



The Current and Future Role of Microbial Culture Collections in Food Security Worldwide

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Food security is the pillar of nutritional wellbeing for food availability, and is necessary to satisfy all physiological needs to thus maintain the general wellbeing of populations. However, global agricultural deficiencies occur due to rapid population growth, causing an increase in competition for resources; such as water, land, and energy, leading to the overexploitation of agro-ecosystems, and the inability to produce a suitable quantity of efficient food. Therefore, the development of sustainable agro-biotechnologies is vital to increase crop yield and quality, reducing the negative impacts caused by intensive non-sustainable agricultural practices. In this way, the genetic and metabolic diversity of soil and plant microbiota in agro-ecosystems are a current and promising alternative to ensure global food security. Microbial communities play an important role in the improvement of soil fertility and plant development by enhancing plant growth and health through several direct and/or indirect mechanisms. Thus, the bio-augmentation of beneficial microbes into agro-ecosystems not only generates an increase in food production but also mitigates the economic, social, and environmental issues of intensive non-sustainable agriculture. In this way, the isolation, characterization, and exploitation of preserved beneficial microbes in microbial culture collections (MCC) is crucial for the *ex situ* maintenance of native soil microbial ecology focused on driving sustainable food production. This review aims to provide a critical analysis of the current and future role of global MCC on sustainable food security, as providers of a large number of beneficial microbial strains with multiple metabolic and genetic traits.

Keywords: agriculture, biological control agents (BCAs), microbial inoculants, sustainability, climate change, plant growth-promoting microorganisms (PGPM)

INTRODUCTION

The rapid growth of the human population will increase the current food demand over the coming years, but intensive non-sustainable agricultural practices place food security, the economy, and the environment at a risk worldwide. Thus, in recent years, global society has faced new challenges related to the development of ecological, efficient, and sustainable alternatives to satisfy increasing

food demand (Martínez-Castillo, 2016). For example, the abrupt changes in climatic conditions at a global scale have had immense negative impacts on agricultural production. The Intergovernmental Panel on Climate Change (IPCC) predicts a global average temperature increase of 1.4 to 5.8°C during the current century (2001–2100), decreasing the production of major cereal crops such as maize (20–45%), rice (20–30%), and wheat (5–50%) (Arora, 2019). In addition, climate change will modify the lifecycle stages and the development rates of phytopathogens and pests (Gupta et al., 2018), which will reduce annual agricultural production by up to 30% (Sharip et al., 2012).

On the other hand, soil degradation is the most significant environmental problem for food production, causing poverty and hunger in developing countries (Pereira et al., 2017). Approximately 52% of the land used for agriculture worldwide is moderately or severely affected by soil degradation (ELD, 2015), due to erosion, salinization, acidification, contamination, or compaction (Kopittke et al., 2019). Soil erosion is the largest contributor to land degradation worldwide, leading to the loss of 75 billion tones of fertile soil per year with an annual economic cost of about USD 400 billion (ELD, 2015; International Atomic Energy Agency (IAEA), 2015). Thus, farmers have relied on the use of high amounts of synthetic agro-inputs to fertilize crops and maintain phytosanitary control, which negatively impact human and environmental health (Villarreal-Delgado et al., 2018). In this sense, in the past 40 years, the use of these agro-inputs in agriculture has increased drastically, i.e., nitrogen (N) has increased by 7.4 times but the yield has only increased by 2.4 times in the same period, indicating that crops have reduced their ability to use N efficiently (Hirel et al., 2011), which increases the economic and environmental cost of food production (Sharip et al., 2012). Therefore, the development of innovative and sustainable agro-biotechnologies focused on solving environmental, economic, and social issues associated with current intensive non-sustainable agricultural practices is needed to contribute to food security (Cano et al., 2017).

Through time, microorganisms have been studied due to their fundamental importance in the maintenance of multiple functions and ecosystem services in the biosphere (Delgado-Baquerizo et al., 2016). Microorganisms are an essential part of human wellbeing, participating in medicine, agriculture, aquaculture, food industry, and biotechnology, among others (Weng et al., 2005; Díaz-Rodríguez et al., 2017). Since microbiota is found in every place on the planet, it plays vital roles in ecosystems, such as; (i) social and ecological sustainability, (ii) adaptation and mitigation of climate change, (iii) as a biotechnological resource for humanity, (iv) water cycling and nutrients, and (v) the increase of food production (Kalia and Gupta, 2005; Pajares et al., 2016).

In agro-ecosystems, microbial communities interact with crops through direct or indirect action mechanisms, regulating their growth and productivity by increasing tolerance to abiotic and biotic stress, plant nutrition, and antagonism against phytopathogenic agents (Santoyo et al., 2019). This particular group of microorganisms are commonly named plant growth-promoting microorganisms (PGPM). PGPM inhabit soil and plants, colonizing roots in 10^5 - 10^7 colony forming units (CFU) per gram of fresh root. These interactions have beneficial impacts

on health and plant growth (Mishra et al., 2017; Valenzuela-Aragon et al., 2018).

Currently, some members of several microbial genera have been studied for their ability to produce phytohormones, and to solubilize phosphates, such as *Micrococcus*, *Pseudomonas*, *Ralstonia*, *Enterobacter*, *Pantoea*, *Acinetobacter*, *Bacillus*, *Aeromonas*, *Burkholderia*, and *Microbacterium* (Lara and Negrete, 2015; Ali et al., 2017). Additionally, others are related to the tolerance of different types of biotic and abiotic stress, such as *Pseudomonas*, *Bacillus*, and *Azospirillum* for salinity stress; *Burkholderia* and *Rhizobium* for water stress; and *Azotobacter* and *Bacillus* for nutrient uptake efficiency (Rokhzadi and Toashih, 2011; Choudhary et al., 2016). Moreover, a group of microorganisms known as biological control agents (BCA) have shown the ability to inhibit the growth of phytopathogens and mitigate the incidence of plant diseases, i.e., *Bacillus amyloliquefaciens* and *Microbacterium oleovorans* have demonstrated the ability to control *Fusarium verticillioides* (Etcheverry et al., 2009); *Trichoderma asperellum* controls *Fusarium* wilt; *Metschnikowia pulcherrima* inhibits the development of *Botrytis cinerea*, *Alternaria alternata*, and *Penicillium expansum* (Köhl et al., 2019); bacteriophages control *Erwinia amylovora* and *Ralstonia solanacearum*; and agriphage controls *Pseudomonas syringae* and *Xanthomonas campestris* (Olanrewaju et al., 2017).

However, the agro-ecosystems are undergoing accelerated deterioration worldwide due to erosion, loss of organic carbon, nutrient depletion, soil sealing, climate change, and other threats, generating a loss of those promising PGPM genera (FAO, 2015a). Therefore, the conservation of this biological diversity is essential for its re-incorporation into agro-ecosystems. Thus, the role of microbial culture collections (MCC) is crucial in achieving this goal (Valenzuela-Ruiz et al., 2018). In this way, the emergence of biological concerns, world food insecurity, and the continuous discovery of new microbial species or subspecies (de los Santos Villalobos et al., 2019) creates the need not only to preserve these microorganisms but also to study them for the development of new agro-biotechnologies (de los Santos-Villalobos et al., 2018). Unfortunately, at present, almost all promising microorganisms are not fully exploited and correctly preserved, which impedes achieving a positive impact on the food security of the world in a sustainable way.

This review aims to highlight the importance of soil microbial resources for the development of sustainable agricultural practices, as well as to highlight the role of MCC as reservoirs and providers of PGPM. Finally, we critically analyze the current status and perspectives to increase the use, exchange, and exploitation of promising microbial strains preserved in these culture collections for sustainably contributing to global food security.

GLOBAL AGRICULTURAL ISSUES FOR FOOD SECURITY

It is estimated that 38.5% of the surface of the planet is dedicated to agriculture, which has increased 1% per year, while food production has increased between 2 and 4% per year (FAO,

2017c). In addition, around 800 million people in the world, or 1 in every 9 humans, suffer from hunger; also, more than two million people suffer from nutrient deficiency, which is known as “hidden hunger” (FAO, 2017a). This is strong evidence of the global food security crisis, which is understood as the failure of nutritional wellbeing through the availability of food necessary to satisfy all physiological needs and maintain the health of the population (Wheeler and Von Braun, 2013). On the other hand, it is estimated that the global population will increase up to 10 billion people by 2050; therefore, agricultural production will have to increase between 50 and 100% to meet global food demands (FAO, 2017c).

The constant increase in the global human population has caused an increment in competition for resources such as water, land, and energy, leading to the overexploitation of agro-ecosystems. This scenario results in the inability to produce enough nutritious and equitable food, awakening the need to develop sustainable alternatives (Godfray et al., 2010; FAO, 2017b). For example, during the green revolution (1960–1980), crop production patterns changed considerably to meet the food demand of the growing world population between 1950 and 1998 (from 2.6 to 5.9 billion people, respectively) (Sunding and Zilberman, 2001). Thus, intensive non-sustainable agricultural practices such as the increased use of synthetic fertilizers and pesticides, large-scale irrigation, and new varieties of high-yield crops were implemented (Gliessman, 2002; Matson, 2012). However, food demand is still on the rise, and intensive non-sustainable agricultural practices have failed to continuously enhance crop yields and quality, generating serious *in* and *ex situ* environmental, economic, and social consequences (Matson, 2012; FAO, 2019).

Intensive non-sustainable agriculture exerts significant internal and external effects. There are two types of external effects: (1) outside the agro-ecosystem, where there is a depletion of groundwater and environmental contamination by the usage of synthetic agro-inputs; and (2) global effects, which result in greenhouse gas emissions, and animal, plant, and human diseases. In addition, as an internal effect (in the agro-ecosystem) soil degradation causes salinization, the reduction of organic matter content, and lowers plant nutrient use efficiency (Lal, 2015; Struik and Kuyper, 2017). For example, <40% of applied nitrogen fertilizers are used efficiently by plants, where the remaining 60% results in volatilization, accumulation in soils, leaching in rivers, lakes, and streams, among others (FAO, 2017d; Chandini et al., 2019). Moreover, according to Tsiafouli et al. (2015), intensive non-sustainable agriculture reduces the microbial diversity and population, which leads to processes of biological and chemical degradation in the soil. At present, soil degradation is increasing at a rate of 5–7 million hectares per year worldwide (International Atomic Energy Agency (IAEA), 2014), and is largely due to its exploitation to satisfy the rising food demand (Maura and Febles, 2018). This reduces the global food productivity by 12%, increasing food prices by 30% (ELD, 2015).

On the other hand, climate change presents a huge challenge for agriculture. It is estimated that by 2050 the temperature of the planet will increase by an average of 3.5–4.7°C, causing

warm winters and summers in many countries. This will have negative consequences for water supply, cooling, and food production (Leahy, 2019). However, agriculture also has a part in the contribution to global climate change through the production of synthetic agro-inputs, an activity that uses a lot of energy by burning fossil fuels and emitting CO₂ into the atmosphere. Agriculture contributes 20% of the CO₂eq emissions globally, while at the regional level, Africa and Latin America contributed the largest amount to the total CO₂eq emissions due to agriculture, with a share of ~60% (FAO, 2020). In this way, climate change has different negative effects on ecological and physiological events in crops, such as changes in the soil microbial ecology, plant-microbiome interactions, plant growth rates, alterations in the distribution regimes, and proliferation of new phytopathogens, pests, and weeds (Mall et al., 2017). These problems will lead to increased crop production costs with lower yields (Nelson et al., 2009; Thomson et al., 2010). Thus, one of the main challenges for agriculture is the adaptation to anthropogenic and natural changes to increase crop yields by sustainable agro-biotechnologies (Foley, 2011), where one of the most promising alternatives is the use of the genetic and metabolic diversity of native microbiota in agro-ecosystems.

MICROBIAL DIVERSITY IN AGRO-ECOSYSTEMS

Soil is the thin layer that covers the Earth, made up of organic substances, living organisms, air, water, and mineral particles. Soil is a vital natural resource from which most of the global food is produced (Hartemink, 2016). Food production requires essential nutrients, metabolites, and water, among others, that are provided by soil to plants. Thus, soil fertility is directly related to the quantity and quality of produced food (FAO, 2015b). In addition, this matrix provides ecosystem services, such as water purification, degradation of pollutants, flood and climate regulation, food, fiber, and fuel supply, carbon retention, nutrient cycling, a source of pharmaceuticals, and genetic resources (Adhikari and Hartemink, 2016). Soil contains a large reservoir of microorganisms (1×10^9 microbial cells g⁻¹ dry soil) and microbial diversity (1×10^5 microbial species g⁻¹ dry soil) (Bodelier, 2011; Bhattarai et al., 2015). These microbial communities are responsible for carrying out between 80 and 90% of its biological processes, including biogeochemical cycles (indispensable for maintaining the equilibrium of agro-ecosystems), organic matter decomposition, soil formation, primary production, climate regulation, and disease control, among others (Nannipieri et al., 2017; Saccá et al., 2017).

Besides, microbial communities play an important role in improving soil fertility, where microbial genera such as *Azotobacter*, *Azospirillum*, *Heliobacterium*, *Bradyrhizobium*, *Bacillus*, *Gluconacetobacter*, *Methylobacterium*, *Nitrosomonas*, *Nitrobacter*, *Klebsiella*, and *Pseudomonas* are involved, for example, in the N cycle including N₂ fixation, nitrification, denitrification, and ammonification (Pajares and Bohannan, 2016). On the other hand, microorganisms are involved in the land-atmosphere carbon (C) exchange, through the balance

between respiration and photosynthesis by carbon fixers, such as autotrophic (chemoautotrophic and photoautotrophic) microbes (Gougoulis et al., 2014). These communities are also important in the phosphorus (P) cycle, due to their ability to solubilize phosphates, i.e., fungal (some species of *Aspergillus* and *Penicillium*) and bacterial (some species of *Bacillus*, *Micrococcus*, and *Pseudomonas*) genera are involved in phosphate solubilization by the production of organic acids and the excretion of protons during NH_4^+ assimilation (Mullen, 2019). Thus, in recent years, more attention has been paid to the function of microorganisms in agro-ecosystems, since they play a fundamental role in plant health and food production, as well as the improvement of soil fertility (Johansson et al., 2004).

THE ROLE OF PLANT GROWTH-PROMOTING MICROORGANISMS (PGPM) IN FOOD PRODUCTION

The use of beneficial microbes, named plant growth-promoting microorganisms (PGPM), as microbial inoculants (biofertilizers) is a sustainable alternative to improve crop yields. PGPM (rhizobacteria, soil or endophytic bacteria, endo- or ectomycorrhizal fungi, cyanobacteria, and many others) can colonize soil and plants in significant quantities (10^5 - 10^7 CFU per gram of fresh root) and exert beneficial effects on plants through several mechanisms (Mishra et al., 2017). They can improve nutrient uptake, plant growth, and plant tolerance to abiotic and biotic stress, as well as biocontrol agents against plant pathogens and pests (Gangwar et al., 2017; Valenzuela-Ruiz et al., 2018).

Microbial inoculants are biodegradable bio-products that contain living or inactive cells of PGPM with the ability to colonize the rhizosphere or inner part of plants, and perform growth-promoting effects on plants (Umesha et al., 2018; Singh et al., 2019). These bio-products are an eco-friendly way to improve the growth of plants by reducing the damage caused by phytopathogens or pests and improving their resistance to abiotic stress (Chávez-Díaz et al., 2020). The use of PGPM in agriculture has gained increasing interest and is currently a sustainable alternative for global food production due to their positive impacts on plant growth (Parewa et al., 2018), mitigation of the pollution generated by agrochemicals, and the reduction of soil degradation (Dubey et al., 2017; Mishra et al., 2017).

In this sense, the earliest microorganisms used as inoculants were the “rhizobia,” diazotrophic bacteria able to colonize the rhizosphere and establish nodules in the roots of host plants (Ciancio et al., 2016; Berg et al., 2017). Currently, several microbial genera are used in the formulation of microbial inoculants due to their metabolic diversity, i.e., many *Bacillus* species induce growth promotion in plants, control phytopathogens, and are spore-forming bacteria-resistant to stressful conditions (Villarreal-Delgado et al., 2018; Ibarra-Villarreal et al., 2021). Some members of the genus *Klebsiella* and *Rhizobium* can fix nitrogen, solubilize organic and inorganic phosphates, produce 1-aminocyclopropane-1-carboxylate (ACC)

deaminase, and produce phytohormones (Suliasih and Widawati, 2019). A large number of bacteria of the genus *Azospirillum* can produce phytohormones, polyamines, and fix atmospheric nitrogen (Cassán et al., 2014; Puente et al., 2018). Some strains of *Enterobacter* are biocontrol agents against phytopathogens, while some *Arthrobacter* strains can degrade a wide variety of compounds, including aromatic molecules, pesticides, and organochloride (Fernández-González et al., 2017). Besides, it has been reported that some *Burkholderia* species can bioremediate pollutants and are applied to biocontrol phytopathogens, can fix atmospheric nitrogen, and promote plant growth (Bolívar-Anillo et al., 2016). Some strains of *Serratia* induce plant growth by stimulating phytohormone production and phosphate solubilization, as well as inducing systemic resistance, enhancing salinity tolerance, and fixing atmospheric nitrogen (Devi et al., 2016; Singh and Jha, 2016; Moreno et al., 2018). However, these positive effects on crops caused by PGPM depend on the soil and climate conditions, crop genotype, plant phenological stage, root exudates, agricultural practices, the ability of PGPM to colonize the soil and plant tissues, and the application modes of beneficial strains, among others (Valenzuela-Aragon et al., 2018).

PGPM improve plant growth and health through direct, indirect, or dual mechanisms (Figure 1). They are considered to be direct mechanisms when bacteria begins to synthesize metabolites or when they increase the availability of nutrients to plants, the most common mechanisms being the production of phytohormones and ACC deaminase, nitrite production, sulfide oxidation, organic phosphate mineralization, and inorganic phosphorus solubilization. On the other hand, indirect mechanisms are related to the inhibition and elimination of phytopathogens through the competition for space and nutrients, the production of antibiotics, antimicrobial substances or lytic enzymes, interference in quorum sensing signaling, induced systemic resistance, and biofilm formation. Furthermore, there are mechanisms with dual activity (direct and indirect), where the most common is the production of siderophores, molecules that sequester iron making it available for the plants but less available to phytopathogens (Moreno et al., 2018; Parewa et al., 2018; Santoyo et al., 2019).

PGPM can exert more than one growth promotion mechanism and may be used in different stages of the plant growth cycle (Gupta et al., 2015; Parewa et al., 2018). For example, strains of *Pseudomonas fluorescens* are the most used bacteria for preventing plant diseases through antibiotics production, which also stimulate plant growth by amino acids, specific growth promoters, and the synthesis of hormones. Additionally, strains of *Bacillus subtilis* promote plant growth by phytohormones and cause resistance against *Fusarium oxysporum* in tomatoes, and *Rhizoctonia solani* and *Phytophthora nicotianae* in tobacco plants (Villarreal-Delgado et al., 2018). Also, *Trichoderma* species produce phytohormones and solubilize phosphates, generating growth-promoting effects, and the control of pathogenic fungi in soil (Peláez-Álvarez et al., 2016; Leal-Almanza et al., 2018). Arbuscular mycorrhizal fungi (AMF) are the most prevalent PGPM found in agricultural soils (Nadeem et al., 2014; Nath and Meena, 2018). These are root obligate symbiotrophs that provide essential nutrients, pathogen protection, and

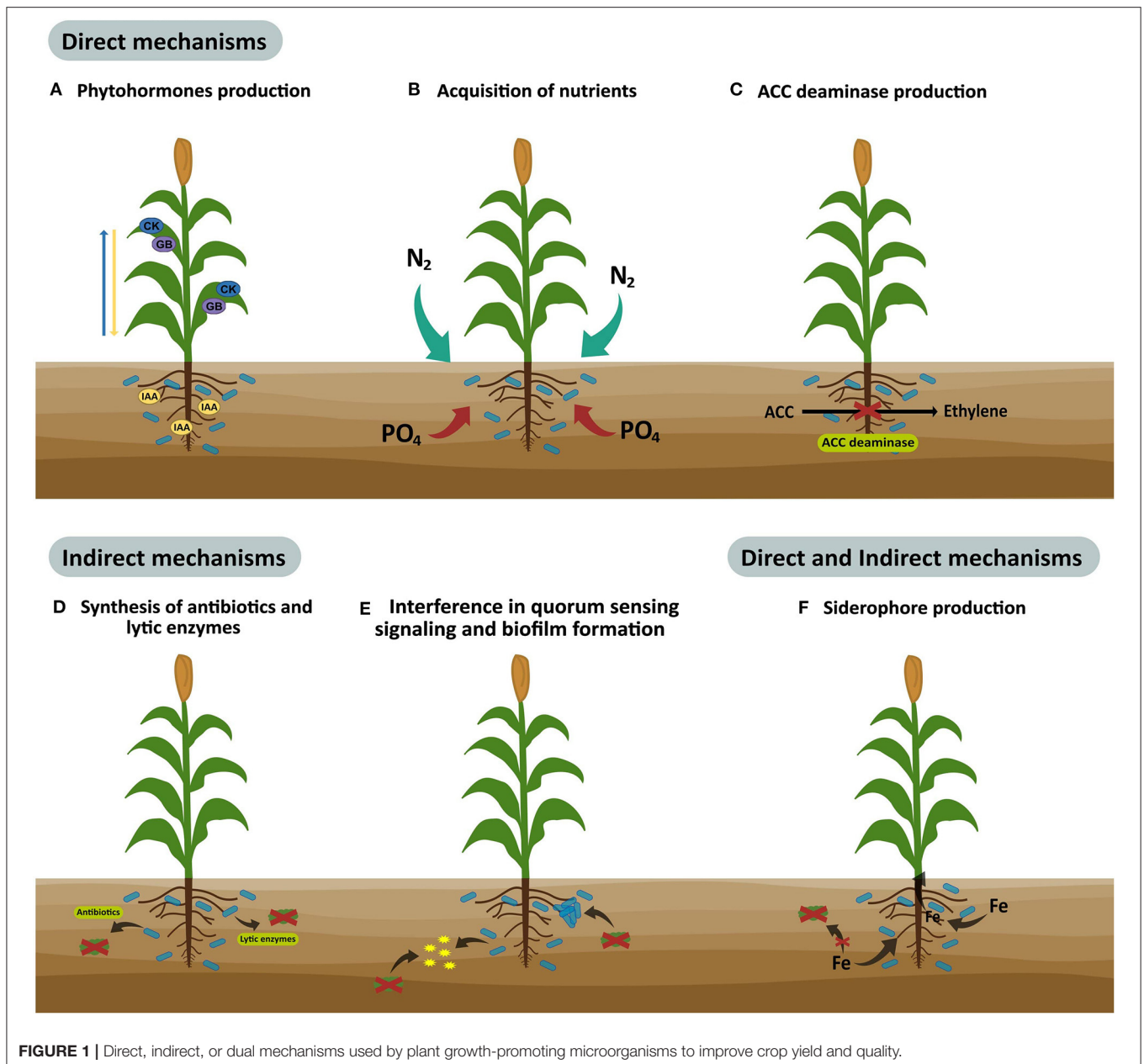


FIGURE 1 | Direct, indirect, or dual mechanisms used by plant growth-promoting microorganisms to improve crop yield and quality.

stress tolerance to the host plant (Begum et al., 2019). AMF, symbiotic, and free-living PGPM have beneficial effects that increase plant health, growth, and yields, under optimal or stressful conditions (Nadeem et al., 2014). Thus, synergistic interactions between AMF and other PGPM can enhance the nutrient uptake and growth-promoting effects, in some cases to a greater extent compared to individual microbial strains. For example, these microbial interactions improve the phosphorus bioavailability and absorption by plants (Nanjundappa et al., 2019), a mechanism used by these beneficial microbial consortia for solubilizing phosphates is organic acid production (acetic, lactic, gluconic, formic, and oxalic acids, etc.), which solubilize

phosphate rocks by acidification processes. Moreover, co-inoculated PGPM can produce chelating substances effective for calcium, aluminum, and iron causing the liberation of inorganic phosphate (Beltrán, 2014; Prabhu et al., 2019). On the other hand, the production of inorganic acids (sulfuric acid, nitric acid, and carbonic acid) by beneficial microbial consortia is involved in phosphate solubilization, but in the absence of acid production, the phosphate solubilization occurs by proton extrusion with nitrogen. The organic phosphate-solubilization by the co-inoculation of beneficial microbes is carried out by enzyme activity, once phosphatase and C-P lyase hydrolyze ester bonds of phosphonates (Prabhu et al., 2019).

Several different studies have suggested that microbial inoculants based on compatible microbial consortia may confer an advantage over formulations based on single strains (Egamberdieva et al., 2013). This is due to the ability for combining different functional metabolites and capabilities to improve soil quality and crop yield (Thilagar et al., 2016). For example, the co-inoculation in black bean (*Phaseolus vulgaris*) with *Trichoderma atroviride* and *Bacillus subtilis* showed a significant growth promotion in plant-dry biomass (43% over the control) compared to un-inoculated plants; while the individual inoculation of *T. atroviride* or *B. subtilis* increased only 2% or 34% in this trait, respectively (Yobo et al., 2011). Similarly, the co-inoculation of *Trichoderma asperellum* and arbuscular mycorrhizal fungi (*Gigaspora margarita* and *Acaulospora tuberculata*) showed a significant increase in plant height (>20 cm), as well as root and shoot fresh weights (>4.7 and >6.9 g/plant, respectively) compared to the un-inoculated treatment (Tchameni et al., 2011). The co-inoculation of *Rhizobium-Azospirillum* in legumes showed a greater production of flavonoids in plants, which triggered the expression of the *Rhizobium nod* gene (Marks et al., 2013; Puente et al., 2018). Puente et al. (2019) confirmed that soybean seeds inoculated (at sowing) with *Bradyrhizobium japonicum* E109 and later foliar-sprayed with *A. brasilense* Az39 showed higher fresh and dry shoot biomass, more nodules, higher leghemoglobin levels, and increased nitrogen and protein content in grains, in comparison with the *B. japonicum* E109-alone treated seeds.

At present, several successful applications of microbial inoculants have been reported, with an increase of up to 10–30% in crop yields, and reductions of the amount of applied chemical fertilizers by up to 50% (Alori and Babalola, 2018; Parewa et al., 2018). In this way, the use of microbial inoculants is growing. The global market for biofertilizers is projected to reach 2.6 billion USD at a CAGR of 14.42% by the end of the year 2023 (Market Research, 2018). Thus, the extensive use of microbial inoculants is an alternative to improve soil fertility, crop quality, and yields, and contribute to mitigating the effects of climate change, as well as to increase the development of regional economies by the establishment of sustainable agribusiness (de los Santos-Villalobos et al., 2018). In this way, the preservation of isolated PGPM and their re-incorporation into agro-ecosystems is vital to maintain their ecological functions (Wood et al., 2015), for which their safeguarding in certified MCC makes them available for bioprospecting (de los Santos-Villalobos et al., 2018; Toader et al., 2019). Therefore, these MCC should focus on the study of metabolic, molecular, and functional traits of promising PGPM for developing sustainable agro-biotechnological alternatives (Smith, 2003; de los Santos-Villalobos et al., 2018).

CONSIDERATIONS AND CHALLENGES IN THE USE OF MICROBIAL INOCULANTS

PGPM can be used as biofertilizers and/or biopesticides, depending on their genetic and metabolic diversity. However, several microbial strains can exhibit different results in the same plant species and vice versa. In this way, there are several

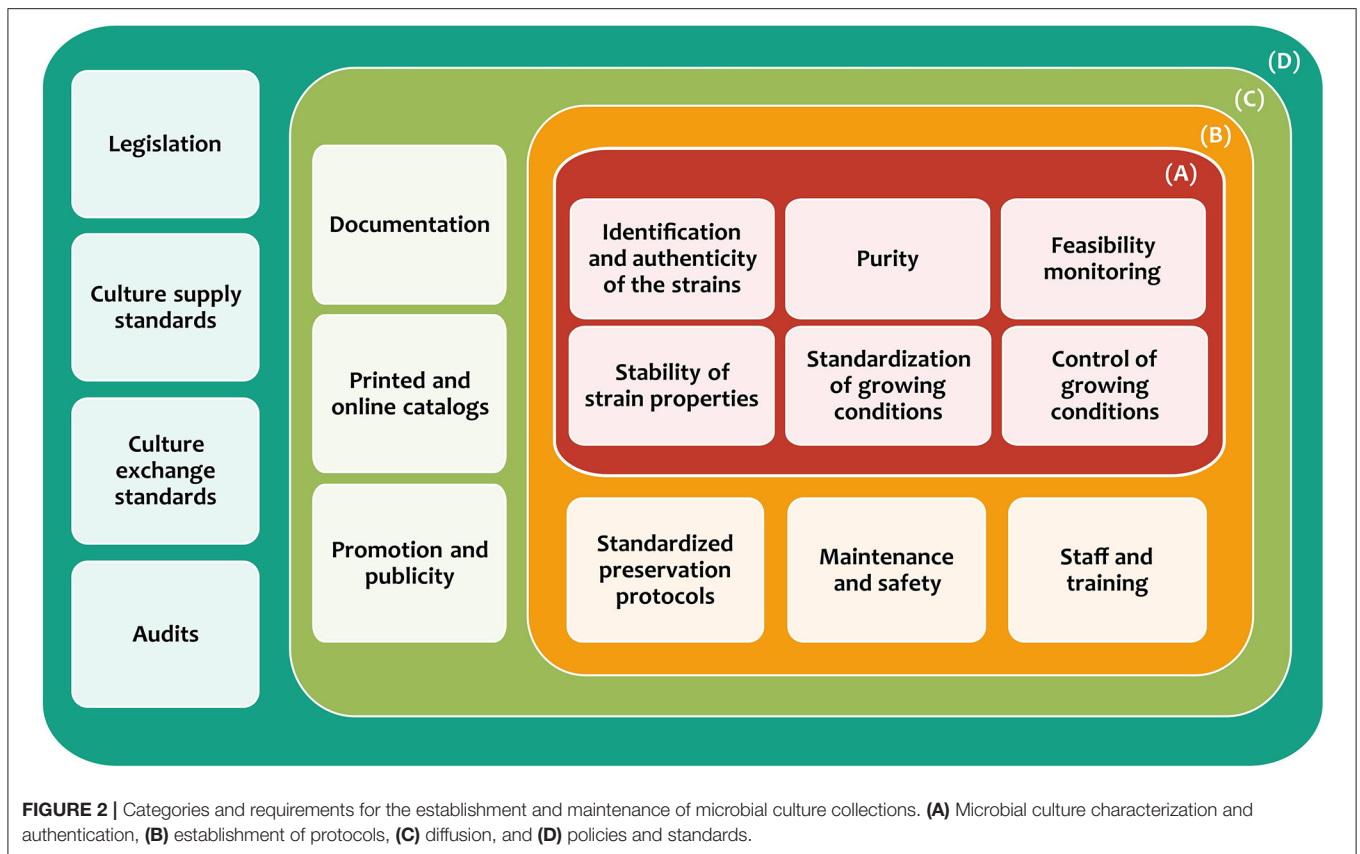
successful experiments at the laboratory and/or greenhouse level; however, those promising results sometimes are highly variable in the field, due to the complexity of the agro-ecosystem (Timmusk et al., 2017). Thus, it is important to select a specific microbial inoculant according to agroecosystem conditions, crop genotype, agricultural practices, climatic conditions, and expected benefits (Martínez-Viveros et al., 2010). The microbial inoculant efficiency depends on the establishment of its PGPM in the host plant and the rhizosphere, which is based on the inoculated PGPM-plant-microbiota competition mediated through the plant exudates (Jin et al., 2019). Besides, the climatic condition is another crucial factor involved in microbial inoculant effectiveness in the field. According to global estimates, abiotic factors lead to crop yield losses of 50%, temperature variations are the main contributor (27%); however, salinity (10%), drought (9%), and other forms of stress (4%) also affect crop yields and the success of microbial inoculants (de los Santos-Villalobos et al., 2018; Kaur et al., 2018; Ibarra-Villarreal et al., 2021). Still, little is known about the factors that control the competition of microbial species in the field; therefore, it is critical to have a higher number of cells to compete with native microorganisms and produce an increase in productivity (Compant et al., 2019). The estimated PGPM concentration required to cause positive effects in plants cannot be established as a general standard because it varies from one species to another; however, some microbial inoculants contain from 10^7 to 10^9 CFU/g of bioproduct, another influential factor is the lack of common international standards (Zayed, 2016).

On the other hand, the success of microbial inoculants depends on their application modes (plant tissues, rhizosphere, seeds, and/or bulk soil). These modes should be defined according to the type of crop, soil properties, climatic conditions, and agricultural practices in the field (Patil and Solanki, 2016; Kaushik and Djiwanti, 2019). Thus, it is important to highlight that the use of microbial inoculants in the field under different biotic and abiotic factors is a promising agro-biotechnological alternative to contribute to food safety sustainably.

ROLE OF MCC IN THE PRESERVATION OF THE BENEFICIAL MICROBIAL DIVERSITY

The progress of microbiology brought the need to establish collections of microbial cultures to study and *ex situ* preserve the biodiversity in ecosystems and the distribution of promising microbial strains to produce goods and services. Subsequently, advances in molecular biology stimulated the development of intensive programs for bioprospecting all these microorganisms (Altier, 2013).

MCC, also known as biological resource centers (BRC), are primary suppliers of culturable microorganisms, replicable parts of these (i.e., DNA, genomes, and plasmids), and viable but not yet culturable microorganisms in biological or environmental matrices (Kurtzman and Labeda, 2009; Smith et al., 2014). According to Smith et al. (2014), the general concept of an MCC or BRC includes “the provision of services and repositories of the living cells, genomes of organisms, and information



relating to heredity and the functions of biological systems.” The importance of MCC has been recognized by the Organization for Economic Cooperation and Development (OECD), which is a promoter of policies to improve economic wellbeing and social welfare at an international level (Smith et al., 2014). Therefore, these MCC have two main functions: (i) the conservation of agro-ecosystems through the isolation and preservation of the microbial diversity, providing a biological safeguard service; and (ii) the study and easy access of microorganisms, reference strains, and microbial resources to the public to generate biotechnological strategies (Mahilum, 2009).

The first MCC that provided a public service was established in Prague in 1890 by Professor Frantisek Král. Some of the strains that were deposited for the first time in this culture collection are still available (Smith et al., 2014). Later, other culture collections were created, such as the Mycothèque de l’Université Catholique de Louvain (MUCL) established in 1894 in Belgium, the Collection of the Centraalbureau voor Schimmelcultures (CBS) in 1906 in Holland, both specialized in fungi. Then, the American Type Culture Collection (ATCC) was established in the United States in 1925, which preserves different types of microorganisms (Sharma et al., 2017). Until 1920, the main role of MCC was initially for their value in carrying out both taxonomic and epidemiological studies; now culture collections have adopted new technologies to characterize and add value to the services they offer. In addition, with the advancement of biochemical and physiological studies, the conservation of

microorganisms has been improving (Malik and Claus, 1987; Sharma and Shouche, 2014).

Thus, specific requirements have been established to maintain and ensure the quality and diffusion of all services provided by MCC (Smith, 1996; González and Jiménez, 2013), which can be divided into four categories (**Figure 2**). The first category is *microbial culture characterization and authentication* (A), which has the purpose of strain identification, as well as their preservation. This should ensure contamination-free cultures, the survival of at least 70% of cells, and stable maintenance of the preserved microorganisms (Escobar et al., 2016). The second category is the *establishment of protocols* (B), which focuses on the standardization of the protocols for the culture collections operation, from the preservation of different types of microorganisms to the maintenance of specialized equipment. Besides, it is necessary to have trained staff in cutting-edge technologies for the preservation, growth, and identification of microbes. The third category is *diffusion* (C), which is focused on all aspects related to achieving a greater scope and accessibility of the generated information (documentation and catalogs) to the general public. The last category is *policies and standards* (D), which seeks compliance with national and international laws, regulations, and policies about the safety, shipping, exchange of microorganisms, and other matters (González and Jiménez, 2013; Sharma and Shouche, 2014).

At present, the World Federation for Culture Collections (WFCC) is the main organization that coordinates the activities

TABLE 1 | Examples of microbial culture collections around the world.

Culture collection name	Acronym	Country	Website
American Type Culture Collection	ATCC	United States of America	https://www.atcc.org
German Collection of Microorganisms and Cell Cultures GmbH	DSMZ	Germany	https://www.dsmz.de
The National Collection of Type Cultures (NCTC) for bacteria	NCTC	United Kingdom	https://www.phe-culturecollections.org.uk/collections/nctc.aspx
Coordinated Collections of Microorganisms/LMG Bacteria Collection	LMG	Belgium	https://bccm.belspo.be/catalogues/lmg-catalogue-search
Refik Saydam National Type Culture Collection	RSKK	Turkey	http://www.hsk.gov.tr
NITE Biological Resource Center	NBRC	Japan	https://www.nite.go.jp/en/nbrc/index.html
All-Russian Collection of Microorganism	VKM	Russia	http://www.vkm.ru/Collections.htm
Centraalbureau voor Schimmelcultures, Fungal and Yeast Collection	CBS	The Netherlands	https://wi.knaw.nl
The Canadian Center for the Culture of Microorganisms	CCCM	Canada	http://cccm.botany.ubc.ca/
The Mexican Culture Collection of Microorganisms recognized as a biological resource center (BRC) by CONABIO	CDBB-500	México	http://cdbb.cinvestav.mx/cdbb/index.html
Colección de Microorganismos Edáficos y Endófitos Nativos	COLMENA	México	http://www.itson.mx/colmena
The Brazilian Collection of Environmental and Industrial Microorganisms	CBMAI	Brazil	https://cbmai.cpqba.unicamp.br
Bioresource Collection and Research Center	BCRC	Taiwan	http://www.bcrc.firdi.org.tw/
Collection Nationale de Cultures de Microorganismes	CNCM	France	https://research.pasteur.fr/en/team/national-collection-of-cultures-of-microorganisms/
Agricultural Research Service Culture Collection	NRRL	United States of America	http://nrri.ncaur.usda.gov/

of MCC worldwide (Sharma et al., 2017). It aims to promote and support the establishment and monitoring of MCC, by providing an information network between affiliated collections and users (Federación mundial de Colecciones de Cultivo, 2010). The WFCC supports the World Data Center of Microorganisms (WDCM) for the compilation of culture collection data, management, services provided, and most recent research with an online international database (Sharma et al., 2017). Currently, the WDCM lists 802 collections in 78 regions, of which 295 are located in Asia, 257 in Europe, 202 in America, 42 in Oceania, and 18 in Africa. The country with the largest number of MCC is Brazil (86), followed by Thailand (66) and China (48) (WDCM, 2020a). These MCC provide different services, such as: consulting, strain distribution, strain identification, patent deposits, storage service, and training (Sharma and Shouche, 2014; WDCM, 2020a). In this way, around the world, culture collections play a fundamental role in the preservation of microbial diversity, and the accessibility of axenic and stable promising strains for agriculture, genetics, industrial and medical microbiology, marine biology, and food safety, among others (Table 1) (Sharma et al., 2017).

The conservation of biodiversity and genetic resources provide essential support for emerging eco-efficient biotechnologies, in both the developed and developing world (OECD, 2009). The most economically powerful countries with the greatest scientific-technological development have created highly-specialized institutions to harbor large culture collections (approximately 98% of known microorganisms are preserved) such as the United States of America, China, Belgium, Japan, and India (WDCM, 2020a). Besides, many countries or individual institutions obtain official support for these culture collections; however, the establishment of MCC requires a constant source of funding that not all of them can obtain. Also, the records that include MCC must be digitized for use in international schemes (CGREA, 2007). For example, in the region of Latin America and the Caribbean, there are valuable specialized MCC created and maintained by universities and research institutes; however, there is not a systematized information source about their progress, limitations, efforts, and initiatives.

Globally, several MCC are recognized for their role in the preservation of microorganisms with international or regional importance, which has a high impact on biotechnology at all

levels, including food security (Table 1). For example, WDCM (at an international level) promotes the development of culture collections of microorganisms supporting the existing ones by providing advice and assistance (González and Jiménez, 2013). Similarly, ATCC safeguards and distributes standard reference microorganisms since they have a wide variety of high-quality biological materials (microorganisms, cell lines, and bioproducts) intended for scientific research (ATCC, 2020). One more example is the Colección de Microorganismos Edáficos y Endófitos Nativos (COLMENA), which is focused on the preservation, characterization, classification, and re-incorporation of native microorganisms to agro-ecosystems in Mexico, to reduce the loss of microbial diversity associated with food production (de los Santos-Villalobos et al., 2018). At present, a total of 3,272,734 microorganisms have been registered in the WDCM, of which 1,429,816 are bacteria (43.7%); 872,094 are fungi (26.6%); 39,491 are viruses (1.2%); and 33,020 are cell lines (1.0%) (WDCM, 2020a). Also, the WDCM has elaborated a catalog of reference strains for easy access, which are recommended for their use in quality control, regulated by different ISO standards. For this, the WDCM assigns a unique identification number to every reference strain, while the culture collection acronyms followed by a number are used as an identifier (at the strain level) for its global identification and tracking (Wu et al., 2016). This catalog contains a total of 196 reference strains of 131 species of bacteria (Table 2), fungi, and yeast (Table 3) (WDCM, 2019). Currently, according to scientific literature, many microbial species preserved in the WDCM could be grouped as PGPM, due to their large diversity of metabolic capabilities with wide agro-biotechnological applications. However, the number of AMF preserved in MCC is lower; probably due to limitations in the specific conservation methodologies since these microorganisms depend on their host plant to complete their life cycle, which makes it difficult to grow in pure synthetic media (Lalaymia et al., 2013). Thus, only two MCC (registered in WFCC) are specialized in these types of microorganisms holding 1,302 AMF strains in total (WDCM, 2020b). Therefore, it is necessary to improve short and long-term preservation methodologies for these microorganisms, which (like others PGPM) play a fundamental role in the growth regulation and nutrients acquisition by plants in ecosystems (Lalaymia et al., 2013; Begum et al., 2019).

On the other hand, the offered services by most of the MCC around the world are limited to the preservation, deposit, and transfer of microorganisms, and do not thoroughly study the strain capabilities; usually, this is left only to interested researchers or professionals. For this reason, more MCC focused, not only on microbial preservation, but also dedicated to the research, teaching, and characterization of promising strains for biotechnological applications are needed (de los Santos-Villalobos et al., 2018). Furthermore, only a few culture collections have a public catalog containing information about preserved microorganisms grouped by function, biosafety, taxonomy, and biotechnological applications, among others. This is a strong limitation for the extensive use of PGPM as microbial inoculants since it complicates the selection of promising strains. For this reason, MCC must also make the biological data of

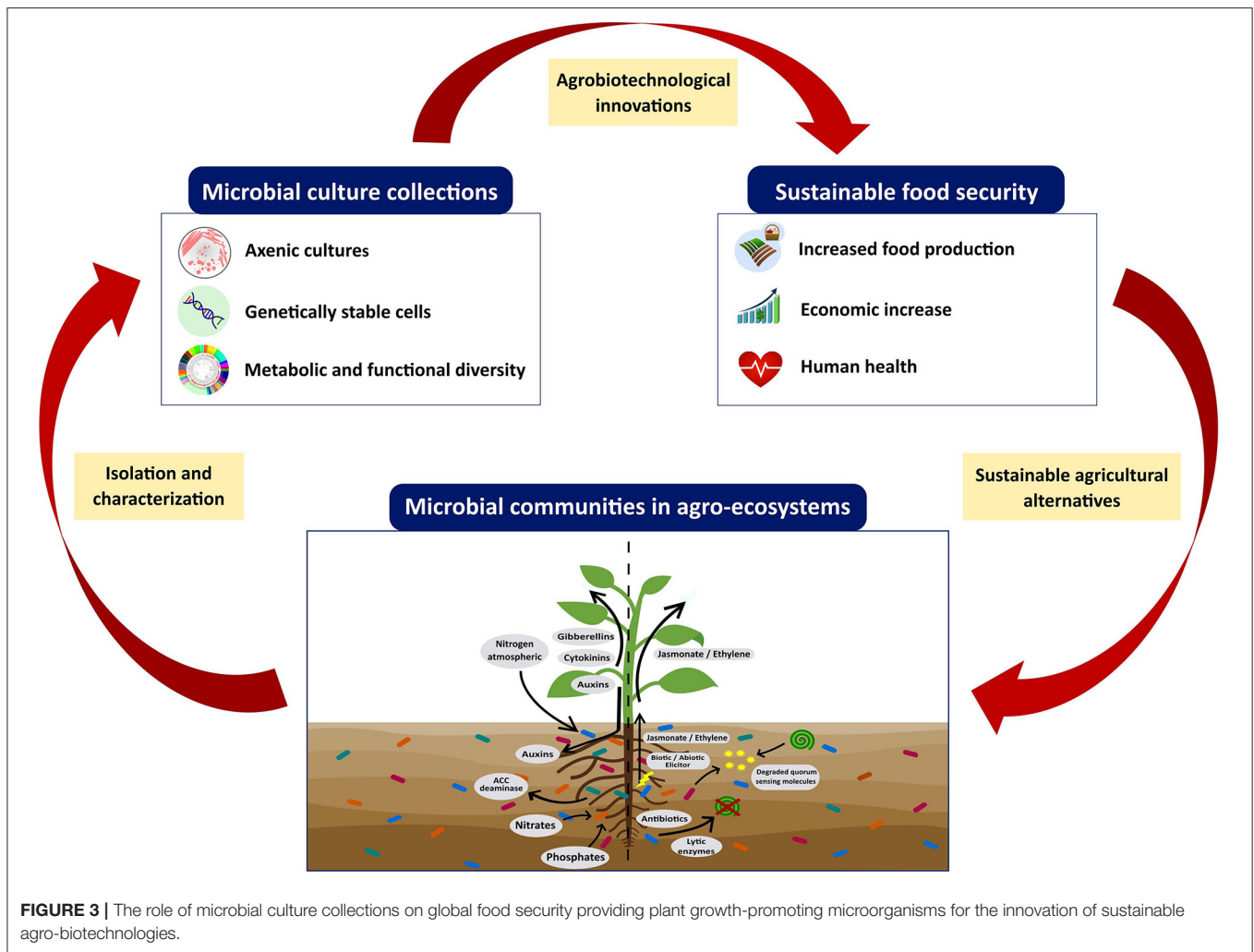
TABLE 2 | The number of bacterial species in the WDCM reference strain catalog that have identifier numbers for the reference strains (WDCM, 2019).

Genus	Species Identifiers	Genus	Species Identifiers
Bacteria			
<i>Acinetobacter</i>	1 3	<i>Lactococcus</i>	1 18
<i>Aerococcus</i>	1 13	<i>Legionella</i>	3 25
<i>Aeromonas</i>	3 29	<i>Leuconostoc</i>	1 10
<i>Arcobacter</i>	3 22	<i>Listeria</i>	6 54
<i>Bacillus</i>	8 92	<i>Micrococcus</i>	1 16
<i>Bifidobacterium</i>	3 13	<i>Morganella</i>	1 11
<i>Brochothrix</i>	1 11	<i>Pantoea</i>	1 9
<i>Campylobacter</i>	4 45	<i>Pediococcus</i>	2 20
<i>Camobacterium</i>	2 18	<i>Photobacterium</i>	1 9
<i>Citrobacter</i>	1 18	<i>Proteus</i>	1 9
<i>Clostridium</i>	5 41	<i>Pseudomonas</i>	4 120
<i>Cronobacter</i>	2 7	<i>Rhodococcus</i>	1 17
<i>Desulfotomaculum</i>	1 6	<i>Salmonella</i>	6 60
<i>Enterobacter</i>	1 20	<i>Shigella</i>	2 20
<i>Enterococcus</i>	3 109	<i>Staphylococcus</i>	4 146
<i>Escherichia</i>	2 77	<i>Streptococcus</i>	2 18
<i>Geobacillus</i>	1 10	<i>Thermoanaerobacterium</i>	1 4
<i>Hafnia</i>	1 11	<i>Vibrio</i>	6 57
<i>Klebsiella</i>	4 34	<i>Weissella</i>	1 11
<i>Lactobacillus</i>	8 102	<i>Yersinia</i>	4 32

TABLE 3 | The number of filamentous fungi and yeasts species in the WDCM reference strain catalog that have identifier numbers for the reference strains (WDCM, 2019).

Genus	Species Identifiers	Genus	Species Identifiers
Filamentous fungi and yeasts			
<i>Aspergillus</i>	5 37	<i>Penicillium</i>	5 18
<i>Candida</i>	1 30	<i>Pleurotus</i>	1 4
<i>Cladosporium</i>	1 4	<i>Rhizopus</i>	1 3
<i>Coniophora</i>	1 7	<i>Saccharomyces</i>	1 26
<i>Eurotium</i>	2 5	<i>Serpula</i>	1 2
<i>Gloeophyllum</i>	1 5	<i>Trametes</i>	1 11
<i>Lentinus</i>	1 2	<i>Trichophyton</i>	1 3
<i>Mucor</i>	1 2	<i>Wallemia</i>	1 2
<i>Oligoporus</i>	1 6	<i>Zygosaccharomyces</i>	1 3

microorganisms more accessible to the community, including (i) taxonomy, (ii) source of isolation, including the biological and environmental context in which strains were found, (iii) evolution, (iv) metabolic-functional traits, and (v) ecological relationship. All these data should be accessible to the general public through an online catalog (databases) with open access to make it easier to transfer microbial strains (Caktu and Turkoglu, 2011; Cruz-Leyva et al., 2015). However, at present, only 53% of MCC have a digital catalog of preserved microorganisms (WDCM, 2020a), the digitization and update of information for each preserved microorganism is one of the major limitations of culture collections. Thus, the expected positive impacts of preserved PGPM in MCC to global food security will be reached when, at least, three stages are linked: (i) the isolation of



microbial strains in agro-ecosystems, (ii) the preservation of these strains in an MCC, and (iii) bioprospecting these promising strains to transfer and develop sustainable agro-biotechnological alternatives (Figure 3). Finally, rules and procedures have been established for the transfer and exploitation of genetic resources preserved in MCC, such as (i) the Budapest Treaty that mentions the International Recognition of the Deposit of Microorganisms for the Patent Procedure, established in 1980 (Organización Mundial de la Propiedad Intelectual (OMPI), 2017); and (ii) the Nagoya Protocol (implemented in October 2014), which aims for the fair and equitable sharing of the benefits derived from the use of genetic resources (Sharma et al., 2017). The Budapest Treaty regulates the process of patent deposits in an international framework; thus, a patent deposit made with one International Depository Authority (IDA) is sufficient and recognized by all member states of Budapest. Nonmember countries may also accept deposits according to the Budapest Treaty as per the norms of the country (Bussas et al., 2017). On the other hand, the Nagoya Protocol is an agreement that complements the Convention on Biological Diversity. It provides a transparent and legal framework to effectively implement the beneficial

sharing between providers and users of genetic resources, by contributing to the establishment of more predictable conditions to access the genetic resources, conservation, and sustainable uses of biodiversity (Convention on Biological Diversity, 2015).

CONCLUSIONS

The concern for sustainable food production that meets the needs of the global human population has become a crucial issue in the agricultural sector. Thus, the development of new sustainable agro-biotechnological alternatives to increase crop yields and quality, and restore soil fertility, is vital to satisfy the current and future food demand worldwide. In this way, several PGPM represent a feasible and eco-friendly strategy to combat challenges of food security and climate change, due to their metabolic and genetic diversity. Regarding the agro-biotechnological potentials of PGPM, microbial communities in agro-ecosystems have become more relevant in recent years for the development of new microbial inoculants. These bioproducts can increase nutrition and stress tolerance in

crops. Thus, the use of microbial inoculants can contribute to reducing the economic, environmental, and health costs of food production, but there are many considerations and challenges to address in order for them to be effective in the field. Besides, since there is no single universal solution for all these issues, the integration of microbial inoculants with other technologies (sustainable soil management, new genetic varieties of crops, and efficient use of agro-inputs, among others) are necessary to enhance the expected positive effects.

In this sense, the success of the extensive use of microbial inoculants depend on the isolation, identification, and characterization of promising PGPM, which should be preserved in MCC for (i) the *ex situ* conservation of these biological components of agro-ecosystems, (ii) the study of these microbial resources, and (iii) the transfer of these biological cultures to develop new agro-biotechnologies. Thus, it is essential to solving bottlenecks in the functioning of MCC, mainly the digitization, easy access, and dissemination of biological information for each preserved microbial strain (including metabolic and genetic diversity). This will lead to the extensive use of PGPM for the development of new strategies to increase sustainable food production. Thus, the role of global MCC is vital to provide biological resources that directly support soil health, sustainable food generation, and the wellbeing of the human population.

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AUTHOR CONTRIBUTIONS

Conceptualization, supervision, and validation were developed by SS-V. All authors contributed to manuscript revision, and have read and approved the submitted version. All authors wrote, visualized, and edited the manuscript.

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