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Review

Overviewing Drought and Heat Stress Amelioration—From Plant Responses to Microbe-Mediated Mitigation

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Abstract: Microbes (e.g., plant-growth-promoting rhizobacteria, arbuscular mycorrhizal fungi and endophytes) are the natural inhabitants of the soil-plant-environment ecosystem having the potential to ameliorate the negative effects of environmental extremities. Plant-microbe interactions are integral events of agricultural ecosystems which must be studied in order to modulate the systemic mechanisms in field crops. Under changing climatic scenarios, drought and heat stresses tend to induce numerous physiological, morphological, metabolic and biochemical alterations in crop plants, while microbes hold the potential to mitigate these adverse impacts in a sustainable way. However, plant-microbe interaction mechanisms remain understudied owing to their complexities in the rhizosphere and within the cellular systems of plants. In this review, we have attempted to summarize microbes' interactions with crop plants that tend to influence hormonal and nutrients balance, and the biosynthesis of metabolites and phytohormones, etc. In particular, focus has been kept on the underlying mechanisms related to plant-microbe interactions which confer abiotic stress tolerance. Moreover, various physiological, morphological, metabolic and biochemical responses of plants subjected to water scarcity and elevated temperatures have been synthesized objectively. Lastly, from the perspective of microbes' application as biofertilizers, both challenges and future research needs to develop microbe-mediated tolerance as a biologically potent strategy have been strategically pointed out.

Keywords: abiotic stresses; biochemical responses; heat amelioration; morphological alterations; rhizobia

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1. Introduction

Plants tend to intimately intertwine, with numerous microbial communities residing around the roots network in the rhizosphere (soils in close proximity to roots, and influenced by root exudates) [1–3]. Microbes such as endophytes (which live within plant tissues without causing any harm to the host plants), plant growth promoting rhizobacteria (PGPR) (microbes colonizing plant roots) and arbuscular mycorrhizal fungi (AMF) can impart numerous alterations in the host plants [4–9]. The plants' health is closely tied to associated microbial activity, while a plant's species also determines the diversity and composition of its associated microbial communities [10–15]. Microbes might be utilized to develop a potent, economical and ecofriendly strategy for offsetting the adverse impacts of environmental extremes [16–19], for instance, PGPR modulate plant hormones for boosting biomass production through enhanced nutrient uptake and biosynthesis of antioxidants and numerous osmolytes [20–22]. These include proline, sugars, polyamines, betaines, quaternary ammonium compounds, polyhydric alcohols, and other amino acids [17,20].

The effective rhizosphere–rhizobacterial interaction attracts microbes in the roots' vicinity [23,24] due to the secretion of root exudates which contain amino acids, organic acids, sugars, enzymes, peptides, vitamins and numerous primary and secondary metabolites [21,24]. The in-depth study of plant-microbe interaction has become even more pertinent because abiotic stresses have raised interest in developing microbe-based stress mitigation strategies [25–27]. The abiotic stresses, especially drought stress (DS) and high temperature stress (HS), have caused serious losses to the productivity of farming systems [28–32], which necessitates research efforts in order to devise plant-microbe-interaction-based strategies. Figure 1 elucidates different types of abiotic stresses (e.g., heat, drought, salinity, water logging, heavy metals toxicity), especially drought-induced alterations in crop plants (e.g., plasma membrane deterioration, impaired photosynthesis, transpiration losses) and in microbes (Psychrophilic microbes population decreases under elevated temperatures, in contrast to Psychrotrophic microbes). However, a vital caveat to note is that, so far, our understanding regarding key processes that trigger microbe-mediated plant adaptations under abiotic stresses remains scant.

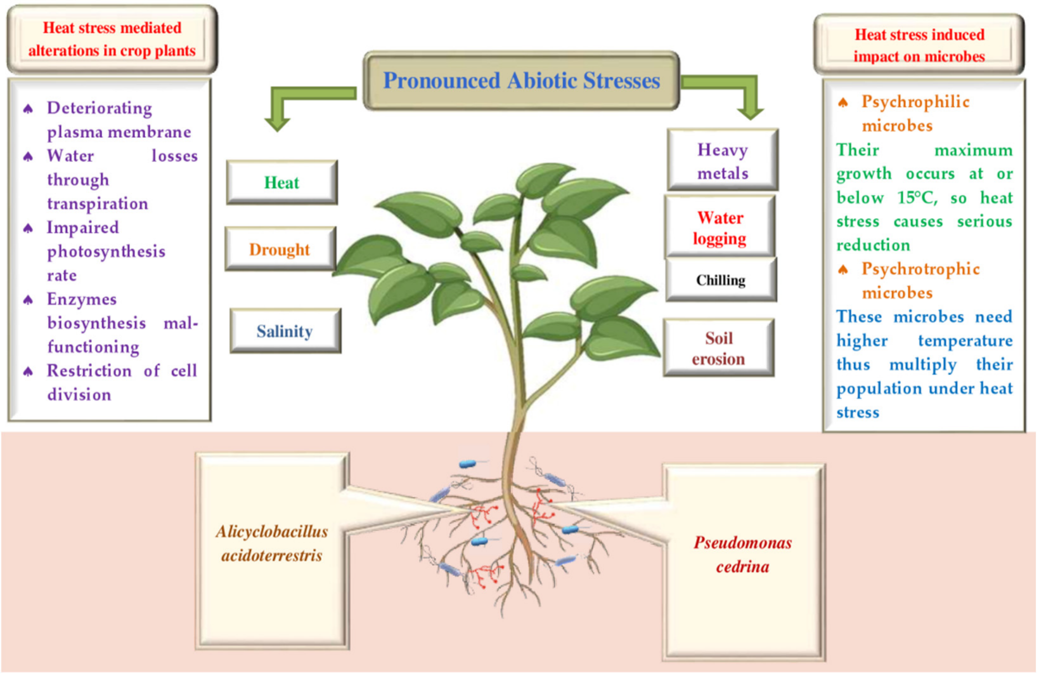

Figure 1. Pronounced abiotic stresses, especially heat-induced alterations in crop plants and various types of microbes.

In this review, a robust but critical attempt has been made to objectively synthesize and elaborate the latest advances on the morphological and physiological alterations imparted by DS and HS in crop plants. However, the prime focus revolves around plant responses to these abiotic stresses along with highlighting the underlying mechanisms of plant-microbe interactions which confer tolerance. The study culminates with a brief discussion on perspectives of microbial application such as bio-fertilizers (BFs) and potential development of a microbes application strategy.

2. Morphological and Physiological Effects of Drought Stress and Plant Responses

Drought occurs when humidity in the soil and atmosphere becomes disproportionally low while the ambient air temperature is high [33]. Resultantly, DS occurs, given the greater evapotranspiration flux, coupled with the reduced water intake [34]. The DS tends to trigger a cascade of morphological, physiological and bio-chemical alterations in plants. For instance, DS significantly reduced germination rate and seedling establishment of sunflower and wheat [35,36]. Likewise, DS hampered the roots development and hypocotyl length in rice (*Oryza sativa* L.), field peas (*Pisum sativum* L.) and alfalfa (*Medicago sativa* L.) [37–39]. Additionally, plant height, leaf diameter, and the stem girth were greatly reduced in maize and canola (*Brassica napus*) under DS [40,41]. This reduced growth is usually owing to disruption in nutrients such as N, Ca, Mg, etc. movement via diffusion and mass flow which leads to retarded plants growth [42]. Similarly, reduced absorption of less mobile nutrients was attributed to thinner leaves having much smaller leaf areas [43]. Overall, drought induced yield reduction was in the range of 21–40% for maize and 20–63% for wheat at 40% water deficiency [44].

Interestingly, plants exposed to DS develop leaves having smaller cells and higher stomatal density [45–48]. In addition, drought damages the photosynthetic pigments and the thylakoid membranes [49], while the reduction in chlorophyll content under DS was caused by the ceasing of chlorophyll biosynthesis and the degradation of existing chlorophyll [50]. Furthermore, the impaired cell elongation restricted the flow of water from xylem to adjacent cells [51]. Besides, DS imparts mitosis and cell elongation impairment [52] along with loss of turgor, which reduces the photosynthesis rate [53–57]. Furthermore, reduced transpiration rates and leaf water potential [58] disrupted water use efficiency (WUE) (ratio of accumulated dry matter to the total consumed water) in drought-sensitive cultivars of Eastern cottonwood (*Populus deltoides*) [54]. In contrast to cereals, legumes roots witness impaired flux of oxygen and CO_2, coupled with greater N accumulation which inhibits N fixing capacity [55]. Additionally, microbial colonies' composition and functioning in the soil are adversely influenced, which eventually disturbs plant-nutrient relations [56]. The DS disturbs assimilated balance [57,58] and net reduction in the sucrose content restricts assimilates' flow towards sinks [59]. Likewise, sink capacity for utilizing the imported assimilates in an efficient way declines [60]. Moreover, disruption of acid invertase activity restricts the phloem loading-and-unloading process, which in turn causes disturbance in partitioning of the assimilates and dry matter accumulation. However, there is a dire need to study nutrients' relations in terms of interactive effects among themselves and overall physiological alterations caused by nutrients deficiency under DS.

In response to DS, plants trigger stomatal closure in order to avoid water losses through transpiration [61,62]. This reduces CO_2 intake, causing severe oxidative damage and ceasing of carbohydrates' assimilation process [53,62]. Additionally, heat dissipation in the leaves of crop plants under DS is a vital growth-restricting phenomenon [63]. Moreover, stomatal closure under DS has been attributed to biosynthesis of abscisic acid (ABA) in roots [64]. However, crop-specific studies are required, because stomatal responses differ across plant species under water scarcity [65]. Interestingly, drought-resistant wheat cultivars recorded higher WUE by enhancing dry matter accumulation and reducing the transpiration rate [66]. In contrast, drought-sensitive genotypes of potato (*Solanum tuberosum* L.) had lesser WUE under early season DS, which reduced biomass and tuber yield [67]. Another pertinent response of crop plants to DS is incremental growth in root length and surface area, along with alterations in roots architecture which facilitate uptake of mobile nutrients [55]. Estill et al. [68] recorded enhanced chlorophyll content in alfalfa and some cultivars of black gram [*Vigna mungo* (L.) Hepper] [69]. This varied response was attributed to different enzymes' biosynthesis which trigger chlorophyll formation. Similarly, chlorophyll-a remained higher as compared to chlorophyll-b under DS [70], while a significant decrease in the chlorophyll a/b ratio in *Brassica* species has also been reported [71].

Besides, plants respond to drought by synthesizing ethylene, reactive oxygen species (ROSs), and triggering leaf senescence [72,73]. Moreover, DS manifests through free radicals' accumulation, which induces disruptions in membrane functions, denaturation of amino acids and proteins, lipid peroxidation and lastly, cell death occurs [72]. Figure 2 depicts sugarcane response in terms of morphological alterations such as production of leaves with thick cuticle, a leaf hair named pilosity, and physiological changes such as reduced leaf transpiration, increased root hydraulic activity, biosynthesis of osmolytes and various growth hormones under DS [58]. However, future research is still needed to explore the underlying mechanisms which enable crop plants to survive short-to-moderate periods of drought [73,74].

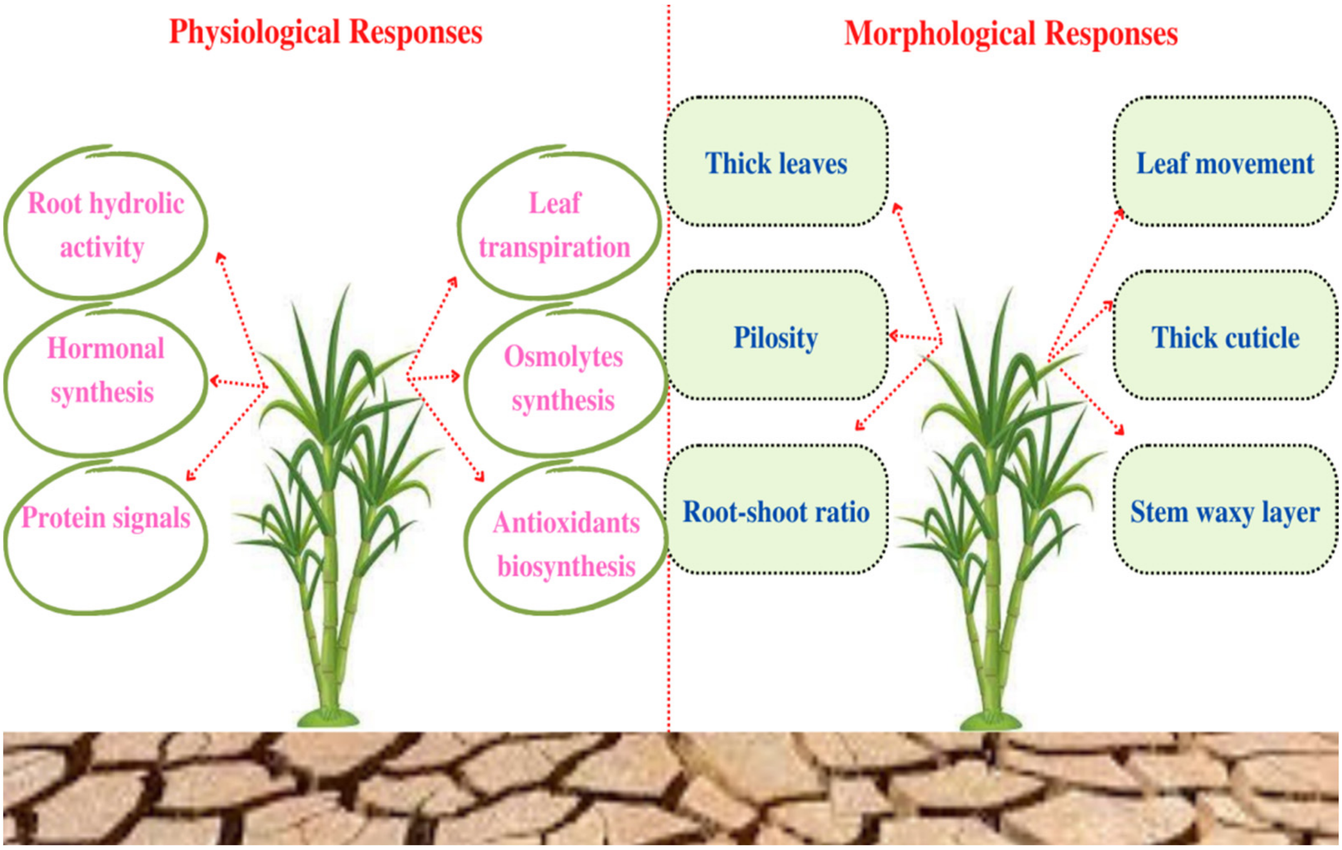

Figure 2. Sugar cane response in terms of morphological and physiological alterations to water-scant conditions.

3. Heat Stress Induced Morphological and Physiological Effects and Plants Responses

Heat stress (HS) occurs when air and soil temperatures rise beyond an optimum threshold level for a determined time span, restricting crop growth [75–79]. Among the most pronounced morphological impacts of elevated temperatures include leaves' and twigs' scorching with visual sunburn symptoms, leaf senescence, stunted growth and discolored leaves and fruits [80–82]. However, reduced germination and planting density are the first impacts of HS [83–85]. In addition, HS-restricted growth of spikes and florets occur in rice along with disturbing seed-set in sorghum [86]. Likewise, anthers and pollens inside the florets remained highly susceptible in comparison to ovules under HS. Moreover, heat-induced floret sterility was attributed to diminished dehiscence of anther, poor pollens shedding, reduced pollen germination on the stigma, and declined pollen tubes elongation [87].

Maize and sugarcane (*Saccharum officinarum* L.) plants, in response to elevated temperature, recorded lesser inter-nodal length owing to restricted net assimilation rate [88–90]. Likewise, reduced fresh and dry weights of sugar beet plants were observed owing to restricted photosynthetic rate caused by denaturation of photosynthetic pigments and multiplication of malondialdehyde content [91]. However, reduced leaf area, leaf yellowing, necrosis, epinasty and leaf abscission in cape gooseberry were the prime impacts of HS [92]. In contrast, wheat yield was reduced owing to substantially reduced grain weight and grain number per spikelet [93]. Likewise, rice growth, development and paddy yield were reduced by HS, especially tillering, the stage most sensitive to elevated temperature [94]. Moreover, reduced grain weight reduced paddy yield [95], while in tomato (*Lycopersicum* *esculentum* Mill.), disruption of fertilization, meiosis, and reduced embryo growth ultimately led to decline in yield [96]. Along with cereals, the HS remained equally drastic for legumes such as common beans (*Phaseolus vulgaris* L.) and peanut (*Arachis hypogea* L.) which seriously hampered vegetative and reproductive growth [97,98]. Similarly, decline in roots number, mass and growth occurred under HS [99]. However, very scant information available related to the direct impacts of elevated temperatures on crops-nutrient relations [100,101]. Future studies may investigate the reduced nutrients uptake under HS as influenced by restricted root growth.

Besides morphological alterations, HS also induces numerous physiological disruptions in crop plants such as deterioration of plasma membrane, enhanced transpiration, impaired photosynthesis rate, restriction in enzymes biosynthesis and cell division. Additionally, changes in the hormonal concentrations, such as increases in jasmonic acid, suppress uptake of nutrients [81,82,102,103]. Other pronounced physiological impacts of HS include protein de-structuring, inactivation of enzymes, damage to cell membranes, oxidative damage, and decreased photosynthetic rate [27,99]. Especially, photosystem II (PSII) is highly sensitive to HS, which damages the oxygen evolving complex (OEC) and vital proteins (D1 and D2) in wheat and barley [104–108]. Similarly, cotton [109] and rice [87] witnessed disruption in the electron chain and regeneration capacity of RuBP. Further, UV radiation altered biosynthesis of ABA, flavonoids and IAA concentrations in soybean [110]. Likewise, major enzymes such as nitrate reductase, which is required for nutrient metabolism, was significantly reduced by HS [111]. Additionally, 5-aminolevulinate dehydratase can be deactivated in wheat plants exposed to HS, which results in disruption of the pyrrole biosynthesis pathway [112]. The inactivation of this enzyme at 42 °C also caused chlorophyll biosynthesis reduction by 60% in cucumber (*Cucumis sativus* L.) [81]. Another vital enzyme's (protochlorophyllide) biosynthesis was reduced by 70% under elevated temperatures [113,114].

Plants have evolved many intricate regulatory mechanisms to cope with HS through alteration of physiological processes, such as perception of signal, transduction of signal and ultimately triggering the gene action [81,102], all of which lead to signal response by crop plants, as exhibited in Figure 3. Additionally, plants trigger their response to HS by employing biosynthesis of enzymes and accumulation of osmolytes. Furthermore, biosynthesis of heat shock proteins (HSP-20, HSP-60, HSP-70, HSP-90 and HSP-100) and ROSs-scavenging enzymes, including ascorbate peroxidase and catalase, enable plants to survive short periods of HS [115–117]. Genome editing must be performed, enabling crop plants to maintain water status within plant tissues under elevated temperatures [118,119] as rapid reduction in the water contents of leaf tissues in sugarcane under HS was recorded [89]. However, heat mediated restriction in root conductance owing to disruption of hydraulic activity has been observed in tomato plants [120]. Moreover, wheat genotypes exposed to HS varied significantly in terms of assimilates' partitioning [121] which necessitates further in-depth studies for exploring the wheat gene-pool for heat tolerance.

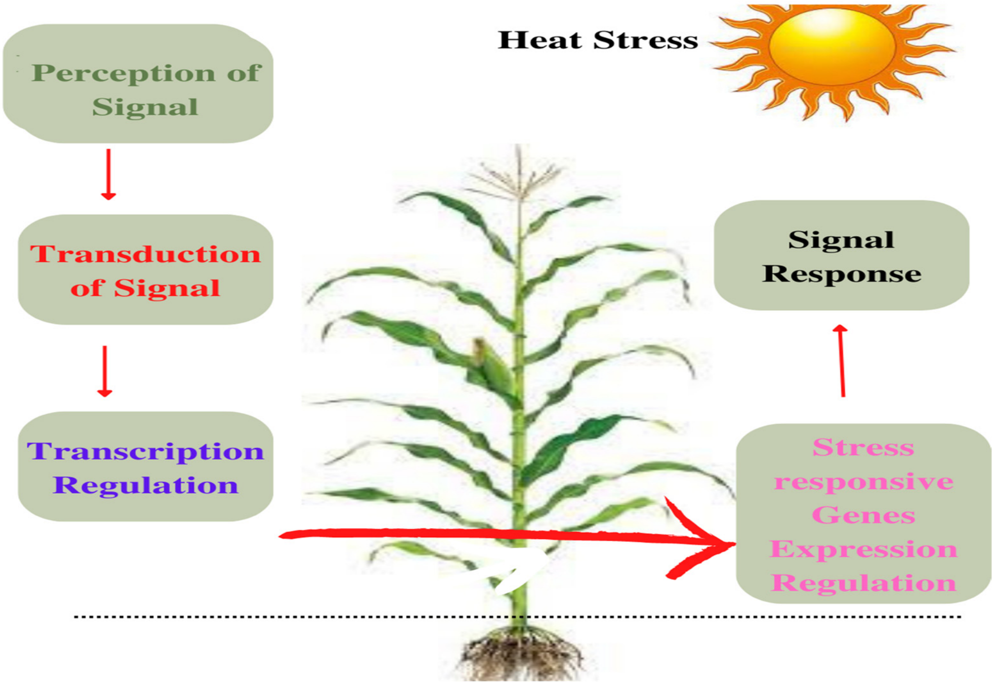

Figure 3. Plant response to heat stress starting from perception of the signal and finally signal response.

4. Plant-Microbe Interaction Conferring Tolerance against Drought and Heat Stress

The rhizosphere harbors a wide range of microbes having plant-growth-promoting abilities [122–124]; the DS-prone rhizosphere in Israel contained a higher population and diversity of PGPR. Additionally, enzymatic activity remained higher in isolates of DS rhizosphere. A variety of direct and indirect biochemical and molecular mechanisms are put to work by microbes to promote plants' growth DS. For instance, PGPR promotes plant growth by effective regulation of hormonal and nutritional balances in plants [125]. In addition, PGPR synthesizes many metabolites and siderophores in the rhizosphere which restricted the availability of iron and ultimately pathogen attack on stressed plants was inhibited [126]. Likewise, PGPR facilitates fixing of atmospheric N through biological fixation process and solubilize clay fixed phosphate [14]. Figure 4 illustrates drought induced alterations in maize plants and microbes along with microbial response to water scarcity as few microbes like actinobacteria multiply under water deficiency while others get depleted, such as planktomycetes.

The PGPR accelerated the flowering phase [127,128], resulted in an earlier seed set and delayed senescence, which assisted crop plants to escape drought [129]. These also stimulated mobilization of vital nutrients within plant tissues and triggered the production of exopolysaccharide and rhizobitoxine [130] through inhibition of ethylene synthesis [131]. Besides, microbes triggered the biosynthesis of key enzymes including glucanase, ACC-deaminase and chitinase [132]. Moreover, microbes have sigma factors (multi-domain subunits of RNA polymerase having critical role in RNA synthesis) to alter the gene expression under stressful environment [133]. Along with PGPR, plant-AM fungi interaction in the root zone of the field crops may improve nutrients' cycling and absorption along with translocation of nutrients. These vital but comparatively lesser studied plant-microbes interaction assist crop plants in maintaining the desired growth under stressful environments. The schematic presentation of plant-microbe interactions under drought and heat stresses has been depicted in Figure 5, where microbes ameliorated osmotic and oxidative stresses through biosynthesis of hormones like ABA and exopolysaccharides (EPS), while drought stress was also ameliorated by N fixing bacteria via enhancement in N and water supply through extensive root network development.

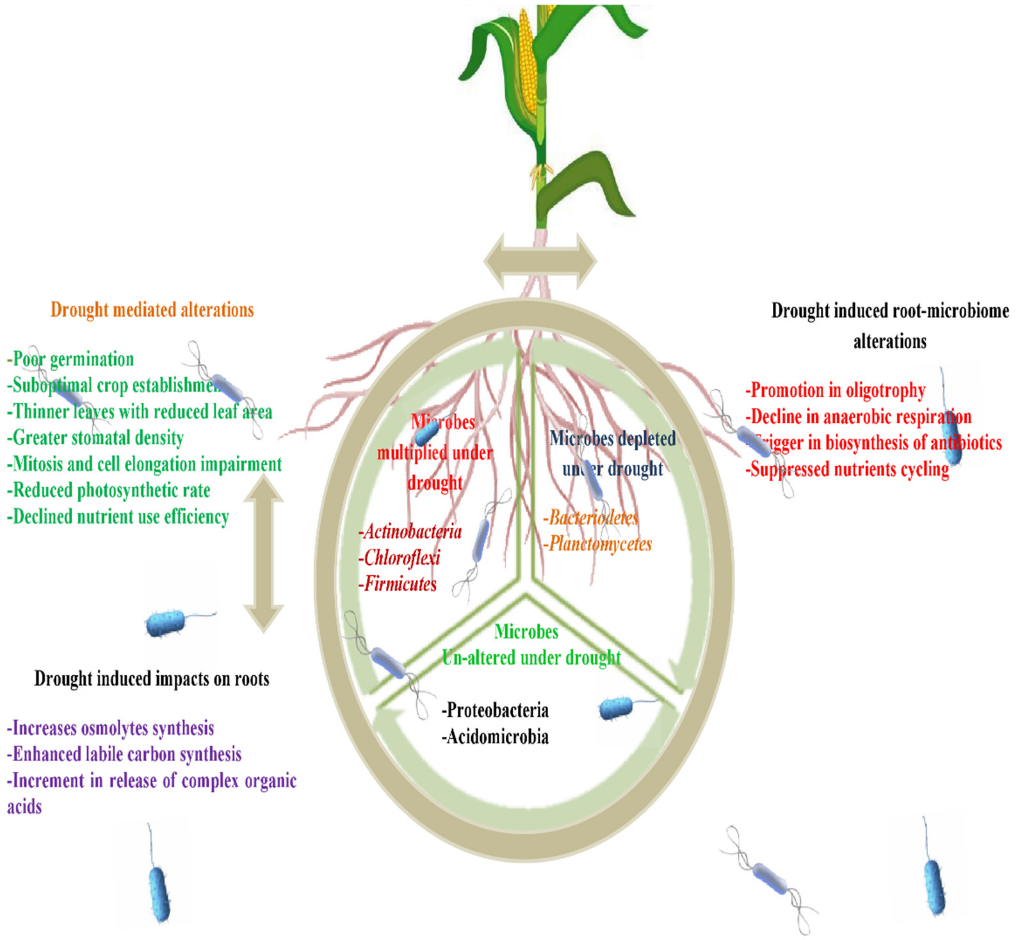

Figure 4. Drought mediated impacts on plants, roots and microbial strains in terms of their differential response (multiplication, depletion and neutral behavior) to water scarcity.

Plants endophytes thrive within plant tissues without causing any damage or disease to the host plants [121]. The phytohormones were synthesized by root endophytes which conferred drought tolerance in pepper [134] through improved nutrient (N, P, Fe, etc.) uptake [135,136]. Maize seeds inoculated with the endophytic microbes such as *Piriformospora indica*, which belongs to root-colonizing type of Sebacinales family, increased root growth, canopy development, SPAD values (indicating differential transmittance of red and an infrared light having 650 nm and 940 nm wavelength respectively through the leaf) and antioxidants (catalase and superoxide dismutase) up-regulation. More importantly, inoculation boosted proline content and suppressed the malondialdehyde (MDA) content [137]. Likewise, wheat-endophytic microbes' interaction significantly boosted PSII efficiency, and triggered increased plant height and seed weight [138]. Additionally, japonica rice interaction with *Paecilomyces formosus* improved the growth traits through down regulation of signaling molecules, ABA and jasmonic acid [139].

Similarly, soybean inoculated with *Paecilomyces formosus* suppressed lipid peroxidation rate and accumulation of linolenic acid, peroxidase (POX), catalase (CAT), and superoxide dismutase (SOD). It was attributed to biosynthesis of phytohormones such as aldehyde dehydrogenase forindole acetic acid, indole-3-acetamide hydrolase, and geranylgeranyl-diphosphate synthase [140]. In addition, plant-microbe interaction promotes synthesis of enzyme including ACC deaminase [141]. Furthermore, plant-microbe interaction created a specific extracellular matrix that maintained hydrated root environment [142]. Similarly, *Paenibacillus polymyxa* heightened the production of biofilm in wheat which enhanced plant survival [143]. Moreover, in the roots of Arabidopsis, *Bacillus megaterium* secreted polyamine spermidine that effectively scavenges ROS along with upregulating the biosynthesis of ABA which led to augmentation of photosynthesis and root architecture [144,145]. Moreover, *Pseudomonas chloroaphis* synthesized butanediol which plays a vital role in drought related signaling pathway allowing stomatal closure in Arabidopsis [146].

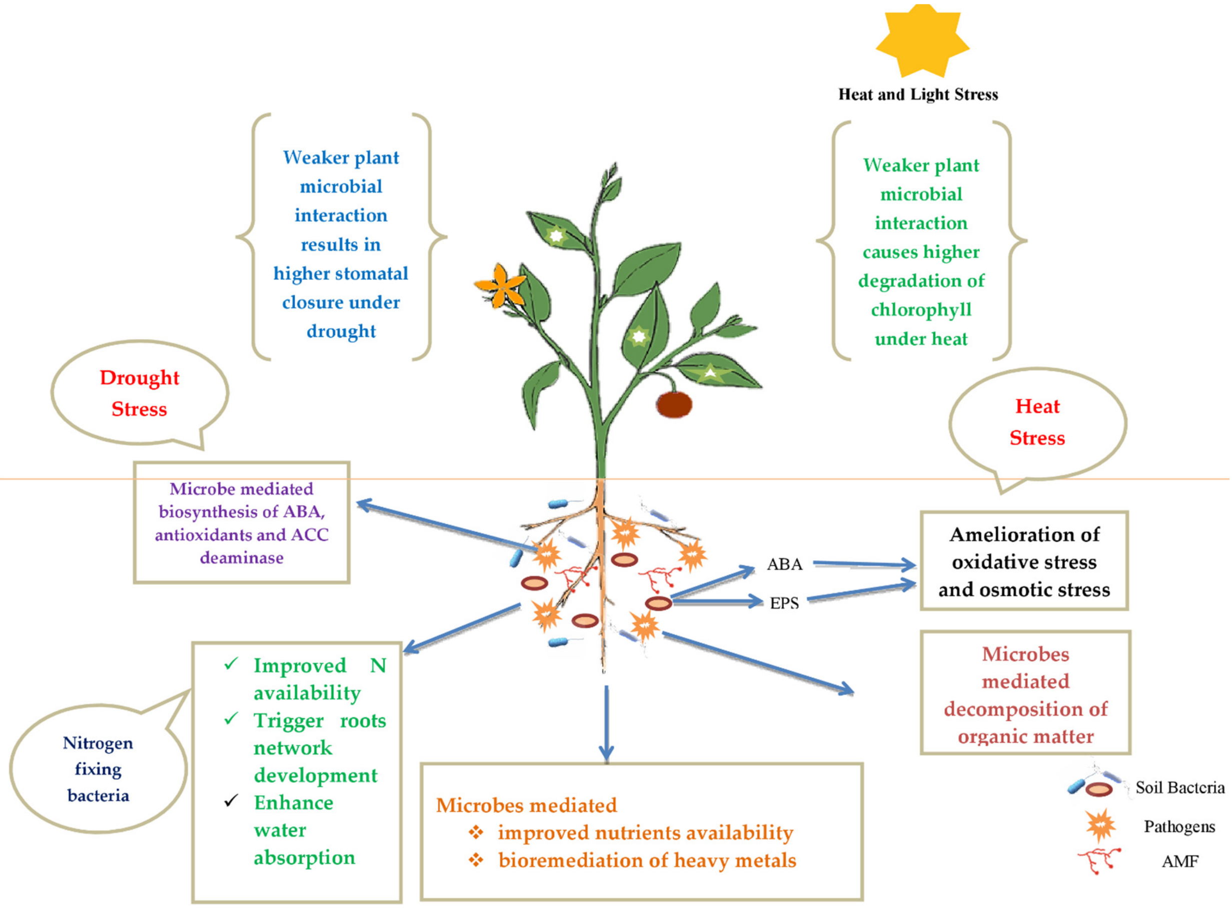

Figure 5. Plants-microbes interaction and microbe-mediated alterations such as biosynthesis of abscisic acid (ABA), 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase and exopolysaccharides (EPS) etc. under drought and heat stresses.

Overall, plant-microbes (e.g., *Bacillus* spp., *Anabaena azollae*, *Azotobacter* spp., *Paenibacillus* spp. etc.) interactions hold potential to ameliorate the adverse effects of HS and DS [147] which might be studied in three different ways. Firstly, microbes' roles in promoting host plant nutritional status must be the subject of future studies and secondly, microbes' mediated antagonism against various pathogens also needs urgent attention. Thirdly, microbes' interaction in the perspectives of their capabilities to stimulate a variety of defense mechanisms in crops and plants must be studied at physiological and molecular levels. Last but not least, the plant-microbes association holds the potential to save over 25–40% cost of chemical fertilizers and pesticides by bolstering soil-available nutrients and triggering natural plant defenses against environmental hazards.

5. Mechanisms of Microbe Survival and Drought Amelioration

The DS-tolerant microbes have evolved and adapted various tolerance mechanisms which enable them to survive through development of thick cell encapsulation, going into dormant phase, accumulation of osmolytes and production of exopolysaccharides (EPS). Interestingly, a significant increment in gram-positive to gram-negative bacteria ratio was observed in a drought-hit rhizosphere [147], while varying impacts of drought on different microbial strains has also been reported [148,149]. Specifically, DS led to sharp declines in gram-negative phyla such as Bacteroidetes, Proteobacteria and Verrucomicrobia [150–152].

Contrarily, gram-positive phyla (Actinobacteria and Firmicutes) recorded significant increase in their population under water shortage [153]. This behavior of microbes might be attributed to substrate preference and capabilities of both types of bacteria which impart distinct drought susceptibilities. Likewise, the oligotrophs microbes tend to thrive well under DS despite being slow growers, and are declared highly specific in terms of substrate requirement [154–156]; contrastingly, copiotrophs microbes need abundant nutrients and a moisture-rich environment. Moreover, the soils experiencing DS tend to contain bacterial strains that degrade complex plant polysaccharides and low microbial-population-targeting oligosaccharides [157]. Different microbes, especially endophytes, ensure their survival by entering into the plant tissues through injured roots, stomata, hydathodes and lenticels openings in leaves, flowers and seeds of different crops (Figure 6).

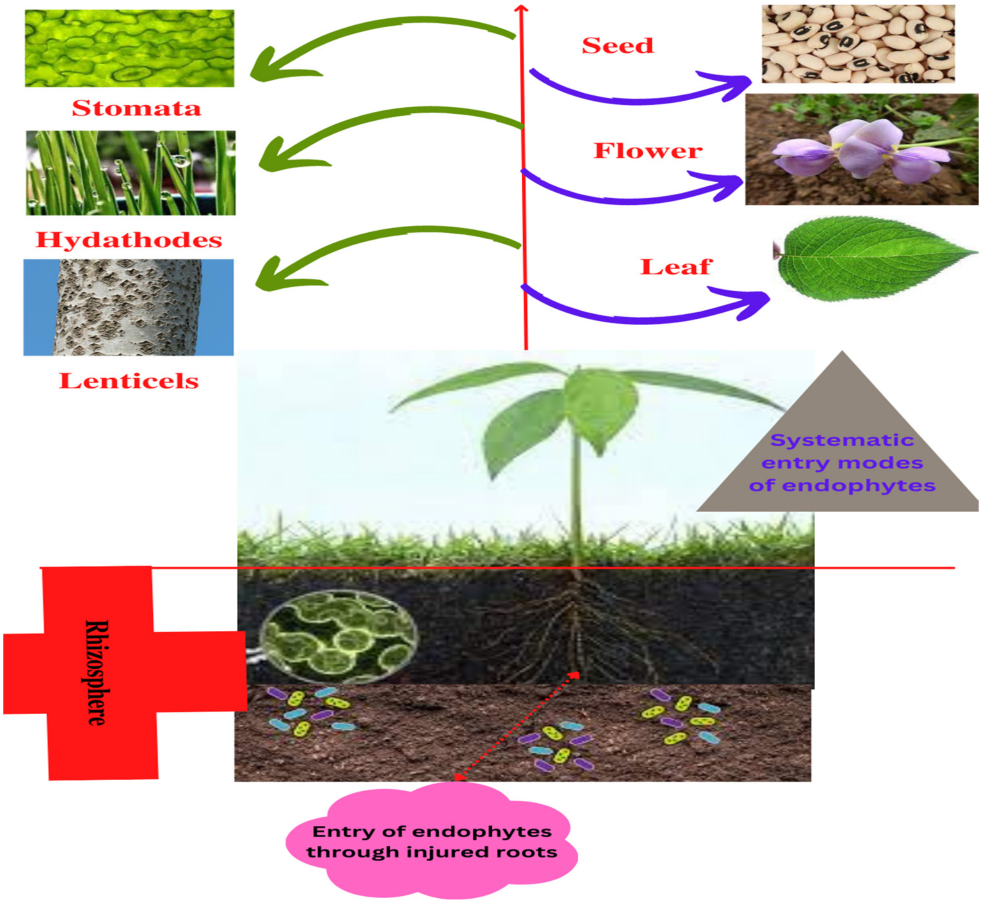

Figure 6. Different modes of entry of endophytes into plant tissues for mediating numerous morphological and physiological alterations.

As far as microbe-mediated drought tolerance is concerned, provision of nutrients and synthesis of various phytohormones (e.g., abscisic acid ABA, indole-3- acetic acid IAA and cytokinins Ck), bacterial exopolysaccharides and ACC deaminase are the major mechanisms [151,154,158]. The PGPR-mediated hormones synthesis stimulated cell division under DS, especially IAA, the most active auxin, which regulates the differentiation of vascular tissues and adventitious roots along with promoting cell division and shoot growth [159]. Moreover, ABA optimized the hydraulic conductivity of roots and regulated the drought-related gene transcription, which enhanced water use efficiency [160]. Likewise, *Azospirillum brasilense* ameliorated drought tolerance in *Arabidopsis thaliana* via ABA synthesis [161]. The ACC deaminase has been recognized as ethylene's precursor under DS, while ACC deaminase synthesized by microbes hydrolyzes ACC into derivatives such as ammonia and alphaketobutyrate, which ultimately promote plants' growth and productivity [161]. For instance, *Pseudomonas aeruginosa*, *Proteus penneri*, and *Alcaligenes faecalis* increased amino acids and proteins along with the sugar content of maize [25]. Moreover, microbe inoculation restricted the antioxidant activity and boosted the synthesis of free amino acids, proline, and sugars in crops plants under suboptimal moisture conditions [162,163]. Furthermore, *Pseudomonas putida* H2-3 inoculation enhanced synthesis of various hormones like EPS which impart tolerance against drought [164]. Along with EPS synthesis, microbe-mediated synthesis of various compatible solutes, including proline, glycine and betain, along with trehlose and spore formation, assist crop plants to survive DS by maintaining the membrane permeability, prevent destructing of enzymes and keep different proteins in the functional form [165]. Various underlying mechanisms of microbe-mediated drought tolerance in cereal crops such as wheat, rice, maize etc. have been described in Table 1. However, consortia of endophytic plants and PGPR must be studied in depth for determining their effectiveness to mitigate the negative effects of water scarcity.

Table 1. Different microbial strains mediated drought tolerance mechanisms for cereal crops under water-limited conditions.

Crops	Microbial Strains	Mechanism of Conferring Tolerance against Drought	References
Maize (*Zea mays*)	*Azospirillum lipoferum*	Enhanced soluble sugars, biosynthesis of amino and proline, along with roots and shoot.	[25]
Maize (*Zea mays*)	*Bacillus* spp.	Greater accumulation of sugars and decline in electrolytes leakage. and enzymes (CAT and glutathione peroxidase) activity.	[130]
Rice (*Oryza sativa*)	*Trichoderma harzianum*	Promotes root network, which delays the onset of drought.	[25]
Wheat (*Triticum aestivum*)	*Azospirillum brasilense*	Triggers attenuation of transcript levels and balances homeostasis.	[147]
Wheat (*Triticum aestivum*)	*Bacillus amyloliquefaciens*	Attenuates the levels of transcript leading to improved homeostasis under DS.	[147]
Wheat (*Triticum aestivum*)	*Mesorhizobium ciceri*	Boosting drought tolerance index under severe water-scant conditions.	[52]
Wheat (*Triticum aestivum*)	*Rhizobium leguminosarum*	Improve biosynthesis of IAA, CAT and EPS.	[147]
Wheat (*Triticum aestivum*)	*Rhizobium phaseoli*	Produce CAT, EPS and IAA which improved the growth, biomass and drought tolerance index.	[52]

Besides cereals, legumes, *Brassica* spp., *arabidopsis'* interaction with microbes also remained effective in mitigating the adverse effects of DS through improved nutrient and water uptake. Moreover, cop plants association with *Pseudomonas putida* and *Bacillus thuringiensis* restricted stromal conductance and minimized leakage of electrolytes owing to proline accumulation in the roots and shoot of stressed plants [166]. Different microbial strains mediated drought tolerance mechanisms for various legumes, *Brassica* and *arabidopsis* have been summarized in Table 2. However, there is dire need to conduct further in-depth studies for exploring the microbes' effectiveness in mitigating the deleterious effects of drought and enhance our understanding related to underlying mechanisms which impart tolerance against water scarcity.

Table 2. Different microbial strains mediated drought tolerance mechanisms for legumes, *Brassica* spp. and other crops under water limited conditions.

Crops	Microbial Strains	Mechanism of Conferring Tolerance against Drought	References
Arabidopsis (*Arabidopsis thaliana*)	*Azospirilum brasilense*	Better plant survival and seed yield owing to proline and malondialdehyde, better water retention capacity and reduced stomatal conductance.	[161]
Arabidopsis (*Arabidopsis thaliana*)	*Phyllobacterium brassicacearum*	Enhanced the level of ABA, delayed reproductive development and improved water and nutrient use efficiencies.	[161]
Barrelclover (*Medicago truncatula*)	*Sinorhizobium medicae*	Improved nutrient absorption, root nodulation and canopy development.	[18]
Chickpeas (*Cicer arietinum*)	*Pseudomonas putida*	Improved accumulation of osmolytes, ROS scavenging capacity and expression of stress related genes.	[72]
French lavender (*Lavandula dentate*)	*Bacillus thuringiensis*	IAA induced higher proline and K-content and decreased glutathione reductase (GR) and ascorbate peroxidase (APX) activity.	[163]
Lettuce (*Lactuca sativa*)	*Azospirillum* spp.	Enhanced chlorophyll, ascorbic acid, chroma functioning and antioxidant potential along with lowering the drought induced browning intensity.	[147,149]
Smooth-stemmed turnip (*Brassica oxyrrhina*)	*Pseudomonas libanensis*	Optimized leaf water contents and pigments synthesis along with reducing proline and malondialdehyde concentrations in leaves.	[165]
Smooth-stemmed turnip (*Brassica oxyrrhina*)	*Pseudomonas reactans*	Increased relative water content of leaves and reduced proline and malondialdehyde contents in leaves.	[165]
Soybean (*Glycine max*)	*Pseudomonas putida*	Lowered abscisic acid, salicylic acid, flavonoids, superoxide dismutase, and free radicals scavenging activity while jasmonic acid synthesis was boosted.	[163]

6. Mechanisms of Microbe-Mediated Heat Tolerance

Before studying microbe-mediated heat tolerance, it is necessary to understand the underlying mechanisms which enable microbes to survive elevated temperatures. The most strategic microbial characteristics are the synthesis of enzymes and structural proteins which ensure membrane integrity and appropriate functioning of nucleic acids under HS [32]. On the basis of survival potential under HS, microbes are classified into psychrophilic (whose maximum growth occurs at or below 15 °C) and psychrotrophic (which need 15 °C or higher temperature for attaining the maximum growth). Interestingly, molecular chaperons are the most effective mechanism to defend microbes against heat. In addition, HS induced gene expression also ensures microbes' survival under HS. For instance, DnaK, the gene present in *Alicyclobacillus acidoterrestris*, is triggered to code heat shock proteins which protect microbes. Future research investigations are needed to explore further HSP expression for adapting microbes to higher soil temperatures [31].

Regarding microbe-mediated heat mitigation, improved nutrient supply and translocation within plant tissues triggered photosynthesis under HS [31]. Additionally, osmotic and oxidative stress amelioration through biosynthesis of ABA and EPS have been depicted in Figure 5. Likewise, synthesis of trehalose multiplied under HS, which protected plants from heat shock injury and oxidative stress [33,34]. Likewise, it plays a critical role in cells proteins' stabilization and resultantly, the survival of field crops under HS becomes possible. Another microbe-mediated heat tolerance mechanism is synthesis of various metabolites, however, very scant information is available about underlying mechanisms. Compared to heat tolerant microbes, more research is available for chilling stress tolerant microbes such as *Brevundimonas terrae*, *Pseudomonas cedrina* and *Arthrobacter nicotianae* [166,167]. Furthermore, psychrophilic bacteria isolated from Antarctica exhibited antimicrobial activity [168] which demands further research to explore the underlying mechanisms. Moreover, thermo-tolerant phosphate solubilizing the microbe's inoculation might act as multifunctional bio-fertilizer. Besides, their function as catalyst to promote biogeochemical cycling of phosphorus in agricultural fields awaits further studies [169–171].

7. Perspectives of Bio-Fertilizers, Challenges and Future Research Needs

Generally, BFs are classified on the basis of their functions N-fixer, P and K solubilizers, and plant growth promoting rhizobacteria. The N-fixing microbes include *Azotobacter*, *Azospirillium*, *cyanobacteria* and various symbionts such as *Anabaena Azolla, Rhizobium, and Frankia*. The legume-associated microbes include members of the genera *Azorhizobium, Bradyrhizobium, Mesorhizobium, Sinorhizobium,* and *Allorhizobium*. For non-legumes crops, N-fixing microbes include genera of *Arthrobacter, Acetobacter, Azomonas, Enterobacter, Lignobacter* and *Mycobacterium*. Although hundreds of microbial genera have been isolated from the rhizosphere, for the most part, only members of *Azospirillum* and *Azotobacter* have been widely tested. The microbe-based bio-fertilizers (BFs) which are the formulation-adjustable products encompass untapped potential to supply essential nutrients to plants under DS and HS. Few of the most prominent microbial candidates include *Azotobacter*, *Acetobacter*, *Anabaena azollae*, *Azospirillum*, and *Pseudomonas*, which can effectively ameliorate the adverse effects of abiotic stresses through biosynthesis of vitamins, growth hormones, antioxidants, antibiotics and phosphate solubility [172–175] (Figure 7). Additionally, *Bacillus* spp. containing BF might be investigated in terms of most efficient dose, plant species, time of application, crop growth stage etc. under unfavorable environmental conditions [131]. Furthermore, in vivo screening studies for isolating putative PGPR from drought-hit plants for preparing BFs might be used as potent strategy in order to confirm the effectiveness and extent of their growth promotion effects under abiotic stresses [123].

More importantly, BFs containing stable microbial consortia might have synergistic effects in alleviating drought and heat effects than do individual microbial genera. For instance, a consortium entailing 10 endophytic strains ensured plant survival of hybrid poplar under water-scarce conditions through unknown drought-responsive pathways [171,172]. These findings indicate that environmental extremities might be confronted using multiple microbes-based BFs because they trigger many tolerance-imparting activities and this aspect direly requisites more research studies to explore the underlying mechanisms. However, the prime challenge in promoting BFs for drought and heat mitigation are to identify, isolate and culture microbes from drought-hit plants for subsequent use as BFs. In addition, research findings are scant regarding microbial strains' potential to convert atmospheric N into available ammonia along with solubilizing P in the rhizosphere under water limited conditions [175]. It is important to note that crop modeling which involves mathematical presentation of biological systems in agro-ecosystems may also assist to evaluate BFs efficacy as influenced by multiple factors such as intensity and duration of abiotic stress, crop species, microbial strains suitability etc.

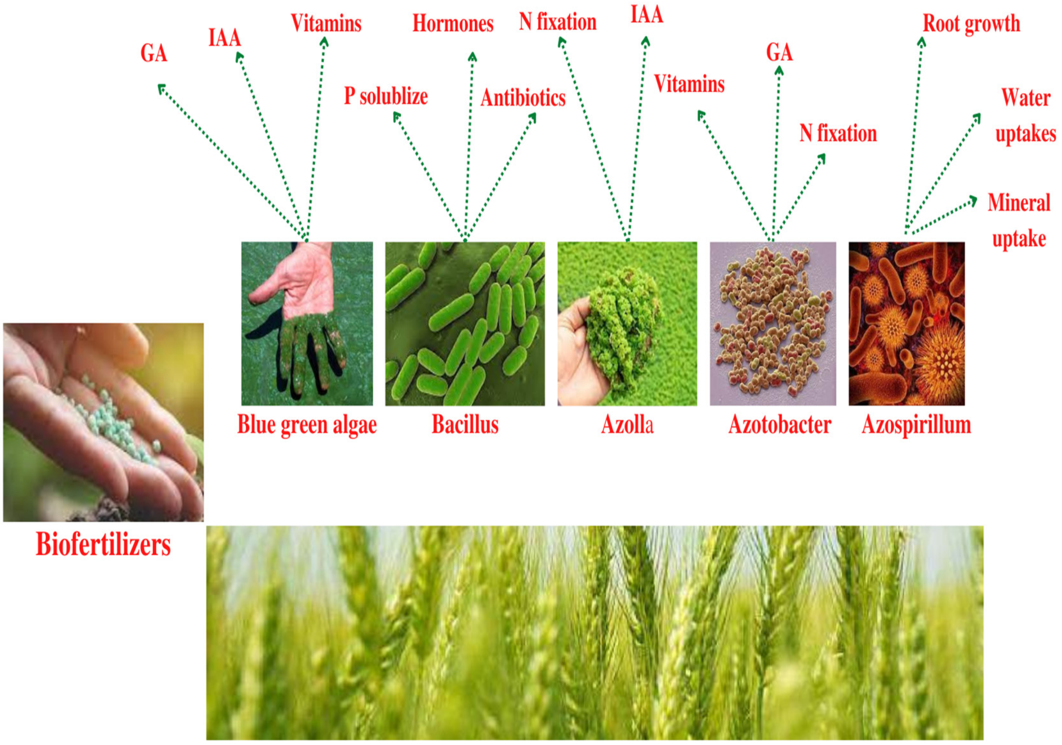

Figure 7. Different microbes (blue green algae, *Bacillus* spp., *Anabaena azollae*, *Azospirillum* spp., *Azotobacter* spp.) and their associated effects in crop plants.

Some of the prime constraints which have restricted the application of BFs on a large scale include competition of local flora with bio-inoculants for niche, non-supportive soil characteristics, presence of soil pollutants, climatic extremities, and unavailability of specific strains and effective carriers. Moreover, a shortage of skilled staff in BFs production unit, a scarcity of research funds, meager research on storage and transport necessities, and insufficient farmer awareness and marketing constraints, along with non-establishment of production standards are future challenges [171,173,175]. A real-time series of BFs-root relationship under DS and HS can highlight trends of accumulation and/or depletion of microbe's taxa, along with revealing the impacts of plant developmental stage on microbial recruitment leading to devising of effective mitigating strategies for ensuring food security under a changing climate.

8. Conclusions

A wide array of factors influence microbe-mediated tolerance in field crops, especially crop type, growth stage, intensity and duration of abiotic stresses, and particularly microbes' species (gram-positive or gram-negative, and oligotrophy or copiotrophy). Additionally, microbes present in the rhizosphere, or their exogenous application, can impart resilience against drought and heat stress, while their efficacy can be further enhanced through microbe-based biofertilizers application. However, a single microbe-mediated mechanism may not be declared as universally linked for drought and heat mitigation. The research gaps exist related to underlying mechanisms which impart resilience in microbes to survive abiotic stresses along with microbe-induced alterations in crop plants which confer stress tolerance. New insights into plant-associated microbial taxa might assist in identifying the potential strains for boosting plant growth. Under changing climate scenarios, microbial-based mitigation strategies involving soil and foliar application of microbial consortia can effectively alleviate the adverse effects of drought and heat stresses in arid and semi-arid regions, thus ensuring food security.

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