





# The Importance of Microbial Inoculants in a Climate-Changing Agriculture in Eastern Mediterranean Region

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**Abstract:** Climate change has gained importance due to its severe consequences for many aspects of life. Increasing temperature, drought and greenhouse gases affect directly or indirectly the productivity of agricultural and natural ecosystems as well as human health. The nutrient supply capacity of the soil is diminishing, while food requirements for the growing population are increasing. The ongoing application of agrochemicals results in adverse effects on ecosystem functioning and food chain. Now, more than ever, there is a need to mitigate the effects of agricultural activities on climate change using environmentally friendly techniques. The role of plant beneficial microorganisms on this global challenge is increasingly being explored, and there is strong evidence that could be important. The use of functional microbial guilds forms an alternative or even a supplementary approach to common agricultural practices, due to their ability to act as biofertilizers and promote plant growth. Application of microbial inocula has a significantly lower impact on the environment compared to chemical inputs, while the agricultural sector will financially benefit, and consumers will have access to quality products. Microbial inoculants could play an important role in agricultural stress management and ameliorate the negative impacts of climate change. This short review highlights the role of microbes in benefiting agricultural practices against climate-changing conditions. In particular, the main microbial plant growth-promoting functional traits that are related to climate change are presented and discussed. The importance of microbial inoculants' multifunctionality is debated, while future needs and challenges are also highlighted.

Keywords: microbial inoculants; climate change; multifunctionality; drought; nutrient efficiency

# 1. Introduction

The Eastern Mediterranean and Middle East (EMME) has been classified as a climate "global hot-spot", and concerted actions are urgently needed to face climate change challenges. Indeed, the Cyprus Government's Initiative for Coordinating Climate Change Actions in the EMME region aims at the development of a Regional Action Plan to address the specific needs and challenges that countries are facing in the EMME region, to address and ameliorate the impact of climate change and finally to advance mitigation actions according to the Paris Agreement. Extreme temperatures, intense and frequent precipitations, drought periods, high salinity, and soil erosion are a few of the phenomena that can be observed globally, regardless of region or season. Particularly for the EMME region, historical and modeled data show a strong drying trend starting in the early 1960s, with the lowest precipitation rates being recorded in the late 1990s [1]. It is expected that the overall warming across the region of EMME will be gradual, ranging from 3.5 to 7 °C by the end of the century [2].

Historical data also showed that in the Mediterranean region, there was a substantial decrease in precipitation during winter [3] and projections indicate that this will further decrease [2]. These main climatic components are expected to significantly affect the productivity of agricultural ecosystems and, subsequently, food security. Traditionally, the increase in agricultural production relied on plant breeding and farming technologies [4,5]. During the last few years, the intensification of agriculture for yield increase has led to the extreme overuse of chemical fertilizers and the depletion of natural resources (i.e., water). Thus, natural ecosystems are being progressively threatened by air, soil and water pollution [6].

Therefore, it has become evident that the increasing need for crop production should be paired with practices and strategies focused on the adaptation of agriculture on climate change [7] and the implementation of tools that also mitigate the adverse effects of agriculture on climate change. The Food and Agricultural Organization (FAO) of the United Nations introduced the concept of climate-smart agriculture (CSA) at the 2010 Hague Conference on Agriculture, Food Security and Climate Change, and since then, it has gained international interest and support [8]. The main objectives of CSA are (i) the sustainable increase of agricultural systems' productivity and income, (ii) to adapt the agricultural ecosystems to a climate-changing environment, and (iii) the development of tools that reduce greenhouse gas emissions (GHG) [9].

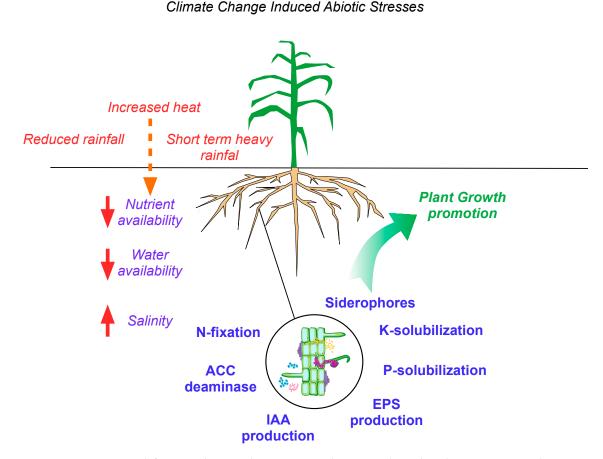
The cornerstone for achieving these objectives is the proper management and utilization of soil genetic resources and functions. The exploitation of soil genetic resources for the isolation and inoculation of beneficial microbial strains to crops has been extensively explored over the past few decades [7]. Moreover, recent studies have suggested that microbial communities can mitigate GHG emissions from agricultural soils [10–12]. Indeed, microbes regulate various soil functions, thereby affecting crop growth [13–15]. Soil microbes occur in immense numbers and exhibit vast genetic diversity and variation. It is well known that soil bacteria and fungi promote plant growth and can be found both free-living and symbiotic with plants [16,17]. Plant growth-promoting microorganisms (PGPM) increase plant productivity through their ability to fix nitrogen, solubilize soil phosphorus and potassium, and produce siderophores and phytohormones [18]. Moreover, such host-microbe interactions are crucial for plant health since microbes affect different plant growth stages (i.e., germination, flowering) [19,20]. Besides this, it has been well established that plants acquire defense/tolerance mechanisms against biotic (i.e., pathogens and pests) and abiotic (i.e., drought and nutrient limitation) stresses through their ability to establish symbiotic relationships with microbes [20,21].

The objective of this short review is to discuss the role of microbes in benefiting agricultural practices against climate-changing conditions. In particular, the main microbial plant growth-promoting functional traits that are related to climate change like drought and reduced soil fertility are presented and discussed. The importance of microbial inoculants' multifunctionality will be debated while future needs and challenges are also highlighted.

## 2. Microbial Functions Benefit the Adaptation of Crops to Climate Change

The direct mechanisms of PGPM functions and traits that support plant growth and are related to the adaptation of crops to climate change are diverse (Figure 1). For example, water is the main critical factor controlling the productivity of agroecosystems in arid and semi-arid regions because its availability determines largely the performance of both plants and microbial communities, which in turn control nutrient cycling. Recently, a meta-analysis showed that the overall effect of water limitation on plant N and P content was negative and this was associated with the duration of the drought [22]. Previously, it was suggested that crop growth is suppressed under drought stress by reducing N and P uptake, transport, and distribution of these nutrients within plants [23]. Besides this, low water soil content causes a reduction in plant nutrient uptake due to a suppression of the mineralization process and by reducing mass flow and nutrient diffusion in the soil [24,25]. The reduction of annual rainfall as a result of climate change and the subsequent reduction in soil moisture amplifies climate

warming in the EMME region [26]. This effect is expected to intensify the duration and level of extreme temperatures causing substantial reductions in plant performance and crop productivity. In addition, long-term irrigation and fertilization have caused a substantial increase in soil salinity in agricultural areas. It has been estimated globally that 50% of the irrigated agricultural area is affected by salinity, causing a significant reduction in crop productivity [27]. The reduction in water precipitation and increase in temperature due to climate change is expected to increase further the frequency and the duration of irrigation, increasing thereby salinity risks. It is therefore evident that targeted solutions should be developed to face the main effects of climate change in the EMME region and these should be mainly related to water limitation, salinity, and nutrient uptake. Microbial functions and traits are linked to the alleviation of water and salt stress and enhanced nutrient uptake; the efficient accession of plants to essential nutrients like nitrogen, phosphorus, and potassium, the production of phytohormones, siderophores, and exopolysaccharides [28–33]. Through these functions, microbes help crops to adapt to abiotic stresses. In the following section, we present the key traits of PGPM that are related to enhanced water and nutrient efficiency under conditions that are mainly driven by climate change.



**Figure 1.** Bacterial functional traits that promote plant growth under abiotic stress conditions induced by climate change. ACC: 1-aminocyclopropane-1-carboxylic acid, IAA: Indolyl Acetic Acid, EPS: exopolysaccharides.

2.1. Nitrogen Fixation Serves as a Mechanism against Nitrogen Deficiency in Soils—An Indirect Effect of Climate Change

Nitrogen (N) is the main limiting factor for an agricultural ecosystem, and this is the reason for the excessive use of nitrogenous chemical fertilizers during the last few decades. Nitrogen fertilizers' overuse leads to environmental problems such as eutrophication of water, loss of biodiversity, global

warming, and stratospheric ozone depletion through the emissions of greenhouse gases [28]. It has been reported that the cost of environmental N pollution exceeds the added value due to N fertilization [34]. Precise and accurate sustainable practices that aim to reduce the excess of external nitrogen input are fundamental to reduce the release of NO<sub>3</sub><sup>-</sup>, N<sub>2</sub>O, and NH<sub>3</sub> in the environment, mitigating therefore the negative effects of N fertilization on climate change. Practices like minimum tillage strategies [35], cover crops [36], the application of organic N sources [37], and the integration of biological nitrogen fixation in agricultural ecosystems [38,39] have been identified as practices that could promote environmentally friendly agriculture. Microbial communities are responsible for biological nitrogen fixation, which is distinguished as symbiotic and free-living [40]. The symbiotic nitrogen-fixing bacteria belonging to genera *Rhizobium, Mesorhizobium, Sinorhizobium, Bradyrhizobium* have been considered as PGPM [41]. All these form associations with legume plant species (pea, alfalfa, soybean), while *Frankia* species form mutualistic associations with non-leguminous plant species [42].

On the other hand, the non-symbiotic nitrogen-fixing bacteria include inter-alia *Azotobacter*, *Azospirillum, Pseudomonas, Bacillus, Agrobacterium, Enterobacter, Erwinia, Burkholderia* [43]. The presence of nitrogen-fixing bacteria in a plant's rhizosphere improves N availability, leading to increased crop yield [28,44], especially when N is limited or not applied [45–47]. The reduction of N inputs in agricultural ecosystems is the main mitigating action for climate change due to the reduction of direct and indirect greenhouse gas emissions. Although the reduction of direct soil N<sub>2</sub>O emissions is expected after the inoculation of efficient N-fixing bacteria due to an overall reduction in N fertilization, the latter should be proven with more studies [48]. Moreover, the isolation of bacteria able to reduce N<sub>2</sub>O to N<sub>2</sub> is a promising strategy to mitigate soil direct N<sub>2</sub>O emissions (Figure 2). Indeed, recently, Akiyama et al. [10] reported a reduction in N<sub>2</sub>O soil direct emissions from a soybean crop when inoculated with *Bradyrhizobium* isolates carrying *nosZII* genes. These findings further support the notion that more research is needed to isolate bacteria able to consume N<sub>2</sub>O produced in the soil [49].

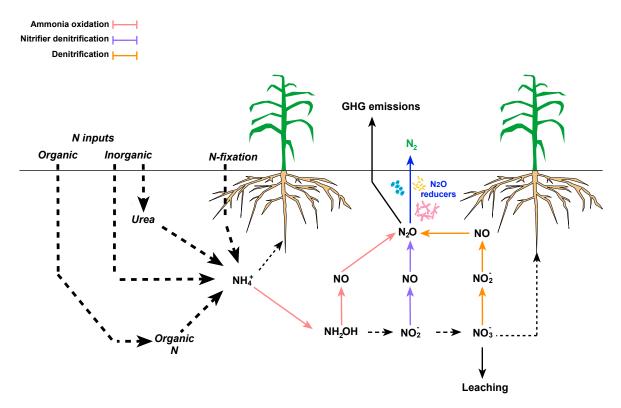


Figure 2. Simplified N cycle in soils and the potential use of  $N_2O$  reducers to mitigate  $N_2O$  emissions. Arrows with different colors denote the different N transformation processes in the soil leading to  $N_2O$  formation.

In addition, several studies demonstrated the beneficial effect of co-inoculation of free-living nitrogen-fixing bacteria with symbiotic N fixers in legumes, indicating that free-living fixers support nodulation and further stimulate plant growth [50–52]. Besides N-fixation, most of these bacteria harbor the molecular cascade for other functions and traits that promote plant growth. Moreover, several studies reported the positive effect of bacteria species having additional traits on various plant species grown under drought. The reported traits include P-solubilization and the biosynthesis of plant hormones, ACC deaminase, siderophores, and exopolysaccharides [53–60]. These findings clearly show that the beneficial effect of N-fixing bacteria on plants grown under stress is related not only to one trait but also to complementary functions that promote plant responses under abiotic stress conditions.

## 2.2. Phytohormone Production: A Multitask Mechanism to Mitigate Drought and Salt Stress

Plant hormones are critical compounds in the response of plants to drought and salt stress [60,61]. They regulate the biochemical, physiological, and morphological levels of the plant and enhance agricultural production [62,63]. Several rhizospheric microorganisms can produce indole-3-acetic acid (IAA) and cytokinins, thus playing an essential role in the plant-microbe interaction [61]. Recently, it has been shown that IAA-producing bacteria reduce abscisic acid/1-aminocyclopropane-1-carboxylate (ABA/ACC) content and enhance the expression of genes that improve plants' tolerance to salt and drought stress [64]. Moreover, auxins affect root morphological traits like the root length, root surface area, and number of root tips. Overall, these traits determine plants' ability to exploit soil resources like nutrients and water, which are critical when plants experience abiotic stress [65]. Indeed, previous studies demonstrated that the inoculation of several plant species grown under salt or water-limited conditions, with bacterial species with high IAA or cytokinin production, resulted in better performance compared to non-inoculated controls. For example, *Medicago truncatula* plants responded better to the effects of high salt stress when inoculated with a *Sinorhizobium meliloti* strain that produced high levels of IAA [29].

Similarly, under salt stress conditions, the inoculation of sunflower plants with two *Pseudomonas* IAA-producing strains caused an increase in fresh plant weight compared to non-inoculated plants [66]. In another study, Naveed et al. [67] reported that two maize cultivars became more resistant to drought stress when inoculated with two different plant growth-promoting rhizobacteria. This response was associated with IAA biosynthesis [68]. The levels of IAA produced by *Bacillus megaterium* have been significantly correlated with root growth and the better response of *Trifolium* plants grown under stress [69]. The drought tolerance of alfalfa plants inoculated with a *Sinorhizobium meliloti* strain that overproduced cytokinins was substantially high compared to control plants [70]. This response was associated with low accumulation of  $H_2O_2$  in alfalfa leaves, while the transcripts of genes associated with antioxidant mechanisms were substantially higher compared to non-inoculated controls. These findings clearly show that cytokinin-overproducing strains can improve the tolerance of plant species to drought. Indeed, the shoot biomass of lettuce plants grown under water-limited conditions when inoculated with a cytokinin-producing *Bacillus* strain was substantially higher compared to non-inoculated plants [71]. The authors suggested that replacing the concentration of loss of plant cytokinins due to drought stress with those produced by the *Bacillus* benefits above-ground biomass.

## 2.3. Regulation of Inhibitory Ethylene Levels in Plant Tissues

Ethylene regulates key plant processes like seed germination, fruit ripening, senescence, root development, and elongation as well as nodule formation [72]. Under plant stress conditions, ethylene production is induced and triggers the senescence mechanisms of plants [73]. A wide range of microorganisms have the molecular cascade which encodes a deaminase that assimilates the precursor compound of ethylene, the 1-aminocyclopropane-1-carboxylate (ACC). The activity of this enzyme has been reported mainly in bacteria and some fungi, while an in silico search of metagenomes revealed that very few archaea harbor the gene encoding ACC deaminase biosynthesis [74]. The importance of these

bacteria is due to the positive effect that ACC deaminase has on preventing the accumulation of ethylene in plants under several stress conditions. Under drought, high temperature, and salt conditions, studies have shown that inoculating plants with ACC deaminase-producing bacteria had a better response to these stresses [75–78]. Besides the direct effect of ACC deaminase bacteria on plant root elongation and shoot growth, ACC deaminase-producing bacteria improved beneficial plant–microbe interactions. Indeed, the modulation of inhibitory plant ethylene levels after the inoculation of plants with ACC deaminase bacteria seems to be critical for the nodulation process in legumes [79]. Earlier, Tavares et al. [80] reported that the bacterial ACC deaminase-producing endophyte *Serratia grimesii* BXF1 promotes the early nodulation and growth of common beans. It is evident that the isolation of bacterial consortia, harboring such functional microorganisms, will improve our efforts to deal with the negative effects of climate change.

## 2.4. Improved Phosphorus Availability and Acquisition Efficiency

Phosphorus (P) is the third most crucial nutrient (after N and K) for plant growth since it participates in almost all metabolic processes of plant cells, including energy conversion, respiration, molecular biosynthesis, and photosynthesis. However, phosphorus in soils is present in forms that are not available to plants, and it could be a great challenge to provide them with adequate P when grown in alkaline and calcareous soils. These soil types are common in areas with low rainfall, such as those of arid and semi-arid regions. Under these conditions, phosphate ions are not available to plants, and traditionally, farmers apply higher quantities of P fertilization than needed to cover crop needs [81]. P-fertilizers' overuse caused an increase in P pools in the soil, which is a potent risk for eutrophication of surface waters. Indeed, sporadic heavy rainfalls and winds during dry seasons in arid and semi-arid areas could cause non-point source pollution with large amounts of P. It is therefore evident that increasing P fertilization is not a sustainable solution and other management practices should be proposed to reduce P inputs without reducing the productivity of agricultural ecosystems. Specific microbial guilds like P-solubilizing bacteria and mycorrhizal fungi could be used as alternative tools to solubilize, mineralize and facilitate the more efficient acquisition of phosphorus and make it available to plants [82]. It has been reported that the inoculation of crops with phosphate-solubilizing microbes could reduce the application rates of P fertilizers by 50% without any significant reduction in crop yields [83,84].

Indeed, Gouda et al. [85] reported that phosphate solubilization and mineralization is a critical function for PGPM that should be examined during their screening process. Early studies reported that 1 to 50% of soil bacteria and around 0.5 to 1% of soil fungi could be characterized as phosphate-solubilizing microorganisms [86]. In particular, bacterial isolates or strains belonging to genera such as *Arthrobacter*, *Bacillus, Burkholderia, Beijerinckia, Flavobacterium, Pseudomonas, Rhizobium, Mesorhizobium* have been characterized as phosphate solubilizers and are able to promote plant growth [30,87–89]. For example, inoculation of *P. sativum* L. plants grown in soil under soluble phosphate-limiting conditions, with bacterial isolates that produced medium-high levels of gluconic acid, resulted in beneficial plant growth [30]. These findings are in line with the general notion that the release of organic acids into the soil by bacteria facilitates the conversion of phosphate complexes into soluble phosphates, an available form of P for plant uptake and assimilation [90]. On the other hand, fungal isolates belonging to *Penicillium* and *Aspergillus* genus have been considered as the most effective phosphate solubilizers isolated from soil samples [91,92].

Besides P solubilization, increasing the acquisition of the phosphorus soil available pools, especially under water-limited conditions, is another strategy to improve crop yields in a climate-changing environment. The role of mycorrhizal fungi is crucial to meet this challenge. Notably, for P acquisition, arbuscular mycorrhizal fungi (AMF) could dominate the total P uptake pathway in plants, even in plants that do not grow better when colonized with AMF [93]. Early studies showed that inoculation of plants grown under stress with AMF causes improved performance, and this was attributed inter alia to improved P acquisition [94]. Indeed, in a field study, inoculation of watermelon grown under

stress conditions with AMF caused a significant increase in P root content [95]. In this study, the root P content was significantly higher in inoculated plants compared with the non-inoculated plants, irrespectively of water treatment. Interestingly, the amounts of P found in roots of non-inoculated but well-irrigated plants were higher than those of plants inoculated with AMF and grown under water-limited conditions. These findings suggest that the functionality of native AMF fungi, as well as the P uptake mechanisms, control P acquisition [96]. Recently, Bowles et al. [97] demonstrated that mycorrhizal plants acquired more P during wet/dry cycles than the more stable soil moisture conditions. Indeed, under drought conditions, the transcripts of specific PHT1 transporters in tomato plant roots, which are mainly involved in P uptake from the soil in AMF plants, were upregulated [98]. However, this was AMF species-dependent, suggesting that no "visible" positive response of plants should be expected under field conditions. Apparently, the plant genotype has a significant effect on P acquisition and the regulation of AMF able to colonize plant roots. Recently, under drought stress conditions, a chickpea genotype tolerant to drought was found to have a different AMF community structure, and the P content was not correlated with AMF colonization [99].

Other studies reported a clear synergistic effect of phosphate-solubilizing bacteria and AMF on plant growth both under water-limited and non-limited conditions [100–102]. Indeed, phosphate-solubilizing bacteria have been detected on AMF hyphae surface [103]. It has been suggested that phosphate solubilizers increase P availability, which can subsequently be absorbed by AMF hyphae. However, the enormous variation among the bacterial strains in their growth on AMF and their combined effect on P acquisition by plant roots should be taken into account during the development of such inoculants [104].

## 2.5. Potassium Solubilization

From the primary essential macronutrients, potassium (K) is the second most important and plays a vital role in plant growth, development, and metabolism. Lack of potassium retards plant growth, and crops exhibit yields of lower quantity and quality. It has a central role in water and nutrient transport in plants [105]. In detail, potassium regulates the opening and closing of stomata, thereby affecting photosynthesis directly, while it is also known to maintain cell turgor and to adjust osmotic levels in plant cells [106]. In the soil, K availability depends on the soil type and, importantly, despite the ample amount of K in the soil, only a soluble/dissolved fraction is available to plants. This is the reason that large agricultural areas suffer from K deficiencies [107]. Indeed, K binds strongly between clay minerals and its release into the soil solution is a relatively slow process [108]. In order to increase and adapt agricultural ecosystems to abiotic stresses that are mainly derived from climate change, like water shortage and salt deterioration of soil, K availability holds a critical position for plant performance. Potassium solubilization is facilitated in the plant rhizosphere either by plant or microbial excretion of organic acids or other compounds, i.e., polysaccharides, which facilitate the dissolution of soil minerals to release potassium [31,109,110]. In soils, a wide range of bacterial and fungal species can release potassium in a plant-available form. Microorganisms such as Acidithiobacillus ferooxidans, Arthrobacter sp., Azotobacter sp., Bacillus sp., Klebsiella sp., Paenibacillus sp., Pseudomonas sp., Rhizobacterium sp. [111–113] are known for their potential role in mobilizing an insoluble native K-source as an effective biofertilizer, which could reduce the level of K fertilizers providing high crop yield with eco-friendly, low-cost crop production [114]. Indeed, Pindi [115] showed that the application of *Frateuria aurantia* could reduce the use of K fertilizers by up to 60%. Other studies also demonstrated that the inoculation of different plant species with potassium-solubilizing microorganisms resulted in improved performance [116–119]. Although there is increasing interest in isolating potassium-solubilizing bacteria, more efforts and research should be focused on co-inoculation studies to reveal any interactive positive effects between K-solubilizing bacteria and fungi with other promoting bacteria with different traits.

# 2.6. Siderophore Production: Another Mechanism to Assist Plant Growth under Stress Conditions

In calcareous and alkaline soils, iron (Fe) availability is limited, causing nutritional disorders in crops grown under these conditions. In particular, Fe has a direct effect on plant development and has

a substantial impact on crop yield and quality [120]. To overcome Fe deficiency, plants have developed several strategies [121], including the biosynthesis and secretion of various chemical substances in the rhizosphere, which solubilize Fe from soil [122]. Similarly, microbes produce low molecular chelating compounds called siderophores to mediate Fe uptake into the cell [123]. According to Boukhalfa and Crumbliss [124], more than 500 different siderophores have been identified. It has been reported that the microbially derived siderophores are more effective than synthetic chelators that are currently in use in agricultural systems [125,126]. Numerous studies report that bacterial and fungal microbes belonging to the genus of Aspergillus, Azotobacter, Azospirillum, Bacillus, Flavobacterium, Rhizobium, Pseudomonas and Trichoderma can produce and secrete siderophores [127–132]. Siderophore production is a tool of bacteria to be more competitive to other microorganisms, thereby restricting their growth, and several studies have highlighted their contribution to the control of plant pathogens [133,134]. Siderophore-producing bacteria could increase the Fe content of plants. Previous studies showed that inoculation of plants with siderophore-producing bacteria could improve the biofortification with iron, improving thereby the nutritional value of crop products [135–138]. In most of the studies, the bacterial species which are reported to enhance plant growth under abiotic stress conditions produce siderophores. Indeed, Azotobacter strains able to secrete siderophores substantially increased the iron content and shoot dry biomass of maize under drought stress conditions compared to non-inoculated control plants [139]. In another study, a *Trichoderma* strain induced physiological protection of cucumber plants grown under salt stress [32]. These results clearly show that the presence of siderophores could potentially promote plant response and performance under adverse climatic conditions, like drought and saline soil. However, the interaction effects between siderophore-producing bacteria with other microbes harboring different plant growth-promoting traits are scarce. More research is needed to reveal the contribution of siderophore production to plant responses to several abiotic conditions that prevail under different climatic scenarios.

## 3. Multifunctional Inoculants: The Concept of Synthetic Microbial Communities

Tackling climate change requires the redesign of agricultural practices and the application of technologies that enable crops to adapt to these adversities. During the redesign and development of innovative strategies in agriculture, the application of microbial inoculants could be an essential tool to achieve the required objectives. However, the challenge of developing microbial inoculants to assist crops in managing the adverse effects of climate change remains. The global market of microbial inoculants includes formulations containing one or few strains of microorganisms (bacteria or fungi) that have a positive effect on cultivated plants. Although there has been rapid growth in this sector, these formulations do not always have the desired effect for the crop. This is because the microorganisms that make up the formulations are significantly affected by the agro-environmental conditions (agricultural practices, soil environment, climatic conditions, and water availability) of the field where they are applied [140–142]. Under this concept, it is of paramount importance to provide solutions that meet the requirements of the farmers, which is the efficacy of the product. In order to introduce microorganisms to address the adverse effects of climate change, it is necessary to develop synthetic microbial consortia with specific functions that can help plants respond to conditions that affect crop yields. Indeed, Wallenstein [143] reported that it is possible to engineer a plant rhizosphere through inoculation, which eventually assists plants in alleviating abiotic and/or biotic stress conditions. Since plants do not grow alone but in the presence of other organisms and a variety of pedo-climatic conditions, "next" generation inoculants should also form strong associations with the native rhizosphere microbial community structure [144] in a way that plant growth will be promoted. In the context of climate smart agriculture, habitat-specific and functionally appropriate synthetic microbial communities [145] will be instrumental mainly in targeting the drought, salt, or heat tolerance of specific crops. Soil is a vast pool of microbial guilds, and it is well known that autochthonous isolates provide improved plant performance [146,147].

Additionally, the rhizosphere and the roots are rich sources of microbes exhibiting plant growth-promoting functions [148,149], and both are valuable tools for isolating and developing plant-specific microbial multifunctional inocula. Indeed, throughout the literature cited in the current review, most of the studies show that different bacterial and fungal isolates perform more than one function, i.e., nitrogen fixation, IAA and ACC deaminase production, siderophore excretion, P and K solubilization [150–155], which promote plant growth under stress conditions (biotic or abiotic). Thereby, the importance of selecting multifunctional microbial isolates or creating multistrain microbial inoculants is based on the idea that this kind of product could elicit more broadly positive response in inoculated plants when limiting conditions for plant growth are present. Besides this, multistrain and multifunctional consortia could be used in diverse types of soil compared to single-strain formulations, because the microbial isolates included in the formulation respond in a wide range of pH, water, and nutrient availability, making the consortium extremely competent. For example, low P availability is associated with a rapid reduction of nitrogen uptake and, consequently, assimilation [155]. These conditions are often observed in the Mediterranean, like in rainfed agroecosystems, where soil pH is also higher than 8. Under these extremes, plant inoculation of P-solubilizing microorganisms and N-fixing bacteria could enhance tomato productivity [156]. In another study, the productivity of maize was higher when plants were inoculated with several bacterial strains, compared to those inoculated with one single strain [157]. The main challenge for the development of multistrain inoculants is the positive plant response after inoculation under field conditions. Previous studies reported that plant inoculation with more than one species does not always lead to a positive plant response [158], suggesting that microbe-microbe interactions within synthetic communities' inocula should also be taken into account. Recent reports suggested that the identification of a core microbiome, using metagenomic high-throughput screening, and the subsequent isolation and functional evaluation of the main microbial guilds of the microbiome will lead to more efficient microbial inoculants, based on the community structure of high-quality crops [159,160]. Besides efficiency and suitability, the application of microbial inoculant products should be sustainable without disturbing the native microbiome balance and the functions provided in the ecosystem. For example, if an efficient inoculum promotes plant growth but co-currently suppresses the proliferation and the function of other beneficial microbes like AMF and or symbiotic fixing bacteria, then cautions should be taken when using this inoculum [159]. Although invasiveness has been extensively studied in several ecosystems, the persistence of "foreign" microbial strains introduced in a soil has been overlooked and studies should be carried out to facilitate and ensure the appropriateness of using a microbial inoculant in agricultural ecosystems [161].

## 4. Future Research Needs and Challenges

So far, the literature has provided strong evidence that plant growth-promoting microbes enhance plant growth and productivity through a variety of mechanisms and processes. The challenge for the scientific community and the industry is to develop such tools and technologies that will facilitate the efficient use of these microorganisms by the farmers. Efficient formulations of plant growth-promoting microorganisms can improve soil fertility, plant tolerance, crop productivity, and maintain nutrient cycling in agroecosystems. Research efforts should strengthen the isolation of new strains and develop multistrain formulations that could be used in a wide range of environments and conditions. In addition, efforts of mapping microbial diversity should also be encouraged in order to explore and secure the soil genetic resources, thereby increasing terrestrial ecosystems from which beneficial microbes could be isolated.

The need for integrating microbial solutions with other strategies and components of modern agriculture which mainly affect systems' productivity under climate-changing conditions is more than essential. The agricultural sector in the EMME region is particularly vulnerable due to its dependency on water resources and the productivity of agricultural ecosystems is expected to experience high pressure. Droughts at increasingly shorter intervals that have been noticed, for example, in Cyprus since 1990 and the overall expected decline of annual precipitation in the region [162] indicates the

challenge of developing tools that can sustain ecosystem productivity. Microbial inocula able to enhance water use efficiency could be part of a holistic strategy for sustainable crop production and should be linked with parallel efforts aiming to reduce climate-related risks.

To this end, plant breeding is a tool with a central role in food security and should be linked with plant-associated microbes [163]. Novel methods that overcome barriers of conventional plant breeding should be deployed [164] and next-generation plant breeding efforts must include microbial communities that will be able to beneficially interact with the plants. The main challenge to integrate the genotype x microbiota approach in a tool able to provide plants to farmers that suit their individual needs, based on the local environmental conditions can be greatly facilitated when plant breeding is performed on the basis of the individual plant and its root system, exploiting micro-adaptation processes specific for individual fields through innovative experimental designs [165]. Further, it is expected that inoculation of a plant genotype selected under poor soil conditions with a multistrain inoculum could enhance the productivity of the resultant phenotype [166]. Moreover, studies on the impact of microbial inoculants on beneficial microbial guilds should be conducted to ensure sustainability and avoid irreversible changes in soil biodiversity. Besides efforts in research and development, policy tools, i.e., actions through rural development plans, should promote the awareness of farmers regarding the potential benefits of using plant growth-promoting microbes. Finally, initiatives that will promote and highlight the importance of microbial communities in conjunction with appropriate plant varieties for the adaptation and mitigation of climate change in Regional Action Plans, are needed.

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