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Review

Facing Climate Change: Application of Microbial Biostimulants to Mitigate Stress in Horticultural Crops

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Abstract: In the current scenario of rapidly evolving climate change, crop plants are more frequently subjected to stresses of both abiotic and biotic origin, including exposure to unpredictable and extreme climatic events, changes in plant physiology, growing season and phytosanitary hazard, and increased losses up to 30% and 50% in global agricultural productions. Plants coevolved with microbial symbionts, which are involved in major functions both at the ecosystem and plant level. The use of microbial biostimulants, by exploiting this symbiotic interaction, represents a sustainable strategy to increase plant performances and productivity, even under stresses due to climate changes. Microbial biostimulants include beneficial fungi, yeasts and eubacteria sharing the ability to improve plant nutrition, growth, productivity and stress tolerance. This work reports the current knowledge on microbial biostimulants and provides a critical review on their possible use to mitigate the biotic and abiotic stresses caused by climate changes. Currently, available products often provide a general amelioration of cultural conditions, but their action mechanisms are largely undetermined and their effects often unreliable. Future research may lead to more specifically targeted products, based on the characterization of plant-microbe and microbial community interactions.

Keywords: sustainable horticulture; plant-microbe interactions; microbiome; induced systemic resistance; ACC deaminase; auxin; PGPR; mycorrhizae

1. Introduction

Global climatic records have shown an increase in world temperature since 1970, as well as changes in precipitation regimes, leading to several severe consequences for agriculture [1]. In this scenario of climate change, crop plants are more frequently subjected to stresses of both abiotic and biotic origin, since, in addition to direct stress on plants, climate change could expand the range of pathogens and pests, and increase the frequency and severity of disease outbreaks [2,3]. Recent estimations calculated that 50% and 30% losses in global agricultural productions are expected due to abiotic and biotic stress, respectively [4]. These losses, together with the steady increase in human population, indicate that an increase of 60% in agricultural production is required to meet global needs [5], with a consequent drastic increase in deforestation and reduction in natural habitats [6]. To help ensure food security with a limited increase in agricultural land, a sustainable strategy is to increase plant resistance and resilience to counteract climate change-induced stresses. The use of biostimulants could be a valuable option to obtain this objective [7,8]. Compared to xenobiotic agrochemicals, microbial biostimulants do not accumulate in the long term, have a low toxicity, and are less prone to select resistant strains of pests and pathogens, and, therefore, can be considered environment- and human-friendly. Hence, the biostimulant market has steadily increased in the last two decades [9], Europe being the world industry leader, with more than EUR 578 million of total sales in 2015 [10].

The compounds grouped within the 'biostimulant' category are heterogenous, including humic substances, protein hydrolysates, amino acids, seaweed extracts, chitosan and other biopolymers and inorganic molecules. In addition, the subgroup of 'microbial biostimulants' is formed by beneficial microorganisms (i.e., fungi, yeast and eubacteria) sharing the ability to increase plant growth and productivity, promote nutrient uptake and effectiveness, improve abiotic stress tolerance and/or quality of crops [7,10,11].

Microbial biostimulants are particularly interesting since plants harbor a wide and complex range of microorganisms in their phyllosphere, rhizosphere and endosphere. Indeed, microbial symbiosis is a common and fundamental condition of plants. Plants coevolved with these microbial symbionts, which are involved in major functions such as plant nutrition, plant performance and productivity, and resistance to biotic and abiotic stresses [12]. For example, fossil evidence shows that the association between plants and microorganisms is as ancient as the emersion from water, thus, suggesting that arbuscular mycorrhizal symbiosis has played a key role in the terrestrialization process [13].

Microbes exert key functions in ecosystems being involved in nitrogen fixation, carbon and nitrogen cycling, plant nutrient acquisition and soil formation [14]. Thus, several microbial symbionts can also act as biofertilizers, providing to the plant complementary limiting nutrients by synergic mechanisms such as nitrogen fixation (e.g., *Azospirillum*, *Azotobacter*, *Rhizobium*), phosphate solubilization (e.g., *Pseudomonas* spp., *Azospirillum*, arbuscular mycorrhiza), cellulolytic activity (e.g., *Trichoderma*, *Penicillium* spp., *Aspergillus*, *Bacillus amyloliquefaciens*), soil acidification (e.g., *Bacillus subtilis*), and siderophore production (e.g., *Pseudomonas* spp. and *Acinetobacter*) [15].

Among fungi, the endosymbiotic genus *Trichoderma* is the most investigated and applied, due to its ability to promote plant growth and defenses, produce antimicrobial substances, parasitize fungal pathogens and prey on nematodes [16–18]. In the case of Arbuscule-Forming Mycorrhiza (AFM), the difficulties of in vitro cultivation, and the lack of comprehension of host specificity determinants and population dynamics in the agroecosystem may play against their use in commercial products, in spite of the beneficial effects exerted on their host plants, such as the increase in nutritional efficiency and in the protection from biotic and abiotic stresses (Figure 1) [11,18].

Beneficial yeasts are found in the phyllosphere and rhizosphere. Leaf-colonizing yeasts have been reported to control many foliar pathogens through direct antagonism [19] or by elicitation of systemic defenses [20]. Soil yeasts can promote plant growth by decomposing organic matter, solubilizing phosphate, promoting root growth and soil aggregation, and controlling root pathogens [21].

Biostimulant bacteria can be distinguished in Plant Growth Promoting Bacteria (PGPB) or Plant Growth Promoting Rhizobacteria (PGPR), the latter specifically colonizing the rhizosphere. The most studied genera are *Burkholderia*, *Bacillus*, *Pseudomonas*, *Serratia* and *Streptomyces* [15,22].

Recently, biochemical, physiological and molecular studies of the plant–microbe interactions revealed the existence of microbe-induced plant responses to stress [23], which could activate an Induced Systemic Tolerance against abiotic stresses [24] or Induced Systemic Resistance against the biotic ones [25]. It is worth noting that many commercial products based on useful microbes or microbial consortia, such as Subtilex® (BeckerUnderWood, Inc., Ames, IA, USA), Kodiak® (Gustafson, Inc., Plano, TX, USA), Biota Max® (CustomBio, Inc., Deerfield Beach, FL, USA), Trianum-P® (Koppert, Srl, Verona, Italy) and Custom GP® (CustomBio, Inc., Deerfield Beach, FL, USA), express multiple functions (competition with pathogens, induction of plant defenses, hormonal stimulation, nutritional exchange) with synergistic and additive effects.

In the current scenario of rapidly evolving climate change, microbial biostimulants represent a sustainable option to support plants coping with biotic and abiotic stresses. While laboratory research and technological development of plant-associated microbes have highlighted their beneficial functions, these have often been generically defined, or have not been efficiently reproduced in field conditions. As a consequence, microbial biostimulants have generally been adopted as accessory treatments, rather than expressing the full potential of microbiome control. The aim of this work is to present the current knowledge on microbial biostimulants, to review their uses in horticulture, and to prospect the development of innovative products to be employed under chronically unfavorable conditions, in particular those exacerbated by the ongoing climate crisis. The information on commercially available microbial species or microbe-based biostimulants has been drawn from online archives based in the European Union and in the USA [26,27]. The understanding of plant–microbe interaction under stressing conditions, together with the identification of limitations and weaknesses in the use of microbes in the current agronomical practices, are pivotal to identify specific scientific questions that need to be addressed, and were therefore investigated.

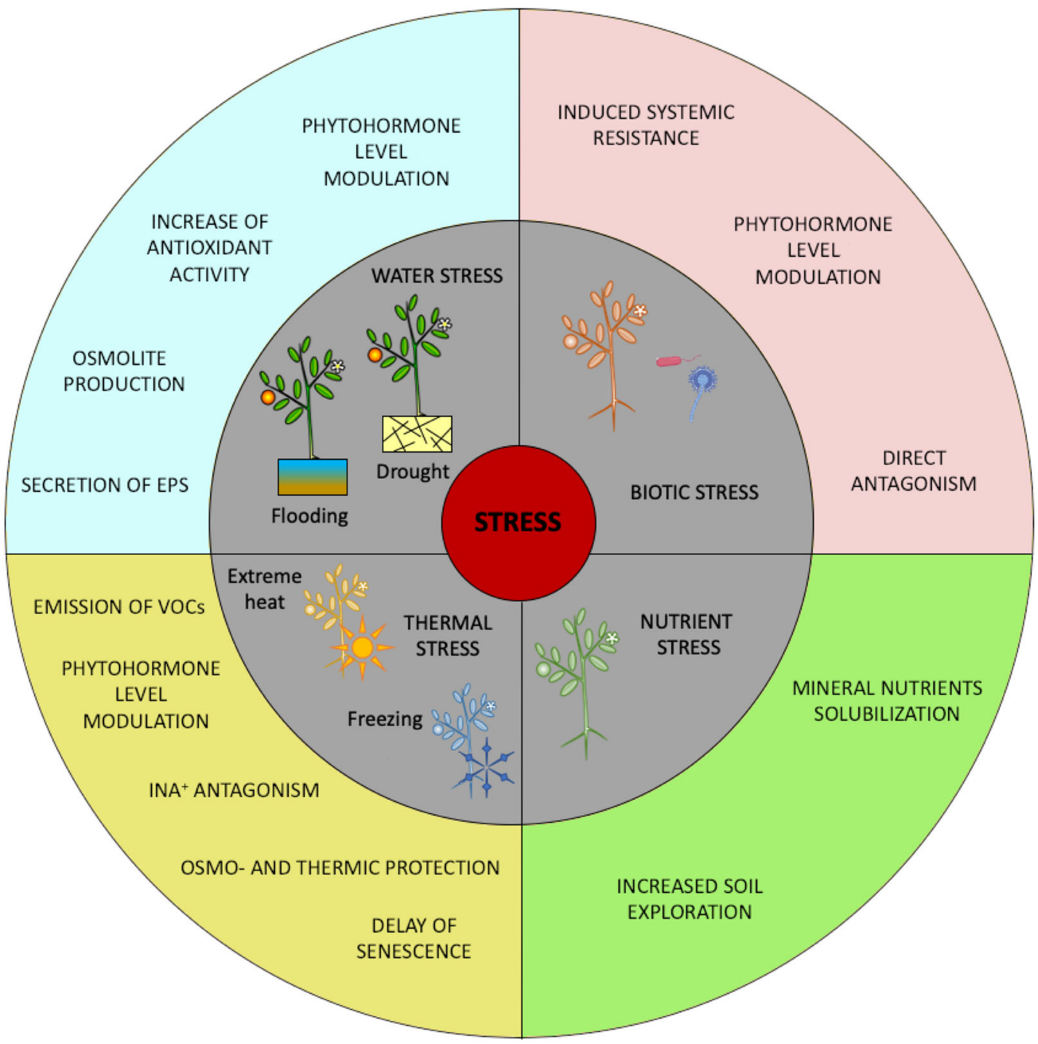

Figure 1. Schematic view of the protective mechanisms exerted by microbial biostimulants in relation to the stresses to which plants are subjected. Exopolysaccharides (EPS), Volatile Organic Compounds (VOCs), Ice-Nucleating Activity (INA^+).

2. Effect of Climate Change-Induced Stress on Plant and Role of Microbial Biostimulants

2.1. Stress Induced by Extreme Thermal Events

In comparison to the last 1000 years, the twentieth century has experienced a high climate variability and extreme temperature events, since the frequency of summer heat waves and spring frost has substantially increased [28]. Table 1 summarizes the results obtained in inducing protection against high or low temperature by use of microbes, along with the mechanisms underlying the stress protection.

2.1.1. High Temperature and Heat Waves

High temperatures impact on plant physiology increasing leaf transpiration and respiration rates, affecting photosynthesis (especially in C3 plants), and modifying allocation of photosynthates [29,30]. At high temperatures, the affinity of Rubisco to O_2 increases, while it decreases for CO_2 [31]. The increase in temperature also reduces CO_2 solubility more than O_2, thus, reducing the concentration of CO_2 relative to O_2 in the chloroplast [32]. Moreover, at high temperature, plants tend to close the stomata to reduce water losses by evapotranspiration. When the stomata are closed, CO_2 concentration rapidly drops, becoming the main limiting factor for photosynthesis, while O_2 concentration, in high irradiation conditions, rises due to the high rate of water photolysis by PSII [33,34]. Under these conditions, photosynthetic efficiency is strongly reduced, due both to the limited concentration of CO_2 and to the increased photorespiration activity of Rubisco that can consume up to 25% of the fixed carbon.

When temperature increase occurs during spring, frost risks are lowered, and horticultural crops could find a benefit in early flowering [33]. This applies mainly to annual crops, such as tomato [35] and lettuce [36], in which higher temperatures would allow multiple cycles per year [37,38]. On the other hand, for some horticultural and fruit species, increasing temperatures could represent a problem for flower differentiation. In cucumber, high temperatures promote masculine flower differentiation instead of productive feminine ones [39]. The failure to fulfill cold requirements, needed for flower differentiation in fruit crops as peach, plum [40] and apple [41] can limit the yield [42]. In the long term, temperature variations could shift fruit cultivation areas toward northern regions [42], in which mild winter temperatures can both induce early flowering, exposing plants to late frost, and extend the vegetative season, delaying dormancy. Furthermore, in this condition, a negative impact on fruit set can be also expected due to an insufficient presence of pollinators [43,44]. Finally, an increase in temperatures could worsen agriculture in environments, such as tropical areas, characterized by extreme conditions [45], thus, causing the total disappearance of particularly sensitive crops.

In plants, heat stress induces complex molecular, biochemical and physiological responses [46], which could lead to the production of heat shock proteins, enzymes involved in the degradation of Reactive Oxygen Species (ROS), osmoprotecting molecules, amino acids, sulfur compounds and sugars [47]. Heat stress responses are governed by hormonal signaling. Among them, ethylene plays a key role [6,46,48], not only in the physiology, development and senescence of plants but also in response to biotic and abiotic stresses [49]. Microbial biostimulants can strengthen plant response to heat stress through different mechanisms (Table 1). Production of ROS-degrading enzymes (peroxidases, superoxide dismutase, catalase), reduction in H_2O_2 levels and lipidic peroxidation are mechanisms that promote heat stress tolerance and that have been observed in bacteria of the genera *Pseudomonas* and *Bacillus* and in mycorrhizal fungi in tomato [50]. SoilPro® (Liventia, Inc., San Antonio, TX, USA) is a soil improver reinforced with high concentrations of *Pseudomonas fluorescens* and *Ps. aeruginosa*, commercialized for its multiple beneficial properties such as phytostimulation, bioremediation and soil fertility enhancement. *Bacillus* spp. have been thoroughly investigated, and several of them have been included in commercial products. Besides registered biopesticides (several *B. amyloliquefaciens* strains, *B. pumilus*, *B. firmus*, *B. subtilis*, *B. licheniformis*, *B. thuringensis*, *B. sphaericus*), biostimulant products only containing *Bacillus* species are available, among them Endox® (Scam, Spa, Modena, Italy) and Activate® (Natural resources Group, Inc., Woodlake, CA, USA). While many commercial products are based on these microbes, either alone or in combination, protection from heat stress is not generally mentioned among their beneficial effects.

The application of microorganisms that reduce ethylene emission has a great potentiality, since the reduction of ethylene in stress conditions could avoid the negative impact of heat stress on plant growth. In particular, the use of bacteria with 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase activity seems very promising. Indeed, ACC deaminase degrades the ethylene precursor, thus, impairing its production in the plant tissues (Figure 2). The inoculation of the ACC deaminase-producing bacterium *Paraburkholderia phytofirmans* PsJN in potato allowed the maintenance of normal plant growth under heat stress conditions [51]. Although it has promising beneficial activity, this bacterial species has not found application in commercial products.

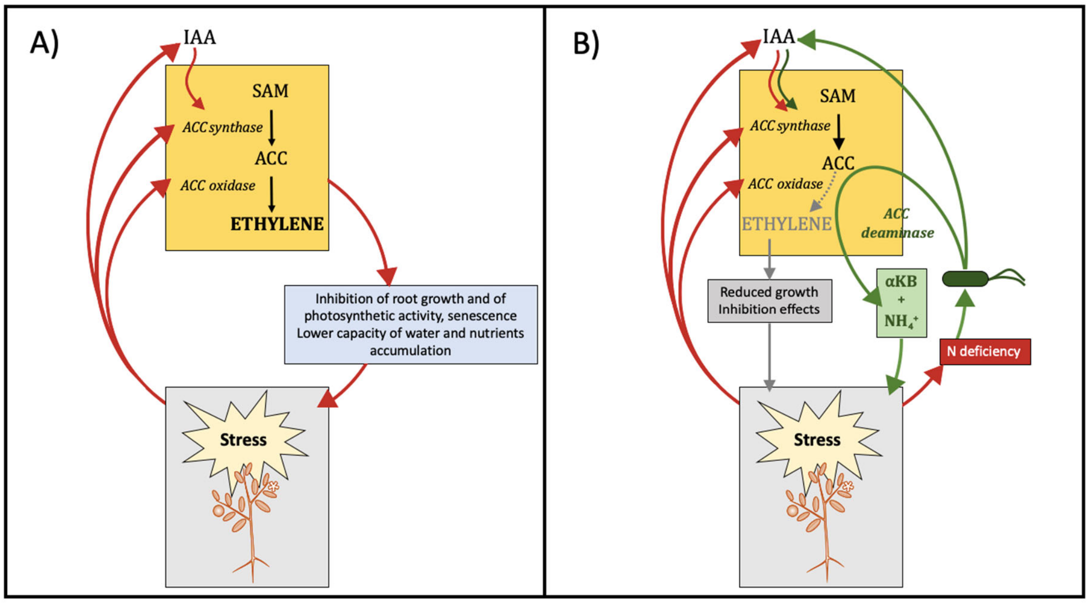

Figure 2. Effect of 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase-producing bacteria on ethylene metabolism of stressed plants. (**A**) Biotic and abiotic stresses stimulate the production of ethylene and indole-3-acetic acid (IAA) by the plant. Through the enzyme ACC synthase, S-adenosyl methionine (SAM) is converted into 1-aminocyclopropane-1-carboxylate (ACC). ACC synthase converts ACC into ethylene, which causes a general growth inhibition. IAA induces the expression of ACC synthase and contributes to the stimulation of ethylene production. (**B**) Following the colonization of the plant by ACC deaminase-producing bacteria, ACC is shunted from ethylene to ammonium (NH_4^+) and α-ketobutyrate (αKB) production. In addition, nutrient stress (including N shortage) stimulates the production of IAA in bacteria. As a result, plant growth promotion is achieved by increased IAA and reduced ethylene contents.

2.1.2. Low Temperature and Frost

Unusually low temperatures are also an important source of stress for cultivated plants. In recent years, frost events causing severe injuries and economical losses to horticulture crops occurred in France, Germany, Italy, Belgium, Switzerland and USA [52–54]. Above freezing conditions, low temperatures slow down plant metabolism, resulting in diminished photosynthetic levels, foliar growth and early senescence [55]. Below freezing conditions, bud development can be impaired since low temperatures can destroy rehydrated and sprouting buds [56]. Finally, frost can cause dehydration of plant tissues, increase in cell cytoplasm osmolyte concentrations and consequently, plasma membrane disruption [56]. Cold damages are promoted by ice core formation, which can occur even at temperatures close to zero. In plants, the formation of ice cores can be caused by the presence of microorganisms with ice nucleating activity (known as INA^+), which can live on leaves, fruits or roots [57]. The cell wall or the extracellular polymeric substance (EPS) of these microorganisms contain proteins, which promote ice crystal formation by acting as ice nucleation centres on their bacterial cell wall [58]. These microorganisms primarily include bacteria, but also ice-nucleating fungi have been described [59], which can colonize the plant both at the epiphytic and endophytic level. The first INA⁺ bacterial strain identified belonged to *Pseudomonas syringae* species [60]. Experimental tests showed that the presence of *Pseudomonas syringae* INA⁺ strain increased susceptibility to cold damage in tomato and soy plants [61]. In addition to *Ps. syringae*, other species such as *Erwinia herbicola* (syn: *Pantoea agglomerans*) [62], *Xanthomonas campestris* [63] and the Gram-positive bacterium *Lysinibacillus* sp. [64] showed some INA⁺ activity.

The use of microbial biostimulants able to outcompete INA⁺ microorganisms has become an important method to minimize the losses caused by frost damages (Table 1). Among them, the use of *Pseudomonas syringae* mutants with inactivated ice nucleating gene reduced frost damages [65,66]. Furthermore, several bacterial strains can efficiently compete with INA⁺ bacteria and prevent plant colonization [67–69]. An example of a widely used product to prevent frost damage is Blightban A506® (Nufarm Americas, Inc., Sugar Land, TX, USA), which is based on lyophilized *Ps. fluorescens* A506 [70]. This product is also applied for the biological control of fire blight (*Erwinia amylovora*) in apple and pear trees.

Microbial biostimulants can also mitigate the effect of above-freezing temperatures. In fact, microbial symbionts producing growth hormones, such as auxins or gibberellins, can counteract plant growth inhibition due to low temperature. Among auxins, indole-3-acetic acid (IAA) is produced by several microorganisms [71]. Furthermore, IAA production can be induced by cold temperatures. For example, in *Pantoea dispersa* 1A and *Serratia marcescens* SRM strains from the Himalayan northwest, IAA production is induced between 4 and 15 °C. Wheat seeds inoculated with these strains and grown in cold conditions showed significantly higher yield and nutrient absorption capacity in comparison to untreated seeds [72,73]. Similar results were obtained with *Pseudomonas* sp. PGERs17 and NARs9 strains [56,74]. Finally, cold stress increases ethylene production, which further contributes to reduction of plant growth and productivity [75]. Despite encouraging results, *Pantoea* and *Serratia* species have not found technological application, possibly because of their relatedness to human pathogens. In grapevine, application of *Paraburkholderia phytofirmans* PsJN, which expresses ACC deaminase activity, increased cold resistance by reducing cell membrane damages [76,77]. Bean plants (*Phaseolus vulgaris*) exposed to freezing temperatures and inoculated with psychrophilic, ACC deaminase-producing bacteria, such as *Pseudomonas fragi*, *Ps. chlororaphis*, *Ps. fluorescens*, *Ps. proteolytica* and *Brevibacterium frigoritolerans*, showed reduced frost damage, lower membrane lipid peroxidation and low ROS production [78]. Among these bacterial species, *Ps. chlororaphis* and *Ps. fluorescens* are the only ones that found a market outlet, the first being the active ingredient of several registered biopesticides (Cedomon®, BioAgri AB, Uppsala, Sweden; AtEze, Eco Soil Systems Inc., San Diego, CA, USA), whereas the second is found in combination with other PGPR in products such as BFMS® (Tainio, Cheney, WA, USA), BioStrain® (Monty's Plant Food Company, Louisville, KY, USA), HyperGalaxy® (Holmes Enviro, Llc., Philomath, OR, USA) and SoilBiotic® (SoilBiotics, Reddick, IL, USA).

Table 1. Microorganisms used against stress induced by extreme thermal events.

Microorganism	Crop Plant	Mode of Action	Ref.
	Protection from High Temperatures		
Paraburkholderia phytofirmans	Potato	ACC deaminase production	[51]
Mycorrhizae	Tomato	Reduction in lipid peroxidation and H_2O_2, higher ROS scavenging activity in leaves and roots	[50]
Bacillus amyloliquefaciens, *Azospirillum brasilense*	Wheat	ROS reduction, pre-activation of heat shock proteins	[79]
Bacillus aryabhatthai SRBO2	Soy	ABA production	[80]

Pseudomonas putida AKMP7, *Pseudomonas* sp. AKMP6	Wheat, sorghum	ROS reduction, increase in proline, chlorophyll, sugar, starch, amino acid and protein content, production of phytohormones	[81,82]
Protection from Cold and Frost			
Ps. fluorescens A506	Apple and pear	Competition with INA$^+$ bacteria	[70]
Pantoea dispersa 1A, *Serratia marcescens* SRM, *Pseudomonas* spp. PGERs17, NARs9	Wheat	ACC deaminase production	[56,72–74]
Paraburkholderia phytofirmans	Grapevine	ACC deaminase production	[76,77]

1-Aminocyclopropane-1-carboxylic Acid (ACC), Ice Nucleating Activity (INA$^+$), Abscisic Acid (ABA), Reactive Oxygen Species (ROS).

2.2. Stress Induced by Water Scarcity or Waterlogging

A list of microorganisms investigated for their ability to protect from stresses linked to water availability is shown in Table 2.

2.2.1. Drought and Salinity Stress

Water stress, caused either by drought or high salinity, occurs when losses by leaf transpiration exceed root absorption, causing a reduction in water content in plant tissues, and consequently, loss of turgor [83]. Since the 1980s, drought events have become more intense and frequent, particularly in the northern hemisphere and in semi-arid areas [84,85]. Furthermore, when rainfalls are of low intensity and sporadic, salt accumulation in the soil can exacerbate the damages due to drought stress [86], since the increase in solutes in saline soils reduces the osmotic potential of soil liquid phase, thus impeding water absorption by roots [87]. Currently, soil salinization has affected about 30% of total arable land and is a very serious problem in the whole Mediterranean area [88]. Additionally, in overexploited areas, drought stress and the consequent soil salinization are the main drivers of desertification. Indeed, drought conditions alter soil composition and edaphic biodiversity, contributing to vegetation degradation and spare soil coverage, which enhance soil erosion [89,90]. Drylands currently cover 46% of the global land area, directly affecting 250 million people in developing countries [91,92].

Drought stress affects plants both morphologically and physiologically, and can cause detrimental ROS accumulation [93], ethylene emission [94] and reduce availability, assimilation and transport of mineral nutrients [95]. Microbial biostimulants containing soil microorganisms can improve plant tolerance to drought or salinity through different direct or plant-mediated mechanisms.

Direct mechanisms consist in the alteration of soil composition and structure by the microorganism, improving water uptake. Bacterial exopolysaccharides (EPS) can improve soil structure, through the formation of micro and macro-aggregates [96], playing a key role in promoting plant growth under water stress [51]. Additionally, EPS, through the formation of a hydrophilic biofilm, create a microenvironment which increases water retention by protecting microorganisms from drying [97], and binding Na^+ ions, limit their absorption by the plant and favor resistance to saline stress [98]. Examples of such protective effects have been described in several strains of *Pseudomonas* spp. [98,99].

Mycorrhizal fungi can strengthen the root capacity of exploring soils [100,101], allowing the increase of root biomass, improving soil structure, increasing water retention and decreasing mineral nutrient leaching [102]. Arbuscular mycorrhizae of the genus *Glomus* produce a glycoprotein (glomaline) with an aggregating effect on soil structure, inducing better growth and water stress resistance in orange plants [103,104]. Similarly, cucumber plants, colonized by different ascomycetes (*Phoma glomerata* LWL2, *Penicillium* sp. LWL3, *Exophiala* sp. LHL08, *Paecilomyces formosus* LHL10)

[101], showed increased chlorophyll content and leaf growth. Besides the enhancement of root growth, mycorrhizal fungi are also able to induce a better water uptake via aquaporins, a large family of integral membrane transporters that allow water passage through cell membrane phospholipid double layer. Plant aquaporins mediate roots water absorption and turgor pressure recovery [105]. Studies on *Phaseolus vulgaris* mycorrhized by *Glomus intraradices*, and subjected to water or saline stress, showed that the fungus regulated aquaporin activity, leading to a better root water conductivity [106]. *Glomus intraradices*, grown in symbiosis with carrot plants, showed a high expression of two fungal aquaporins (GintAQPF1 and GintAQPF2), which improved water transfer between the two symbionts, thus, conferring to the plant a greater resistance to water scarcity [107]. Among the abovementioned microbes, *Glomus intraradices*, together with several other mycorrhizae, and *Paecilomyces* spp., are the only ones that have been brought to the market. In commercial products, *Glomus intraradices* is mainly found in combination with other beneficial fungi and bacteria, such as in MycoApply® All Purpose (Mycrrhizal Applications, Inc., Grants Pass, OR, USA), and OroSoil® (Fomet, Spa, Verona, Italy), but it has been marketed in single formulation (Agtiv®, PremierTech, Rivière-du-Loup, Canada, and Groundwork®, GroundWork BioAg, Ltd, Hashahar, Israel) as well.

Concerning the plant-mediated effects, microbial biostimulants can influence the associated plants at several levels, including the modulation of phytohormone levels, the antioxidant defenses, the production of protective osmolytes such as glycine betaine, and the emission of volatile organic compounds (VOCs), which in turn, influence and coordinate the ecological contour (neighboring plants, rhizosphere microbiome, associated insects) of the plant [26,108–112].

Water limitation also impairs nutrient uptake by plant roots, including nitrogen compounds. This multistress condition promotes ethylene production, that, triggering stress responses, inhibits plant growth and carbon availability for associated microbes (Figure 2A). Thus, mechanisms enacted by plant symbiotic microbes can be based on ACC subtraction, reducing ethylene production and relieving ethylene-mediated inhibition [75], and/or IAA production to stimulate plant growth and root branching (and consequent exchange of resources with rhizospheric microflora). IAA production was found to be responsible for plant growth promoting effects by several microbes under nitrogen shortage conditions [113,114]. Notably, some of the identified genera (*Sinorhizobium*/*Ensifer*, *Serratia*, *Arthrobacter*, *Alcaligenes*, *Bacillus*) are likely N-fixing bacteria. In addition, IAA- and ACC deaminase-based metabolisms are mutually integrated, since IAA may stimulate ACC synthase, and ACC deaminase recirculates ammonium, making it available for other plant or bacterial metabolic needs (Figure 2B).

The bacterium *Pseudomonas chlororaphis* TSAU13, an IAA producer strain, when inoculated on salt stressed tomato and cucumber plants, can increase plant water conductance and resistance to salinity and drought [115]. Similar results were obtained in orange trees treated with the mycorrhizal fungus *Funneliformis mosseae*, which showed to increase root IAA levels, root hair growth and plant performance under drought stress [116]. *Funneliformis mosseae* is one of the active ingredients of Biologic Systems Wettable Mycorrhizae Blend® (BioLogic Crop Solutions, Inc., Santa Rosa, CA, USA), a commercial product improving the plant's ability to absorb water and nutrients. Similarly, gibberellin- and cytokinin-producing bacteria showed their efficacy in controlling water stress damages, stimulating shoot growth and stomatal opening in conditions of low water availability [117,118]. *Burkholderia*, *Promicromonospora*, *Acinetobacter* and *Pseudomonas* spp. strains have been described as Plant Growth Promoting Rhizobacteria (PGPR) that can produce active gibberellins. These bacteria, when inoculated on horticultural plants, such as cucumber, can increase plant growth in drought and salinity conditions [119]. Despite their promising beneficial activity, no commercial product has been released based on these species.

The production of abscisic acid (ABA) is physiologically stimulated in plants following water stress to induce stomatal closure. In soybean, the inoculation with *Pseudomonas putida* H-2-3 reduced the production of ABA, substantially mitigating the effects of drought stress on plant productivity [120]. *Ps. putida* is marketed in combination with *B. subtilis* in the commercial product N-Texx® (CXI, Coppell, TX, USA) for its ameliorative effect on soil fertility, although not specifically for drought stress relief. In lettuce, the inoculation with *Glomus intraradices* decreased ABA concentration and reduced salt stress susceptibility [121]. Both ABA and water scarcity increase ethylene production in plants. High ethylene concentration can reduce plant growth, especially at the root level, further increasing plant sensitivity to water scarcity. Therefore, the application of microorganisms showing ACC deaminase activity may alleviate these negative effects. For example, *Achromobacter piechaudii* ARV8 in tomato and pepper [122], or *Pseudomonas fluorescens* TDK1 in peanut seedlings [123], have been successfully used to enhance fresh and dry weight of yielded crops under drought or salinity stresses. *Achromobacter* spp. in combination with *Pseudomonas* spp. and other beneficial microbes are responsible for plant growth promotion and soil improvement of SOS® and SSB® (Liventia, Inc., San Antonio, TX, USA) products.

ROS production, and consequent oxidative damage to proteins, lipids and nucleic acids, is frequently observed under water stress. Several microorganisms can reduce negative effects resulting from ROS increase via the production of antioxidant molecules, or the enhancement of antioxidant enzyme activity, such as catalase or peroxidases [124]. Basil plants grown in conditions of water deficit showed an increase in catalase activity when inoculated either with *Pseudomonas* sp. alone or by microbial consortia composed by *Pseudomonas* sp., *Bacillus lentus* and *Azospirillum brasilense*. In the latter condition, also glutathione peroxidase and ascorbate peroxidase activity increased [125]. These microbe combination is the base for several successfully commercialized products, such as BFMS® (Tainio, Cheney, WA, USA), Environoc® (Biodyne, Llc., Wayne, IN, USA) , SoilBiotics® (SoilBiotics, Reddick, IL, USA) and HyperGalaxy® (Holmes Enviro, Llc., Philomath, OR, USA).

Osmocompatible solute accumulation is a reaction to stress, which involves the accumulation of organic or inorganic solutes respectively in the cytosol or in the vacuole, thus lowering the osmotic potential of the cell and maintaining its turgor potential under water stress [126]. Several bacteria can produce osmolytes [127], which can act in combination with plant osmolytes, showing also a detoxifying action on ROS (such as proline) and/or stabilizing proteins, enzymes and cell wall components [128]. When inoculated in tomato plants, proline production by the phosphate-solubilizing bacterium *Bacillus polymyxa* was observed, thus reducing the negative effects induced by water stress [124,129]. In rice, betaine produced by rhizosphere osmotolerant bacteria acted in concert with that produced by the host plant, increasing water stress tolerance [108]. Despite encouraging results, *B. polymixa* has not landed on the market yet.

Some microbes can interact with plants by means of VOCs, that stimulate adaptation responses to stress conditions. Such responses include root expansion, water saving and activation of mineral uptake systems [130–133]. The mechanisms underlying plant-microbe interactions under stress are largely obscure, although the implication of hormone signaling cascades has been observed [134–136]. Since the discovery of the effects of the microbial metabolite 2,3-butanediol on plant fitness [134], including regulation of stomata closure and production of osmoprotectants [132,133], other beneficial VOCs have been identified. For instance, 2-undecanone, 1-heptanol and 3-methyl-butanol from *Parabulkholderia phytofirmans* [137] contribute to salt tolerance, while 1-butanol and butyrolactone promote root development and carbon exchange in the rhizosphere [138]. Future exploitation of VOC-based plant promotion will probably depend on the clarification of signaling pathways induced by stress conditions.

Despite the relatively high number of microbial species able to protect plants from water stress, only a few products are specifically commercialized for this purpose. Most of these products (Ryze®, L.Gobbi, Srl, Genova, Italy; Micosat F®, CCS, Srl, Aosta, Italy; Suma Grolux®, RRR Supply Inc., Munger, MI, USA) are based on complex microbial communities, including *Glomus*, *Trichoderma*, *Bacillus* and/or *Pseudomonas* spp., that exert water stress protection, along with the general amelioration of plant growth, nutrition and yield, as a result of interaction of multiple mechanisms, including hormone production or stimulation, enrichment of soil organic matter and nutrients, and production of EPS.

2.2.2. Heavy Rainfall, Flooding and Water Stagnation

Among the consequences of ongoing climate change, seasonal variability and interannual rainfall trends are one of the main problems [139–141]. Currently, flood problems involve 13% of earth's surface [142] and, in the future, extreme rainfall frequency and intensity will globally increase [28]. Heavy rainfall and flood cause water stagnation and root hypoxia or anoxia. Under flooding conditions, roots produce high levels of the enzyme ACC synthase, which is involved in the biosynthesis of ethylene. In the absence of oxygen, the ethylene precursor ACC cannot be converted into ethylene since the enzyme ACC oxidase, which catalyzes the final step in ethylene biosynthesis (Figure 2), is oxygen-dependent. Thus, ACC is translocated through the xylem to the aerial part of the plant [143,144], where it can be converted to ethylene, causing wilting, leaf chlorosis or necrosis, flower and fruit drop, and reduced yield [75].

The use of PGPB can contribute to minimize problems associated with water stagnation due to their ACC deaminase activity, which reduces endogenous ethylene levels [75,145–147]. The pioneering research about microorganism utilization to reduce anoxia stress was conducted on tomato seeds inoculated with ACC deaminase-producing strains of *Enterobacter* and *Pseudomonas* spp., and were submerged for nine consecutive days. The presence of the microorganisms conferred to the germinated seedlings a higher tolerance to this extreme stress condition [145]. Although the application of the commercial product SumaGrow® (RRR Supply Inc., Munger, MI, USA), containing, among others, *Enterobacter* spp. and *Pseudomonas* spp., provides significant yield increase and better stress tolerance; specific protection from waterlogging stress is not claimed. Using *Pseudomonas* sp. on cucumber seeds [146], and the endophytic *Streptomyces* sp. GMKU 336 strain in association with Indian bean plants (*Vigna radiata*) [148], plant elongation, biomass, chlorophyll content, leaf area and adventitious roots formation were promoted, together with a reduction in ethylene levels. *Streptomyces* K61 and *S. lydicus* WYEC 108 are the active substances of Mycostop® (Verdera Oy, Espoo, Finland) and Actinovate® (Mycorrhizal Applications, Inc., Grants Pass, OR, USA), respectively. Although *Streptomyces* spp. are well-known soil beneficial bacteria, commonly used as a base of several commercial products, they are mainly applied for targeting biotic stresses such as seed and soil borne fungi. Unfortunately, the use of the abovementioned bacterial species as stimulators of plant tolerance under anoxic conditions is still poorly investigated.

Table 2. Microorganisms active against water stresses.

Microorganism	Crop Plant	Mode of Action	Ref.
Phoma glomerata, *Penicillium sp.*, *Exophiala sp.*, *Paecilomyces formosus*, *Glomus intraradices*	Cucumber, bean	Greater soil exploration by roots or by fungal hyphae and better water root conductivity	[101,106]
Pseudomonas chlororaphis TSAU13, *Funneliformis mosseae*	Tomato, cucumber, orange	IAA production	[115,116]
Burkholderia, *Promicromonospora*, *Acinetobacter*, *Pseudomonas* spp.	Cucumber	Gibberellin production	[119]
Bacillus subtilis	Lettuce	Cytokinin production	[117]
Ps. putida H-2-3	Soybean	ABA production	[120]
Achromobacter piechaudii ARV8, *B. licheniformis* K11, *Pseudomonas* spp., *Ps. fluorescens* TDK1	Tomato, pepper, pea, peanut	ACC deaminase	[122,123,149,150]
Glomus intraradices	Carrot, soybean, lettuce	Increased aquaporin activity	[107,151]
Pseudomonas sp.	Basil	Increased antioxidant protection	[125]

Ps. putida, *Ps. aeruginosa* PF23, *Glomus mosseae*, *G. versiforme*, *G. diaphanum*	Sunflower, orange	EPS production	[98,99,104]
Bacillus polymyxa, *Glomus intraradices*, *G. versiforme*	Tomato, soybean, tangerine	Osmolyte production	[104,124,129,152]

Indole-3-acetic Acid (IAA), Abscisic Acid (ABA), 1-Aminocyclopropane-1-carboxylic Acid (ACC), Exopolysaccharides (EPS).

3. Role of Microbial Biostimulants in Response to Biotic Stresses

Plant diseases cause losses estimated for 20–40% of global crop [153]. Climate change has a very complex effect on plant-pathogen interactions, since environmental conditions affect the whole disease triangle: they modify plant susceptibility, the biological cycles of parasites and pathogens [154,155], and host–pathogen physiology and interactions [5,156]. Although protection against biotic stresses falls outside the generally accepted definition of biostimulation [11], disease resistance induction is sometimes elicited by *stricto sensu* biostimulants and will be discussed here as a desirable additional trait for future products to be developed. These considerations exclude, however, microorganisms directly acting on pests and pathogens (such as entomopathogenic and antibiotic-producing microbes), which are categorized as biopesticides rather than biostimulants.

Grapevine and potato downy mildew, gray mold and bacterial canker of kiwifruits represent crop diseases whose incidence has been increased due to climate change [157]. The presence of even more frequent frost events during the vegetative season led to an increase in disease incidence of the bacterial canker of kiwifruit (*Pseudomonas syringae* pv. *actinidiae*), as plant tissues were more subjected to frost damages, which can be exploited by the pathogen as entry points [158].

Increase in temperature, CO_2 levels, acid rains and tropospheric O_3 concentration can cause multiple chronical stresses to plants, lowering their ability to respond to a pathogen attack [155]. Furthermore, even though the rise in CO_2 can cause a reduction in stomata density, which are important entry points for several epiphytic pathogens, increase in acid rains and O_3 may reduce the protective efficacy of the cuticles and facilitate pathogen penetration. Climate change is also likely to increase the frequency of pesticide application [159]. In fact, higher winter temperature will anticipate bud break and, thus, the length of the growing seasons and the number of pesticide applications. In addition, changes in temperature and precipitation may alter the dynamics of pesticide persistence on the crop foliage. An increase in the frequency of intense rainfall events could result in increased fungicide wash-off and, consequently, reduced control. The physiological and morphological changes in crop plants resulting from growth under elevated CO_2 could also affect uptake, translocation, and metabolism of systemic pesticide. The CO_2-induced increase in crop growth rate may results in bigger and denser canopy that could negatively affect spray penetration and coverage. The increased use of pesticides (including the variety of compounds applied, their doses and application frequencies) [160,161] and the possible reduction of their efficacy [155] may result in a rise of pathogen resistance [162]. In this scenario, the use of microbial biological control agents will become a key option to prevent the environmental, social and economic impact of the increase in pesticide use.

In addition to the classical biological control, based on a direct effect of beneficial microorganisms against the pathogens, an innovative and sustainable approach applied for plant diseases control is the use of microorganisms which enhance plant disease resistance. Systemic acquired resistance (SAR) and induced systemic resistance (ISR) are two different mechanisms for plant resistance [27,163]. In the case of SAR, after a pathogen attack, salicylic acid is accumulated in infected plant tissues. This hormone activates immune responses, such as the expression of pathogenesis-related (PR) genes, encoding for antimicrobial products [164]. On the other hand, beneficial microorganisms more frequently act via ISR induction, which consists in a plant immune system stimulation (priming) against a broad spectrum of pathogens, leading to a more rapid and intense reaction after pathogen recognition [165], but generally not affecting plant growth and yield.

Bacterial species of the genera *Pseudomonas*, *Serratia* and *Bacillus*, and fungi such as *Trichoderma* spp. and *Piriformospora indica*, are among the most studied organisms for the induction of resistance [27,166,167]. The commercial formulate Trianum-P® (Koppert, Srl, Verona, Italy), for instance, employs a *Trichoderma harzianum* isolate to induce ISR and protection against soil pathogens. In *Pseudomonas* and *Bacillus* spp.-based products, resistance induction effect may as well exist, although not documented. Several microbial molecules can activate ISR, such as flagellar proteins, Gram-negative bacteria lipopolysaccharides, siderophores [167], some antibiotics, N-alkylated benzylamines, VOCs [168] and N-acyl homoserine lactones, a class of signal molecules involved in bacterial quorum sensing [169]. The antifungal compound 2,4-diacetylfloroglucinol [170] and cyclic lipopeptides are also recognized as microbial elicitors [165,171,172]. These elicitors stimulate plant immune response via the activation of the regulatory genes involved in ethylene and jasmonic acid biosynthesis [173,174]. *Enterobacter asburiae* R57 strain, recently isolated from raspberry, showed the ability to control *Botritys cinerea* in vitro via the production of siderophores and acetoin, a volatile precursor of 2,3-butanediol [175]. Other microorganisms can be beneficial for plant resistance, increasing plant constitutive barriers, for example by promoting callose deposition in cell wall [176] following ABA stimulation [177]. Even preventive treatments with ACC deaminase-producing bacteria could help in protecting plants from bacteria, fungi and nematodes [75], impeding the development of symptoms and decreasing disease severity. This kind of response was detected following the application of the ACC deaminase producing *Pseudomonas putida* UW4, which limited damages caused by *Pythium ultimum* in cucumber [178]. A list of resistance-inducing microbes, along with the mechanisms eliciting plant protection and the target pathogens, is presented in Table 3.

Several microbes are registered as active principles of pesticides, acting against plant pathogens through direct antagonism mechanisms. In contrast, broad sense biostimulation (i.e., resistance induction) properties against biotic stresses are less considered for commercial formulates. *Bacillus amyloliquefaciens* (formerly *subtilis*) QST 713 is an EU registered pesticide active substance that, besides directly competing for nutrients on leaf surfaces with fungal pathogens, induces systemic resistance responses in plants, as indicated by peroxidase production [26]. Among complex commercial products, Ryze® (L.Gobbi, Srl, Genova, Italy) and Nutribac® (Chemia, Spa, Ferrara, Italy), containing both mycorrhizae and PGPR, exhibit not only general beneficial properties for the soil, but also enhance plant resistance to biotic stresses. Direct antagonism seems to have been a more appealing strategy for microbe-based products commercialization. Alternatively, resistance-inducing products (such as chitosan, exopolysaccharides and lipopolysaccharides) have been isolated and extracted from their originating organism. While the use of live microbes as resistance inducers may be a less straightforward, thus, possibly less reliable protection strategy, it may as well combine the advantages of a long-lasting and stable plant-microbe interaction and of wide-range protection, possibly improving the baseline health status of crops and reducing the synergism within pathogen consortia.

Table 3. Resistance-inducing microorganisms with their respective plant protection mechanisms.

Microorganism	Plant/Pathogen(s)	Microbial Elicitor	Signaling Pathway	Ref.
Bacillus pumilus SE34	Tomato/*Phytophtora infestans*		depending on ET/JA; SA independent	[179]
B. subtilis S499	Bean/*Botritis cinerea*	Cyclic lipopeptides (surfactin and fengicine)		[163]
Burkholderia gladioli	Cucumber/*Colletotrichum orbiculare*	Exopolysaccharides		[180]
Pseudomonas fluorescens SS101	Tomato/*Phytophtora infestans*	Cyclic lipopeptides	SA-independent	[181]

Ps. fluorescens WCS374	Radicchio/*Fusarium oxysporum* f. sp. *raphani*	Pigment (pseudobactin), lipopolysaccharides		[182]
Rhizobium etli G12	Potato/*Globodera pallida*	lipopolysaccharides		[183,184]
Ps. fluorescens WCS417	Eucalyptus/*Ralstonia solanacearum*	Lipopolysaccharides and siderophores		[185]
Serratia liquefaciens MG1	Tomato/*Alternaria alternata*	N-acyl homoserine lactones	Probably depending on SA and ET	[161]
B. amyloliquefaciens IN937a	Arabidopsis/*Erwinia carotovora*	VOCs (2R,3R-butanediol)	depending on ET/JA; NPR1/SA-independent	[160]
Paenibacillus polymixa BMP-11	Arabidopsis/*Phytophthora capsici*, *Alternaria brassicicola*, *Botrytis cinerea*, *Colletotrichum capsici*, *Fusarium oxysoprum*	VOCs (1-octen-3-ol)		[186,187]
B. amyloliquefaciens IN937a	Pepper, cucumber/*Xanthomonas axonopodis pv. vesicatoria*	VOCs (3-pentanol)		[188]
Trichoderma atroviride TRS25	Cucumber/ *Pseudoperonospora cubensis*		Probably depending on SA and JA/ET	[189]
Bacillus sp. CHEP5 e *Pseudomonas* sp. BREN6	Peanut/*Sclerotium rolfsii*		Increased ACC conversion capacity	[190]
Paenibacillus P16	Cabbage/*Xanthomonas campestris*			[191]

Ethylene (ET), *J*asmonic *A*cid (JA), *S*alicylic *A*cid (SA), Volatile Organic Compounds (VOCs), 1-aminocyclopropane-1-carboxylic acid (ACC*).*

4. Limitations and Future Perspectives in the Application of Microbial Biostimulants

The development of a new microbial biostimulant displays some specific difficulties. Firstly, commercial registration process is usually complex, and a harmonized international legislation is still lacking [192]. Secondly, product efficacy is strictly dependent on the horticultural crop on which it is applied and on its phenological state. The development of phytostimulant products needs to evaluate the relationship microorganisms establish with the host plant. A positive and long-lasting plant colonization is an essential prerequisite for biostimulant effectiveness.

Finally, the best formulation to guarantee products efficacy and conservation has to be defined, to minimize the influences from environmental and cultural conditions [193]. Biostimulants with Gram-positive bacteria allow powder formulations with durable stability and drying tolerance due to spore production by bacteria [194].

Even if there are many examples of the efficacy of microorganism application in promoting plant growth under unfavorable conditions, very few biostimulant products specifically addressing stresses emphasized by climate change are available. In general, the high costs related to the production of the commercial biostimulant and the variability in the efficacy observed in field conditions [195] are major hindrances to the development of biostimulant products, resulting in a relatively low number of commercialized products and a limited diffusion in horticultural practice.

Several parameters in fact have to be considered before the application of a microbial biostimulant:

- Soil and crop characteristics: no microorganisms can be universally applied in any ecosystem [196] or on any vegetable host [197], thus, choosing a particular strain for a biostimulant product needs consideration of soil properties and specific crop requirements, in order to select microbial strains with the best adaptation to each particular condition [198].
- Competition for nutrients and ecological niche occupation between selected microbial strains and indigenous microflora, which can reduce biostimulant efficacy [199–202].
- Mode of application of the microbial biostimulant, that should reduce microorganisms dispersion or death due to abiotic factors (UV, temperature) [203].
- Specific characteristics of the microbial strain: microbial strains with multiple PGP traits are preferable over microbial strains characterized by only one PGP, because they can reduce different stresses simultaneously [194,204].
- Integration of microbial and plant genetic resources: future crop breeding programs should consider the plant's capacity to establish stable symbiotic relationships with useful microorganisms as a highly desirable trait, closely linked to stress resistance, productivity, and resilience. Concurrently, the deeper characterization of microbial functions and mechanisms of interaction may enable the selection of specific biostimulants for a particular crop/cultivar in a given cultural condition.

In-depth characterization of the plant microbial biocoenosis by next-generation sequencing (NGS), the real-time monitoring of the dynamics of microbial functions and the development and optimization of microbial synthetic communities are pivotal strategies to fully achieve the potential of microbial biostimulants. Several studies suggest that microbes isolated from the microbiome of the host plant have a superior efficacy in comparison to non-indigenous microbial inoculants [205]. Thus, the characterization of the native microbiome through the application of high-throughput NGS technologies is a key step for the successful selection of microbial biostimulants. Together with meta-analysis of population association, NGS technologies could lead to the identification of microbes able to persist on the plant under stressful environments [206]. In fact, their persistence would be a likely result of positive selection, due to their beneficial effect on plant growth and protection [207].

Additionally, investigation of the microbiome based on functional markers, besides taxonomic ones, is fundamental to understand and exploit plant–microbe ecological interactions [208]. Indeed, the application of real-time monitoring techniques for beneficial microbial functions could address agricultural practices or conditions to maximize the action of microbial inoculants. Current real-time PCR methods allow broad-range quantification of microbial functional genes, and could be adapted to agroecological functional monitoring in the future [209,210].

Finally, the construction of synthetic microbial communities, i.e., integration of several microorganisms with different PGP functions, presents a unique opportunity to increase the efficacy and reliability of microbial biostimulants, although engineering a microbial community represents a significant challenge [211]. Indeed, the complexity of ecological interactions that occur between microbes (e.g., commensalism, competition) have to be deeply investigated in order to assure success of the beneficial community.

5. Conclusions

Microbial biostimulants potentially represent a sustainable and effective strategy to reduce abiotic and biotic stresses accentuated by climate change. Moreover, the use of microbial biostimulants could contribute to the maintenance of agro-ecosystem ecological balance, minimizing the use of pesticides and/or heavy metals in agriculture. Nonetheless, in pursuing a better product efficacy and a more widespread employment, some issues should be considered both at the regulation level, and at the research and development stage.

The definition of plant biostimulant is claims-based, meaning that the function itself defines the product [212]. Multiple active ingredients can be present in one product, with different functions and targets. Therefore, the intrinsic heterogeneous nature of biostimulants eludes legislative categories (e.g., amendant, fertilizer, fungicide). According to the country of registration, products may undergo long and expensive trial procedures before approval. The lack of a coherent international regulation [192] forms an impediment to product marketing and may discourage the development of new products.

With regard to biological and agroecological research, the use of microbial biostimulants still presents several limitations mainly linked with their lower efficacy and higher sensitivity to the environment in comparison with chemical growth regulators, fertilizers and pesticides. Furthermore, microbial biostimulants often showed inconsistent results from crop to crop or from region to region. Thus, to maximize the efficacy of microbial biostimulants fostering the constancy of the results, future research should be aimed at obtaining better targeted products, for instance, by in-depth exploring plant-associated microbiomes, by characterizing and controlling plant–microbe interactions, by functionally integrating the community of species included in one biostimulant product, by isolating microbes specifically adapted to the agricultural stress or local conditions of interest, or even by allowing on-field selection of useful microbes rather than introducing new ones. Biostimulants should be coupled with agricultural practices able to increase agroecosystem biodiversity and ensure a long-lasting and stable symbiotic relationship with crop plants. In this scenario, the use of microbial biostimulants represents a sustainable and effective solution against plant productivity losses due to changing climatic conditions and could help optimize human inputs in agricultural ecosystem.

Finally, the experimental results obtained by the research on microbial biostimulants should be used to promote pilot or demonstration trials for all the relevant stakeholders, from growers to extension services and policy makers, to ensure the straightforward application of this methodology on different crops, regions and environmental conditions. A close cooperation and a constant exchange of information between the scientific community and the stakeholders is the key to the successful validation of research results in real conditions and their adaptation to practical applications.

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