather regulating availability of phosphate. Frontiers in Microbiology 7: 1–14. https://doi.org/10.3389/fmicb.2016.01785
60. Angulo VC, Sanfuentes EA, Rodríguez F, Sossa KE (2014) Caracterización de rizobacterias promotoras de crecimiento. Revista Argentina de Microbiología 46: 338–347. https://doi.org/10.1016/S0325-7541(14)70093-8
61. Rehman F, Pervez A, Khattak BN, Ahmad R (2018) Growth promoting rhizobacteria impact on *Typha latifolia* and *Phragmites australis* growth and dissolved oxygen. Clean Soil Air Water 46(8):1700353. https://doi.org/10.1002/clen.201700353
62. Penrose DM, Glick BR (2018) Methods for isolating and characterizing ACC deaminase-containing plant growth-promoting rhizobacteria. Physiologia Plantarum 118:10-15. https://doi.org/10.1139/cjm-47-4-368
63. Takishita Y, Charron JB, Smith DL (2018) Biocontrol rhizobacterium *Pseudomonas* sp. 23S induces systemic resistance in Tomato (*Solanum lycopersicum* L.) against bacterial Canker *Clavibacter michiganensis* subsp. *michiganensis*. Frontiers in Microbiology 9: 1–14. https://doi.org/10.3389/fmicb.2018.02119
64. Cappellari L, Chiappero J, Santoro MV, Giordano W, Banchio E (2017) Inducing phenolic production and volatile organic compounds emission by inoculating *Mentha piper*ita with

plant growth-promoting rhizobacteria. Scientia Horticulturae 220: 193–198. https://doi.org/10.1016/j.scienta.2017.04.002

65. Bhattacharyya PN, Jha DK (2012) Plant growth-promoting rhizobacteria (PGPR): emergence in agriculture. World Journal of Microbiology and Biotechnology 28:1327–1350. https://doi.org/10.1007/s11274-011-0979-9
66. Zhao LF, Xu YJ, Lai XH (2018) Antagonistic endophytic bacteria associated with nodules of soybean (*Glycine max* L.) and plant growth-promoting properties. Brazilian Journal of Microbiology 49: 269–278. https://doi.org/10.1016/j.bjm.2017.06.007
67. Sapre S, Gontia-Mishra I, Tiwari S (2018) *Klebsiella sp.* confers enhanced tolerance to salinity and plant growth promotion in oat seedlings (*Avena sativa*). Microbiological Research 206: 25–32. https://doi.org/10.1016/j.micres.2017.09.009
68. Shahid M, Akram MS, Khan MA, Zubair M, Shah SM, et al. (2018a) A phytobeneficial strain *Planomicrobium sp.* MSSA-10 triggered oxidative stress responsive mechanisms and regulated the growth of pea plants under induced saline environment. Journal of Applied Microbiology 124: 1566–1579. https://doi.org/10.1111/jam.13732
69. Shahid M, Mahmood F, Hussain S, Shahzad T, Haider MZ, et al. (2018b) Enzymatic detoxification of azo dyes by a multifarious *Bacillus sp.* strain MR-1/2-bearing plant growth-promoting characteristics. Biotechnology 8: 1–12. https://doi.org/10.1007/s13205-018-1442-5
70. Chatterjee P, Samaddar S, Anandham R, Kang Y, Kim K, et al. (2017) Beneficial soil *bacterium pseudomonas frederiksbergensis* Os261 augments salt tolerance and promotes red pepper plant growth. Frontiers in Plant Science 8: 1–9. https://doi.org/10.3389/fpls.2017.00705
71. Khan MY, Zahir ZA, Asghar HN, Waraich EA (2017) Preliminary investigations on selection of synergistic halotolerant plant growth promoting rhizobacteria for inducing salinity tolerance in wheat. Pakistan Journal of Botany 49(4):1541-1551. https://inis.iaea.org/search/search.aspx?orig_q=RN:48097101
72. Salomon MV, Purpora R, Bottini R, Piccoli P (2016) Rhizosphere associated bacteria trigger accumulation of terpenes in leaves of *Vitis vinifera* L. cv. *Malbec* that protect cells against

reactive oxygen species. Plant Physiol Biochem 106:295–304. https://doi.org/10.1016/j.plaphy.2016.05.007

73. Liu D, Yang Q, Ge K, Hu X, Qi G, et al. (2017) Promotion of iron nutrition and growth on peanut by *Paenibacillus illinoisensis* and *Bacillus sp*. strains in calcareous soil. Brazilian Journal of Microbiology 48: 656–670. https://doi.org/10.1016/j.bjm.2017.02.006
74. Naeem M, Aslam Z, Khaliq A, Ahmed JN, Nawaz A, et al. (2018) Plant growth promoting rhizobacteria reduce aphid population and enhance the productivity of bread wheat. Brazilian Journal of Microbiology 49: 9–14. https://doi.org/10.1016/j.bjm.2017.10.005
75. Turatto MF, Dourado F, Zilli JE, Botelho GR (2018) Control potential of *Meloidogyne javanica* and *Ditylenchus spp*. using fluorescent *Pseudomonas* and *Bacillus spp*. Brazilian Journal of Microbiology 49: 54–58. https://doi.org/10.1016/j.bjm.2017.03.015
76. Rojas-Rojas FU, López-Sánchez D, Meza-Radilla G, Méndez-Canarios A, Ibarra JA, et al. (2019) El controvertido complejo *Burkholderia cepacia*, un grupo de especies promotoras del crecimiento vegetal y patógenas de plantas, animales y humanos. Revista Argentina de Microbiología 51: 84–92. https://doi.org/10.1016/j.ram.2018.01.002
77. Regolamento (UE) 2019/1009 del Parlamento Europeo e del Consiglio del 5 giugno 2019 che stabilisce norme relative alla messa a disposizione sul mercato di prodotti fertilizzanti dell'UE, che modifica i regolamenti (CE) n. 1069/2009 e (CE) n. 1107/2009 e che abroga il regolamento (CE) n. 2003/2003. Gazzetta Ufficiale dell'UE del 25.6.2019. https://eur-lex.europa.eu/legal-content/IT/TXT/PDF/?uri=CELEX:32019R1009&from=HU
78. Regolamento (CE) N. 1107/2009 del Parlamento Europeo e del Consiglio del 21 ottobre 2009 relativo all'immissione sul mercato dei prodotti fitosanitari e che abroga le direttive del Consiglio 79/117/CEE e 91/414/CEE. Gazzetta Ufficiale dell'U.E. del 24.11.2009. https://eur-lex.europa.eu/eli/reg/2009/1107/oj
79. Kandel S, Joubert P, Doty S (2017) Bacterial endophyte colonization and distribution within plants. Microorganisms 5:77. https://doi.org/10.3390/microorganisms5040077
80. Bhatti AA, Haq S, Bhat RA (2017) *Actinomycetes* benefaction role in soil and plant health. Microbial Pathogenesis 111: 458–467. https://doi.org/10.1016/j.micpath.2017.09.036

81. Sousa JA, Olivares FL (2016) Plant growth promotion by *streptomycetes*: Ecophysiology, mechanisms and applications. Chemical and Biological Technologies in Agriculture 3:1–12. https://doi.org/10.1186/s40538-016-0073-5
82. Barka EA, Vatsa P, Sanchez L, Gaveau-Vaillant N, Jacquard C, et al. (2016) Taxonomy, physiology, and natural products of actinobacteria. American Society for Microbiology 80: 1–43. https://doi.org/10.1128/MMBR.00019-15.Address
83. Trujillo ME, Bacigalupe R, Pujic P, Igarashi Y, Benito P, et al. (2014) Genome features of the endophytic actinobacterium *Micromonospora lupini* strain lupac 08: On the process of adaptation to an Endophytic life style?. PLoS One 9(9): e108522 https://doi.org/10.1371/journal.pone.0108522
84. Manivasagan P, Venkatesan J, Sivakumar K, Kim SK (2014) Pharmaceutically active secondary metabolites of marine actinobacteria. Microbiological Research 169: 262–278. https://doi.org/10.1016/j.micres.2013.07.014
85. Traag BA, Sangal V, Mascini N, Hoskisson PA, Goodfellow M, et al. (2013) A novel taxonomic marker that discriminates between morphologically complex *actinomycetes*. Open Biology 3(10): 130073. https://doi.org/10.1098/rsob.130073.
86. Verma M, Lal D, Kaur J, Saxena A, Kaur J, et al. (2013) Phylogenetic analyses of phylum actinobacteria based on whole genome sequences. Research in Microbiology 164:718–728. https://doi.org/10.1016/j.resmic.2013.04.002
87. Salwan R, Sharma V (2020) Molecular and biotechnological aspects of secondary metabolites in actinobacteria. Microbiological Research 231: 126374. https://doi.org/10.1016/j.micres.2019.126374
88. Gomes KM, Duarte RS, Bastos MC (2017) Lantibiotics produced by Actinobacteria and their potential applications (A review). Microbiology 163:109–121. https://doi.org/10.1099/mic.0.000397
89. Bouizgarne B, Aouamar AA (2014) Diversity of plant associated actinobacteria. In: Maheswari, D.K. (Ed.), Diversity of plant associated actinobacteria in bacterial diversity in sustainable

agriculture. (1st edition). Springer, Cham, Switzerland, pp. 99. https://doi.org/10.1007/978-3-319-05936-5_3

90. Lewin GR, Carlos C, Chevrette MG, Horn HA, Mc Donald BR, et al. (2016) Evolution and Ecology of Actinobacteria and their bioenergy applications. Annual Review of Microbiology 70: 235–254. https://doi.org/10.1146/annurev-micro-102215-095748.
91. Wei Y, Wu D, Wei D, Zhao Y, Wu J, et al. (2019) Improved lignocellulose-degrading performance during straw composting from diverse sources with *actinomycetes* inoculation by regulating the key enzyme activities. Bioresource Technology 271: 66–74. https://doi.org/10.1016/j.biortech.2018.09.081
92. Mukhtar S, Zaheer A, Aiysha D, Abdulla-Malik K, Mehnaz S (2017) *Actinomycetes*: A Source of Industrially Important Enzymes. Journal of Proteomics and Bioinformatics 10:12. https://doi.org/10.4172/jpb.1000456
93. Martínez-Hidalgo P, Galindo-Villardón P, Igual JM, Martínez-Molina E (2014) Micromonospora from nitrogen fixing nodules of alfalfa (*Medicago sativa* L.). A new promising plant probiotic bacteria. Scientific Reports Nature 4: 6389. https://doi.org/10.1038/srep06389
94. Vurukonda SS, Giovanardi D, Stefani E (2018) Plant growth promoting and biocontrol activity of *streptomyces spp*. as endophytes. International Journal of Molecular Sciences 19(4): 952. https://doi.org/10.3390/ijms19040952
95. Fierer N (2017) Embracing the unknown: Disentangling the complexities of the soil microbiome. Nature Reviews Microbiology 15: 579–590. https://doi.org/10.1038/nrmicro.2017.87
96. Wagg C, Schlaeppi K, Banerjee S, Kuramae EE, van der Heijden MG (2019) Fungal-bacterial diversity and microbiome complexity predict ecosystem functioning. Nature Communications 10: 1–10. https://doi.org/10.1038/s41467-019-12798-y
97. Richardson AE, Barea JM, McNeill AM, Prigent-Combaret C (2009) Acquisition of phosphorus and nitrogen in the rhizosphere and plant growth promotion by microorganisms. Plant and Soil 321: 305–339. https://doi.org/10.1007/s11104-009-9895-2

98. Barea JM, Pozo MJ, Azcón R, Azcón-Aguilar C (2005) Microbial co-operation in the rhizosphere. Journal of Experimental Botany 56: 1761–1778. https://doi.org/10.1093/jxb/eri197

99. Avio L, Turrini A, Giovannetti M, Sbrana C (2018) Designing the ideotype mycorrhizal symbionts for the production of healthy food. Frontiers in Plant Science 9: 1–19. https://doi.org/10.3389/fpls.2018.01089

100. Bonfante P, Anca IA (2009) Plants, Mycorrhizal fungi, and bacteria: A network of interactions. Annual Review of Microbiology 63: 363–383. https://doi.org/10.1146/annurev.micro.091208.073504

101. Miransari M (2010) Contribution of arbuscular mycorrhizal symbiosis to plant growth under different types of soil stress. Plant Biology 12: 563–569. https://doi.org/10.1111/j.1438-8677.2009.00308.x

102. Johansson JF, Paul LR, Finlay RD (2004) Microbial interactions in the mycorrhizosphere and their significance for sustainable agriculture. FEMS Microbiology Ecology 48: 1–13. https://doi.org/10.1016/j.femsec.2003.11.012

103. Rillig MC, Mummey DL (2006) Mycorrhizas and soil structure. New Phytologist 171: 41–53. https://doi.org/10.1111/j.1469-8137.2006.01750.x

104. Piazza G, Pellegrino E, Moscatelli MC, Ercoli L (2020) Long-term conservation tillage and nitrogen fertilization effects on soil aggregate distribution, nutrient stocks and enzymatic activities in bulk soil and occluded microaggregates. Soil and Tillage Research 196: 104482. https://doi.org/10.1016/j.still.2019.104482

105. Lynch JM, Benedetti A, Insam H, Nuti MP, Smalla K, et al. (2004) Microbial diversity in soil: ecological theories, the contribution of molecular techniques and the impact of transgenic plants and transgenic microorganisms. Biology and Fertility of Soils 40: 363-385. https://doi.org/10.1007/s00374-004-0784-9

106. Sosa-Hernández MA, Leifheit EF, Ingraffia R, Rillig MC (2019) Subsoil arbuscular mycorrhizal fungi for sustainability and climate-smart agriculture: A solution right under our feet?. Frontiers in Microbiology 10:744. https://doi.org/10.3389/fmicb.2019.00744

107. Giovannini L, Palla M, Agnolucci M, Avio L, Sbrana C, et al. (2020) Arbuscular mycorrhizal fungi and associated microbiota as plant biostimulants: Research strategies for the selection of the best performing inocula. Agronomy 10: 106. https://doi.org/10.3390/agronomy10010106

108. Rouphael Y, Colla G (2020) Editorial: Biostimulants in Agriculture. Front Plant Sci 11:40. https://doi.org/10.3389/fpls.2020.00040.

109. Migliorini P, Torri L, Whittaker A, Moschini V, Benedettelli S, et al. (2018) Old and new common wheat (*Triticum aestivum* L.) varieties in organic: connecting agronomic, microorganism, phytochemical and bread sensory characteristics. Journal of Food, Agriculture and Environment 16: 22-27. https://doi.org/10.1234/4.2018.5492

110. Dal Cortivo C, Ferrari M, Visioli G, Lauro M, Fornasier F, et al. (2020) Effects of Seed-Applied Biofertilizers on Rhizosphere Biodiversity and Growth of Common Wheat (*Triticum aestivum* L.) in the Field. Front Plant Sci 11:72. https://doi.org/10.3389/fpls.2020.00072

111. Raiola A, Tenore GC, Petito R, Ciampaglia R, Ritieni A (2015) Improving of Nutraceutical Features of Many Important Mediterranean Vegetables by Inoculation with a New Commercial Product. Current Pharmaceutical Biotechnology 16(8): 738-746. https://doi.org/10.2174/138920101608150603160206

112. Rouphael Y, Cardarelli M, Bonini P, Colla G (2017) Synergistic Action of a Microbial-based Biostimulant and a Plant Derived-Protein Hydrolysate Enhances Lettuce Tolerance to Alkalinit and Salinity. Front Plant Sci 8:131. https://doi.org/10.3389/fpls.2017.00131

113. Colla G, Rouphael Y, Di Mattia E, El-Nakhel C, Cardarelli M (2015) Co-inoculation of *Glomus intraradices* and *Trichoderma atroviride* acts as a biostimulant to promote growth, yield and nutrient uptake of vegetable crops. J Sci Food Agric 95(8): 1706–1715. https://doi.org/10.1002/jsfa.6875

114. Battini F, Turrini A, Sgherri C, Malorgio F, Quartacci MF (2016) Dual inoculation with AMF and associated bacteria improves nutraceutical value of sweet basil grown under commercial conditions. Agrochimica 60: 81-99. https://doi.org/10.12871/0021857201623.

115. Baldi E, Toselli M, Masoero G, Nuti M (2020) Organic and Symbiotic fertilization of Tomato plants monitored by Litterbag-NIRS and Foliar-NIRS rapid spectroscopic methods. Journal of Agronomy Research 3(1): 9-26. https://doi.org/10.14302/issn.2639-3166.jar-20-3363

116. Akhtar N, Naveed M, Khalid M, Ahmad N, Rizwan M, et al. (2018) Effect of bacterial consortia on growth and yield of maize grown in *Fusarium* infested soil. Soil Environ 37(1):35-44. https://doi.org/10.25252/SE/18/872

117. Cameron EK, Martins IS, Lavelle P, Mathieu J, Tedersoo L, et al. (2018) Global gaps in soil biodiversity data. Nature Ecology and Evolution 2: 1042–1043. https://doi.org/10.1038/s41559-018-0573-8

118. Marın C, Bueno CG (2019) A systematic review on South American and European mycorrhizal research: is there a need for scientific symbiosis? In: Pagano M., Lugo M. (eds) Mycorrhizal Fungi in South America (1st edition). Fungal Biology, Springer, Cham, Switzerland, pp. 374.https://doi.org/10.1007/978-3-030-15228-4_5

119. Wall LG, Gabbarini LA, Ferrari AE, Frene JP, Covelli J, et al. (2019) Changes of paradigms in agriculture soil microbiology and new challenges in microbial ecology. Acta Oecologica 95: 68–73. https://doi.org/10.1016/j.actao.2019.02.001

120. Piazza G, Ercoli L, Nuti M, Pellegrino E (2019) Interaction between conservation tillage and nitrogen fertilization shapes prokaryotic and fungal diversity at different soil depths: evidence from a 23-year field experiment in the mediterranean area. Frontiers of Microbiology 10: 2047. https://doi.org/10.3389/fmicb.2019.02047

121. Volpato S, Masoero G, Giovannetti G, Nuti M (2020) Arbuscular Mycorrhizal Biofertilizers Sources in the Potato (*Solanum Tuberosum*) Plant show Interactions with Cultivars on Yield and Litter-bags Spectral Features. Journal of Agronomy Research 2 (4): 9-17. https://doi.org/10.14302/issn.2639-3166.jar-20-3185

122. Liu H, Brettell LE, Qiu Z, Singh BK (2020) Microbiome-Mediated Stress Resistance in Plants. Trends in Plant Science 25(8): 733-743. https://doi.org/10.1016/j.tplants.2020.03.014

123. Ramirez KS, Snoek LB, Koorem K, Geisen S, Bloem LJ, et al. (2019) Range-expansion effects on the belowground plant microbiome. Nature Ecology and Evolution 3: 604–611. https://doi.org/10.1038/s41559-019-0828-z
124. Machado AA, Valyi K, Rillig MC (2017) Potential Environmental Impacts of an "Underground Revolution": A Response to Bender et al. Trends in Ecology and Evolution 32: 8–10. https://doi.org/10.1016/j.tree.2016.10.009
125. Sarabia M, Cazares S, González-rodríguez A, Mora F (2018) Rhizosphere plant growth promotion traits of rhizosphere yeasts and their response to soil characteristics and crop cycle in maize agroecosystems. Rhizosphere 6: 67–73. https://doi.org/10.1016/j.rhisph.2018.04.002
126. Nafady NA, Hashem M, Hassan EA, Ahmed HA, Alamri SA (2019) The combined effect of arbuscular mycorrhizae and plant-growth-promoting yeast improves sunflower defense against *Macrophomina phaseolina* diseases. Biological Control 138: 104049. https://doi.org/10.1016/j.biocontrol.2019.104049
127. Singh S, Tripathi A, Maji D, Awasthi A, Vajpayee P, et al. (2019) Evaluating the potential of combined inoculation of *Trichoderma harzianum* and *Brevibacterium halotolerans* for increased growth and oil yield in *Mentha arvensis* under greenhouse and field conditions. Industrial Crops and Product 131: 173–181. https://doi.org/10.1016/j.indcrop.2019.01.039