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Enhancing Abiotic Stress Tolerance in Fruit Trees Using Microbial Biostimulants

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Abstract

Global climate change has significantly reduced the yield of many crops due to various abiotic stressors. These stressors include water-related issues such as drought and flooding, thermal changes like extremely low and high temperatures, salinity, and adverse soil pH conditions including alkalinity and acidity. Biostimulants have emerged as promising and effective tools for mitigating the damage caused by these abiotic stressors in plants, ultimately enhancing both the quantity and quality of crops. Biostimulants are naturally derived substances that include humic acid, protein hydrolysates, nitrogenous compounds, seaweed extracts, beneficial bacteria, and molds. Even at low concentrations, biostimulants play a critical role in activating important plant enzymes, inducing antioxidant defenses, improving water relations and photosynthetic activity, stimulating hormone-like activities (particularly auxins, gibberellins, and cytokinins), and modulating root system development. This review discusses the physiological effects of microbial biostimulants on the quality and productivity of fruit crops, as well as their experimental applications.

Keywords: Abiotic Stress, Biostimulants, Fruit, Microorganisms

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INTRODUCTION

The horticulture and agriculture sectors face the contradictory challenges of producing high-quality food products and meeting the demands of a global population expected to reach nearly 10 billion by 2050,[1] while also reducing environmental pollution caused by the increased use of agrochemicals such as pesticides and fertilizers. The negative effects of chemical pesticides and fertilizers are significant. They have long half-lives in the soil and environment, impacting both biotic and abiotic factors. These chemicals harm the environment, microflora, soil health, and other living organisms. Additionally, residues often remain in fruits and vegetables, especially when practices such as ignoring the interval between the last spraying date and harvest time or overdosing to achieve better results are followed. Over the past few decades, pesticide residues have accumulated in soils, posing significant ecotoxicological risks.[2] Their use may have detrimental effects on the environment, as well as on animal, plant, and human health.

Different types of plant protection products are used to prevent damage to plants. However, there has been a gradual shift towards using natural preparations to replace chemical and mineral plant protection agents.[3] Growing concern regarding biostimulants arises from their capacity to utilize agricultural, urban, and industrial waste products to promote sustainable production and yield stability.[4] Plant biostimulants contribute to sustainable agriculture by positively affecting plant growth and enabling crops to overcome the negative effects of suboptimal growing conditions. Research by Ruzzi and Aroca,[5] Franzoni *et al*.,[6] Carolina Feitosa de Vasconcelos *et al*.,[7] Rouphael and Colla,[8] and Rakkammal *et al*.,[9] has demonstrated that biostimulants improve plant tolerance to abiotic stresses such as drought, extreme temperatures, salinity, and hypoxia. They also enhance the architecture and biomass of plant root systems. By promoting plant health and vigor, biostimulants can improve crop quality by increasing harvestable yields. In organic farming, where artificial fertilizers are not permitted, biostimulants help reduce the required amount of fertilizer, which is crucial. The biostimulant industry is rapidly expanding within the agricultural sector, with an annual growth rate predicted at 7.4% and a forecasted revenue of USD 4.6 billion by 2030.[10]

The term "biostimulants" is broad and lacks precision. Kauffman *et al*.[11] introduced the term to refer to substances that enhance plant growth at low doses, distinct from fertilizers. Many scientists have defined biostimulants based on regulatory frameworks and the origin of active substances.[12-15] Biostimulants are often described as any substance that positively impacts plants without being a nutrient, pesticide, or soil enhancer. Unlike fertilizers and pesticides, biostimulants are identified by their beneficial effects on plants. Essentially, they are categorized by what they are not and their positive benefits.[16]

Types of Microbial Biostimulants

Biostimulants are natural ingredients or microbes that help plants grow under stressful conditions without causing negative effects.[13] They include enzymes, micronutrients, protein hormones, plant hormone precursors, and amino acids. The term biostimulant also encompasses natural stimulants such as protein hydrolases, phenols, salicylic acid, fulvic acids, and humic acid.[13,17] Both natural and synthetic chemical biostimulants can be supplied to bacteria and fungi to enhance plant growth, regulate production and quality traits, and improve resilience to environmental stressors. For example, PGPRs offer advantages to plants even in the absence of nutrients, pesticides, or soil enhancers. These bacteria exist in various forms, each with its own taxonomic classification, and are categorized based on their agricultural and horticultural benefits. The terms "biofertilizers" and "biocontrol agents" are also used to describe these bacteria in the context of agricultural and horticultural practices. Although biostimulants are often confused with fertilizers, they do not provide direct nourishment to plants. Instead, they support the metabolic processes of both soil and plants, leading to improved nutrient acquisition.[18]

Among the common fungi used as biostimulants, endomycorrhizae, specifically members of the Glomeromycota species, are notable for their benefits in effective plant nutrition, making them crucial for advancing sustainable agriculture.[19] Other symbiotic fungi include *Trichoderma* spp., *Sebacinales* spp., and *Heteroconium chaetospira*.[20-24] Beneficial bacterial species include *Agrobacterium, Arthrobacter, Azospirillum, Azotobacter, Bacillus, Burkholderia, Caulobacter, Chromobacterium, Enterobacter, Erwinia, Flavobacterium, Micrococcus, Pantoea, Pseudomonas*, and *Serratia*.[21,25-27]

These microorganisms support plant growth through several mechanisms:
1. nutrient solubilization: they solubilize essential nutrients, such as phosphorus (P), to facilitate plant uptake.
2. nitrogen fixation: soil microorganisms engage in a symbiotic nitrogen (N) fixation, transforming atmospheric N into ammonium (NH_4-N).
3. iron oxidation: they synthesize siderophores that oxidize iron (Fe), increasing its assimilable form for plants.
4. hormone secretion: microorganisms increase hormone secretion, supporting plant homeostasis and physiological and metabolic functions.

The synthesis of these hormones is linked to increased indole acetic acid (IAA) production.[28] These diverse mechanisms underscore the role of microorganisms in enhancing plant growth and resilience, making them vital components of sustainable agricultural practices.

Vital role of biostimulants on crop plants

Fruit tree crops are essential agricultural commodities, making treatments that support and enhance fruit yield highly significant. Currently, perennial fruit trees are exposed to multiple abiotic stressors throughout their lifespan due to ongoing climate change. Seasonal weather patterns, including heat waves, heavy rainfall, droughts, and intense ultraviolet radiation, can greatly diminish the yield and quality of fruits and vegetables.[29,30]

Low concentrations of plant biostimulants can trigger various plant responses at the molecular, physiological, and biochemical levels. These responses include boosting the blooming process, promoting plant development and abundance, and improving the nutritional and operational uniformity and shelf life of edible crops. Additionally, microbial plant biostimulants have been shown to enhance nutrient use efficiency and increase resilience to abiotic stresses such as salinity, extreme temperatures, and drought.[14,31,32]

Many studies have aimed to elucidate the physiological and molecular mechanisms controlling the effects of biostimulants on plants. These mechanisms include i) activation of essential enzymes to stimulate C and N metabolism, ii) strengthening of the defense mechanism against oxidants, and iii) the development of secondary metabolites. Additionally, biostimulants can iv) encourage photosynthesis and improve water management, v) enhance the physical and chemical properties of soil, and vi) stimulate the production of hormone-like substances, such as gibberellins, cytokinins, and auxins. Furthermore, vii) through their actions, they can improve the populations of microorganisms that exist on the surface of plants and in the soil surrounding their roots. Additionally, they can influence various aspects of the root system, such as density, width, length, size, branching, and quantity of soil or substrate used.[32-36]

Stressors in plants

Abiotic stress refers to environmental conditions that reduce plant growth and productivity below optimal levels. Factors such as extreme salinity, temperature fluctuations, acidity, drought, flooding, soil composition, wind, and UV radiation adversely affect plants, ultimately diminishing both the quality and quantity of harvested yields.[37] Yield quantity encompasses agronomic and organoleptic properties, as well as nutrient and vitamin content. Agronomic properties include fruit size, yield, and resistance to fungal or bacterial rot, while organoleptic properties involve characteristics like fruit shape and firmness. Plants expend considerable energy combating abiotic stress instead of focusing on yield production, resulting in significant yield reductions. Biotic factors, such as infectious bacteria, fungi, or viruses-known collectively as living factors-can also induce various plant disorders leading to yield reductions or complete harvest loss. To mitigate these losses, biostimulants are increasingly employed in agricultural practices.

Approximately 60-70% of yield variation attributed to climate change is caused by abiotic stressors, notably salinity and drought in water and soil.[34,38] Environmental stresses often lead to oxidative stress, disrupting physiological, metabolic, biochemical, and morpho-anatomical processes crucial for growth and economically significant yield reductions.[39] Plant biostimulants play a crucial role in stabilizing crop yields under adverse environmental and soil conditions.[35] One example is seaweed extracts (SWE) from green, red, and brown macroalgae which are widely used microbial biostimulants in agriculture and horticulture, with various commercial products available. Algal inoculation has been shown to enhance the growth of *Vicia faba* crop plants.[40] SWE applications offer multiple benefits, including enhanced plant growth, improved product quality, and increased stress resistance—both biotic (antifungal and antibacterial properties) and abiotic (enhanced water and nutrient availability).[41]

The efficacy of biostimulants in enhancing abiotic stress tolerance in agricultural and horticultural crops is linked to several physiological and biochemical mechanisms. These mechanisms include: i) strengthening the root system to enhance nutrient uptake and assimilation; ii) improving photosynthetic efficiency and leaf-water relations; iii) increasing the accumulation of osmolytes such as sorbitol, proline, betaine, and glycine; iv) reducing oxidative stress by lowering hydrogen peroxide (H_2O_2) and malondialdehyde (MDA) levels, and enhancing antioxidant defenses through increased activities of enzymes like catalase (CAT) and superoxide dismutase (SOD); v) optimizing water use efficiency by reducing transpiration and stomatal resistance, and improving the root-to-shoot ratio; vi) regulating key genes involved in reactive oxygen species (ROS) detoxification and osmolyte synthesis; and vii) influencing epiphytic microbial communities that support plant growth.[36,42,43]

Microbial biostimulants improve water stress tolerance in fruit

Microbial biostimulants enhance plant tolerance to drought and salinity through various direct and plant-mediated mechanisms. Under water stress conditions, microbial biostimulants can produce bacterial exopolysaccharides that improve soil structure by forming micro- and macroaggregates.[44,45] Additionally, these exopolysaccharides bind Na^+ ions, reducing their uptake by plants, and create hydrophilic biofilms that create a microenvironment promoting water retention and protecting microbes from drought stress.[46,47]

Research on the application of plant biostimulants to mitigate water stress in fruit crops remains limited, but promising outcomes have been noted in citrus species. Specifically, SWE from *Ascophyllum nodosum* was found to alleviate the detrimental effects of water stress on newly planted 'Hamlin' variety orange trees (*Citrus sinensis* (L.) Osbeck) grafted onto citrange rootstocks ('Carrizo' and 'Swingle'), under different water regimes (50% and 100% of evapotranspiration), whether applied as a foliar mist or soil drench.[48] In grapevines, foliar application of SWE facilitated photosynthetic recovery following drought stress, whereas soil drench had no significant physiological impact.[49] Regardless of rootstock type, potted trees treated with SWE exhibited enhanced growth, characterized by longer stems, increased leaf area, and higher shoot and leaf weights. Moreover, water use efficiency, whether intrinsic or agronomic relative to total biomass, was notably improved in water-stressed trees grafted onto 'Swingle' rootstock. These effects are likely linked to alterations in hormone metabolism and the accumulation of phenolics, suggesting a plausible physiological mechanism underlying the differential response of rootstocks to water stress.[48]

Arbuscular mycorrhizal fungi (AMF) represent a significant and sustainable approach to enhancing drought resistance in horticultural crops, including flowers, fruits, and vegetables.[50,51] AMF influence the architecture of plant roots, affecting parameters such as diameter, density, length, and the development of lateral roots.[52] Microbial biostimulants based on AMF have demonstrated effectiveness in bolstering the drought resilience of citrus plants. For instance, the fungal species *Funneliformis mosseae* enhances IAA levels in roots, promotes root hair development, and stimulates the growth of orange plants under drought conditions.[53] Studies by Wu *et al.*,[54] extensively analyzed various pathways involved in drought tolerance facilitated by AMF. Inoculation with AMF can alter root architecture, thereby enhancing water absorption efficiency.[55]

Additionally, AMF-inoculated citrus plants exhibit significantly higher water absorption through their hyphal networks under drought stress, compared to non-inoculated plants, irrespective of the specific AMF species used.[56] In trifoliate orange (*Poncirus trifoliata* (L.) Raf.) grown under controlled substrate conditions, AMF applications have induced osmotic adaptations that enhance plant growth efficiency and improve leaf tissue hydration during drought stress.[57,58] Specifically, AMF-treated plants under drought stress show elevated concentrations of inorganic ions (K^+ and Ca^{2+}) and organic solutes (glucose, fructose, sucrose) involved in osmotic regulation. Moreover, AMF-inoculated plants exhibit higher proline levels, crucial for osmotic adjustment, compared to non-inoculated plants where proline-catabolic enzyme activities are more pronounced.[59] AMF have also been effective in enhancing soil aggregate stability and rhizospheric structure, thereby improving water accessibility and growth efficiency. Studies on trifoliate orange have shown a positive correlation between soil hyphal length or root colonization by AMF and the extractable concentration of soil glomalin, a glycoprotein responsible for enhancing soil structure through rhizospheric glue mechanisms.[54] Jia-Dong *et al*.,[60] explored the role of aquaporins—water transport proteins in cell membranes—in enhancing growth efficiency and water status of trifoliate orange plants during AMF inoculation and water stress. The study revealed complex responses of aquaporin genes, both upregulated and downregulated, in mycorrhizal plants under drought stress. Enhanced root system architecture in mycorrhizal plants allows extended exploration of soil by radical hyphae, improving water and nutrient uptake efficiency, particularly for phosphorus (P), zinc (Zn), and copper (Cu), in low-water environments.[61]

Wu *et al*.,[62] examined trifoliate orange (*Poncirus trifoliata* L. Raf.) and reported that when *Glomus versiforme* colonized a plant lacking water, the mineral content of the leaves (N, P, Ca, K, Fe, Zn, and Mn) increased in contrast to control plants. In cultivars of pistachios ('Badami-Riz-Zarand' and *Pistacia vera* 'Qazvini'), AMF (*F. mosseae* and *R. intraradices*) inoculated plants grown under greenhouse conditions increased the utilization of essential minerals like Zn and P, as well as elevated the status of the water in leaves underwater stress.[63] Several studies have revealed that treatment with AMF enhances the ability of citrus plants to withstand drought by decreasing their osmotic potential. This reduction is achieved through the buildup of both inorganic and organic solutes, which can also act as potential protectors against osmotic stress.[38,54]

AMF symbiosis has proven beneficial in enhancing drought tolerance in various vegetable crops. Field studies on AMF-inoculated tomatoes (*Solanum lycopersicum* L.) colonized by *R. intraradices* have highlighted significant improvements in agricultural practices and physiological responses under different drought intensities.[64] Inoculated plants showed substantial increases in fruit yield under excessive, moderate, and mild drought conditions, surpassing non-inoculated plants by 25%, 23%, and 16%, respectively. Enhanced crop productivity in inoculated plants was attributed to improved nutrient uptake (higher levels of nitrogen and phosphorus) and maintained leaf water status. Cesaro *et al*.,[65] confirmed this result in tomatoes colonized by *Funneliformis,* where AMF inoculation significantly increased yield under mild and severe stress conditions. Additionally, *G. versiforme* enhanced the productivity by 20-32%. In greenhouse melon plants (*Cucumis melo* L. 'Zhongmi 3'), inoculation with AMF species such as *G. versiforme*, *R. intraradices*, and *F. mosseae* demonstrated enhanced drought resistance compared to non-inoculated plants. This resulted in improvements in plant height, biomass accumulation, and net photosynthetic rates.[39]

In response to water stress, plant cells release free radicals that can damage cell structures. However, biostimulants reinforce antioxidants, which can mitigate the toxic effects of these radicals and enhance plant defense systems by reducing oxidative stress levels. Plants with elevated antioxidant levels exhibit improved root and shoot growth, maintain high leaf moisture content, and show lower disease susceptibility under both optimal and stressful environmental conditions.[66]

The development of soluble sugars through AMF symbiosis and the enhancement of antioxidant enzymes are associated with increased drought tolerance and agricultural productivity.

Davies *et al*.,[67] investigated the mechanisms underlying drought mitigation using a blend of *Glomus* spp. in Mexican and Chilean ancho peppers. They found that application of ZAC-19 (*G. albidum, G. claroides*, and *G. diaphanum*) improved leaf water potential and the root-to-shoot ratio, suggesting potential use in Chilean pepper transplant systems to mitigate drought impacts in Mexican open-field agriculture. Davies *et al*.,[67] also observed that drought stress promoted the growth of extra-radical hyphae of *Glomus* sp. Deserticola in bell peppers, leading to enhanced water uptake compared to non-mycorrhizal plants. AMF-inoculated plants were also found to regulate abscisic acid (ABA) levels better than non-inoculated plants, improving the balance between root water transport and leaf transpiration during drought stress and subsequent recovery.[68] Research on strawberries (*Fragaria ananassa*) inoculated with *F. mosseae* BEG25, *F. geosporus* BEG11, or a combination thereof showed increased growth, productivity, and water-use efficiency (WUE) compared to non-mycorrhizal plants.[69] AMF inoculation has also been reported to enhance WUE in watermelons,[70] indicating that AMF not only improve water absorption but also increase the efficiency of water use by the host plant. This improvement may be attributed to enhanced transpiration, stomatal conductance, and nutrient availability.[61,71] Asrar *et al*.,[72] demonstrated that AMF-inoculated potted snapdragon (*Antirrhinum majus* 'Butterfly') plants, particularly Deserticola, mitigated the adverse effects of drought stress on flower quality, increasing flower number, diameter, nutrient content (N, P, K, Ca, Mg), water relationships, and chlorophyll content under severe drought conditions, thereby enhancing crop production.

Zamljen *et al*.,[73] assessed the impact of a commercial biostimulant derived from *A. nodosum* extract on water-stressed melon plants. They found that biostimulated plants exhibited improved root water absorption, leading to a 44% increase in yield compared to control plants. In water-limited environments, microbial biostimulants promote root growth over shoot growth. This adaptation allows plants to penetrate deeper soil layers during dry seasons, facilitating the synthesis of compatible solutes that help maintain favorable water potential gradients and enhance water uptake as soil moisture decreases. According to Van Oosten *et al*.,[74] this process involves creating synthetic absorption surfaces around plant roots, which effectively retain soil moisture for the benefit of the plant.

Microbial biostimulants improve salt stresses in fruit

Several reviews have explored the role of AMF in mitigating the adverse effects of salinity on crops in agricultural and horticultural settings.[51,75,76] Previous studies indicate that while salinity can inhibit the growth of AMF,[77] mycorrhizal plants tend to perform better under salt stress conditions. The degree of salt tolerance varies among AMF species, and their ability to withstand such stress can enhance their symbiotic relationships with host plants, especially in challenging environments. For instance, leguminous plants like pea (*Pisum sativum*) and fava bean (*Vicia faba*) responded differently to moderate salt stress when inoculated with various strains of *Rhizobium leguminosarum*. The salt-tolerant strain (GRA19) demonstrated superior performance in terms of salt tolerance and plant growth compared to other strains.[74,78] In grapevine rootstocks (*Vitis vinifera* L. 'Dogridge', '1103', 'Paulsen' and 'Harmony') and citrus seedlings, inoculation with *Rhizobium leguminosarum*, combined with AMF such as *R. intraradices*, *F. mosseae*, and *Paraglomus occultum*, resulted in improved growth characteristics including increased plant height, stem diameter, and biomass of shoots and roots. This enhancement in crop yield was associated with reduced levels of Na and Cl, higher concentrations of K and Mg in leaf tissues, and an increased potassium to sodium ratio.[62,79] Similarly, Porras-Soriano *et al*.,[80] observed significant improvements in shoot and root biomass, nutrient uptake, and salinity tolerance in olive seedlings inoculated with three different AMF strains (*F. mosseae, R. intraradices*, and *Claroideoglomus claroideum*), with *F. mosseae* proving to be the most effective fungus. Selecting the appropriate AMF species is crucial to maximize their effectiveness under specific environmental conditions.

Beltrano *et al*.,[81] demonstrated that mycorrhizal inoculation of pepper plants mitigates salinity damage, stabilizes membranes, and promotes plant growth, likely through improved phosphorus nutrition. However, the impact of salt stress on pepper shoot growth varies significantly among different fungal species.[82] Inoculating zucchini squash (*Cucurbita pepo* L. 'Tempra') with AMF such as *R. intraradices* alleviates salinity stress in greenhouse conditions, enhancing nutrient uptake and leaf hydration. This treatment resulted in increased potassium and decreased sodium concentrations in leaf tissues, facilitating mineral transport and improving plant adaptation to saline conditions.[83] Similarly, applying AMF to onions (*Allium cepa* L.) and basil (*Ocimum basilicum* L.) has been effective in mitigating the negative effects of salt stress on crop productivity and development.[84,85] In leafy vegetables, Jahromi *et al*.,[68] isolated *R. intraradices* strain DAOM 197198, which significantly promoted lettuce growth under two different salinity levels. This effect was associated with higher relative leaf hydration and reduced root ABA levels compared to non-mycorrhizal plants, indicating lower salinity stress and less ABA accumulation in AMF-inoculated plants.

Under saline conditions, AMF symbiosis enhances the upregulation of *LsPIP1*, a gene crucial for regulating water movement across cells. This improved gene expression allows better control over root water permeability, enabling plants to effectively cope with osmotic stress induced by salinity.[68] Porcel *et al*.,[76] have shown that AMF such as *R. irregularis* can mitigate the detrimental effects of salinity on lettuce ('Romana') by modulating hormonal profiles, including increased strigolactone production, which beneficially affects plant physiology, enabling lettuce to thrive even under unfavorable conditions.

Vicente-Sanchez *et al*.,[86] demonstrated that AMF (*G. iranicum var. tenuihypharum* sp. *nova*) effectively mitigated the adverse effects of irrigating lettuce with saline-reclaimed water. This was evidenced by improvements in various physiological aspects such as photosynthesis and stomatal conductance. Furthermore, the positive effects of AMF application under saline conditions extend to ornamental plants. Studies by Navarro *et al*.,[87] and Gomez-Bellot *et al*.,[88] showed that AMF species like *R. intraradices* and *G. iranicum* var. *tenuihypharum* sp. nova enhanced the growth and quality of Euonymus (*Euonymus japonica* Thunb.) and carnation (*Dianthus caryophyllus* L. 'Kazan'). These strains improved the uptake of essential elements such as K, P, Ca, and Mg, while concurrently reducing the translocation of detrimental ions (Na^+ and Cl^-) in the shoot system.

The containment of harmful ions inside root cell vacuoles or within intraradical fungal hyphae of AMF, rather than entering the cytosol of root cells, suggests a mechanism that prevents their translocation to the shoots. Introducing AMF inoculum presents a promising strategy for enhancing plant tolerance to high salinity levels. Apple seedlings (*Malus hupehensis* Rehd.) treated with AMF, specifically *G. versiforme*, showed improved leaf turgidity under saline conditions, although their leaf osmotic capacity was lower compared to non-mycorrhizal plants.[56] These inoculated seedlings exhibited enhanced defense systems against ROS induced by salinity stress, with increased activities of ascorbate peroxidase and CAT. They also displayed elevated K^+/Na^+ ratios, indicating better adaptation to salinity stress. The study suggested that mycorrhizal apple seedlings could tolerate salt concentrations up to 2%, whereas non-mycorrhizal seedlings could tolerate up to 4%. Red tangerines (*Citrus tangerine* Hort. ex Tanaka) also benefit from mycorrhizal associations to enhance salt tolerance.[62] When inoculated with *F. mosseae* and *Pyrodictium occultum* under saline conditions, these plants showed improved vegetative growth and physiological efficiency, evidenced by increased plant height, stem width, overall biomass, and enhanced rates of photosynthesis, transpiration, and stomatal conductance. The authors attributed this increased resistance to saline conditions to the effects of AMF on root morphology and the maintenance of ionic balance within cells, particularly the increased ratios of potassium to sodium and calcium to sodium.

Silicon (Si) could reduce the harmful impacts of grapevine salinity on the physiology of plants.[89] It has been shown that when potassium silicate soil application (2 mM K_2SiO_3'$9H_2O$ solution) was applied to 1-year-old cuttings of the "Cabernet sauvignon" grapevine exposed to salinity (100 mM of NaCl), the cuttings significantly enhanced the rates at which the leaf area expanded and the height of the plant. These benefits have been linked to a reduction in the detrimental effects of salinity on leaf photosynthesis, possibly because Si is crucial for safe guarding the machinery responsible for photosynthesis.[90] The fact that the greatest output and capacity for the photochemical efficiency of photosystem II photochemical processes increased when potassium silicate was administered to vines under salt stress further highlights this impact. In another study, K_2SiO_3-treated plants generally displayed milder water-or salt-stress symptoms under various experimental conditions, most likely because of their increased metabolic antioxidant enzymatic activity against ROS. In addition to potassium silicate, silicon nanoparticles and calcium metasilicate (Wollastonite, $CaSiO_3$) were tested. Mango trees were partially protected from the effects of salt stress using foliar sprays containing Si nanoparticles at high concentrations (5.3 and 10.6 mM Si).[91]

Persimmons (*Diospyros kaki* cv. 'Rojo Brillante') trees grafted onto *D. Lotus* were examined using a calcium protein hydrolysate (CPH) dependent biostimulant product of animal origin, and it was discovered that persimmon trees were able to boost their resilience to salinity stress. Treated trees exhibited a substantial decrease in the absorption of chloride, and the development of necrotic leaves spanned two years and improved stem water capacity. There are two potential explanations for the increased salt resistance of CPH-treated trees: (i) the ability of Ca^{2+} (a component of hydrolysate) to improve the capacity of the plant to keep chloride ions out of the root cells and (ii) improved salt-stress response protein expression caused by the amino acids (betaine, glycine, and proline) contained in the CPH.[92] An AMF inoculum improved the growth of the plants of three strawberry cultivars ('Albion,' 'Charlotte,' and 'Seascape') exposed to salinity (NaCl concentration 0-200 mM). *R. irregularis, F. mosseae*, and *Caledonius.*[93] This effect was higher for *R. irregularis* at the maximum NaCl concentration, demonstrating that the efficacy of AMF was dependent on the genotype and conditions. The negative impact of salt stress (50 mM NaCl) in strawberry was counteracted by immersion of potassium silicate in a solution of essential nutrients (1000 and 1500 ppm) 'The Kurdistan' and 'the Paros'. Plants subjected to salt-induced stress and subsequently treated with potassium silicate showed a reduction in proline content, which served as a mechanism for osmotic adjustment, and a corresponding increase in the activation of antioxidant enzymes. These changes contributed to an elevated salt tolerance index in both cultivars. Most of the variables studied responded best to the application of 1000 ppm K_2O_3Si, which enabled treated plants to produce a 50% increase in ultimate yield in comparison to control plants.[94] *Bacillus, Staphylococcus* and *Kocuria* contain plant growth-promoting bacteria (PGPB), notably boosting (by 51-94%) the final production of strawberry plants. 'Fern' (35 mM NaCl added to the nutritional solution) was used under saline conditions.[95] Salt-stressed plant leaves treated with PGPB exhibited an increase in their leaf relative water values, with an increase of approximately 15% compared to the control group. Additionally, treated leaves displayed enhanced N content.[38] Application of PGPB resulted in substantial reductions in Na^+ and Cl^- levels in the roots and leaves compared to the control stressed plants. This finding suggests that bacterial inoculation in the rhizosphere may alter exopolysaccharides, improving the resistance of plants to salinity stress.[95] Saline water was used to irrigate date palm trees (*Phoenix dactylifera* L.) and when combined with AMF and putrescine amine, PGPB (*Paenibacillus polymyxa, Azospirillum lipoferum*, *Bacillus ciraulans*) was found to enhance the nutritional value and sugar content of the trees.[96] The increased resilience of date palms is associated with a reduction in lipid peroxidation observed in young leaves. Additionally, there was an improvement in diamine oxidase and polyamine oxidase activities. Although the precise physiological processes underlying the resistance of date palm to salinity are still unknown, these results may be the result of many variables (elevated levels of organic solutes and photosynthetic pigments, and/or chosen hormones, and lower formation of polyamines). Biomass, shoot and root length, and seed size were increased in *Pseudomonas putida* strain AKMP7 inoculated plants. Stress therapy also reduces the production of ROS and lowers the expression levels of ROS response genes, such as ascorbate peroxidase, SOD, and CAT.[74,97]

Microbial biostimulants improve thermal stress tolerance in fruit

Temperature stress in plants can be divided into three categories according to the type of stressor they encounter: high, chilling, and freezing. Thermal stress can reduce growth, germination, photosynthesis, and often lead to crop losses in terms of productivity and product quality.[98] However, in response to temperature stress, plants have evolved several molecular systems, including membrane lipids, proteins, antioxidants, metabolites, regulatory factors, and additional protectants. The most crucial processes for environmental adaptation are modifications in the lipid content of cellular membranes and the activation of natural detoxifying processes.[99] Several studies have investigated the use of biostimulants to mitigate the adverse effects of thermal stress on agricultural and horticultural crops. Microbial biostimulants enhance plant responses to heat stress. For instance, plants colonized by beneficial bacteria, such as *Bacillus* and *Pseudomonas*, and mycorrhizal fungi, such as *Septoglomus deserticola* and *Septoglomus constrictum*, have higher levels of ROS-degrading enzymes, which improve heat stress tolerance.[100] *P. fluorescens* and *P. aeruginosa* have been commercialized for bioremediation, phytostimulation, and enhanced soil fertility capabilities, as well as soil quality and heat stress tolerance.[45]

Excessive solar radiation causing temperature elevation at the fruit level can lead to sunburn and reduce fruit quality.[101] Apples are characterized by natural waxes in their cuticle and epidermal pigmentation, which help absorb and reflect UV radiation, thereby mitigating its harmful effects and aiding in coping with abiotic stress.[102] He demonstrated that the detrimental effects of heat stress on various apple cultivars under orchard conditions could be alleviated by applying emulsified natural wax derived from carnauba palm (*Copernicia prunifera*).

Grapevines inoculated with PGPR exhibit greater resistance to lower temperatures.[102-105] Injecting *Burkholderia phytofirmans* (strain PsJN) into chilled Chardonnay plantlets increased plant biomass and photosynthesis, while lowering electrolyte loss from the leaves. In addition, an increase in numerous metabolites linked to cold stress (including phenolics, proline, and starch) has been observed.[103] Fernandez *et al*.,[104] reported that inoculation of 'Chardonnay' vines with *B. phytofirmans* improved cold tolerance. This could be explained by a change in the metabolism of carbohydrates, which stimulates the formation of starch, single sugars associated with cold tolerance, including glucose and sucrose, and sugars such as raffinose and its precursor galactinol. Theocharis *et al*.,[105] conducted a child-stress experiment on 'Chardonnay' vines. The authors reported that *B. phytofirmans* endophytes induced stress-related metabolites, including proline, MDA, aldehydes, and hydrogen peroxide. There has been increasing interest in the significant category of plant biostimulants known as SWE, owing to their favorable effects on plants experiencing abiotic stresses.[106] SWEs have different bioactive components depending on the type of seaweed (brown, green, or red), location of the raw material, and extraction process.[107] To examine the effectiveness of *A. nodosum* extract in promoting the development and adaptation of plants, it was sprayed on grapevine cv. Sangiovese grown in a Mediterranean environment (central Italy), as well as Pinot Noir and Cabernet Franc grapevines in a cool-climate viticulture zone (Michigan, USA). SWE accelerated veraison, enhanced anthocyanin accumulation in all cultivars, and improved phenolic content, especially in Sangiovese'.

The utilization of kaolin, a particulate film composed of alumina and silicate minerals, on pomegranate (*Punica granatum* L.) decreased fruit superficial temperature and sunburn incidence. Compared to untreated fruits, treated fruits exhibited approximately 50% fewer indications of fruit cracking and sunburn. They also had a lower incidence of bacterial blight.[108]

Protein hydrolysates represent a significant category of plant biostimulants that have gained increasing interest due to their beneficial effects on crop output and stress tolerance. They consist of a mixture of polypeptides, oligopeptides, and amino acids, typically derived from plant or animal sources through chemical or enzymatic hydrolysis.[109] According to Bogunovic *et al*.,[110] drenching strawberry plants with a biostimulant containing animal-derived amino acids improved growth and resilience to frost damage. Marfa *et al*.,[111] revealed that the treatment of strawberry plants with an animal hemoglobin hydrolysate-based biostimulant produced more root biomass when the weather was cold. Similarly, soil-based or foliar application of a biostimulant containing 10% boron with PGPR on in strawberries reduced freeze damages and showed higher crop performance, in comparison to the control. Additionally, leaf-level measurements of the antioxidant enzymes CAT, POD, and SOD revealed increased activity.[112] Different strawberry cultivars (Asia, Alba, and Clery) were exposed to extremely cold conditions and to a biostimulator containing animal-derived amino acids (porcine blood). The findings showed that all cultivars responded favorably to biostimulant application in terms of their resistance to cold stress.[110] Foliar application of protein hydrolysates of plant origin (soybean or lupin) or animal origin (dairy mixed-based casein) on grapevines decreased the conductance index, increased leaf temperature, and enhanced anthocyanin content under heat conditions.[113]

AMF inoculation has been shown to increase low temperature tolerance in two varieties of blueberry from *Vaccinium ashei* ('Britewell') and *V. corymbosum* ('Misty'), respectively. The authors highlighted the capacity of AMF to sustain its detoxifying effects by increasing the activity of GMX, APX, and SOD, among other antioxidant enzymes, decreasing the production of superoxide and hydrogen peroxide, and increasing the accumulation of osmoprotectants (proline and soluble polysaccharides) as the reason for the tolerance of AMF-inoculated blueberry plants to low temperatures. In another study, it has been found that AMF stimulated the growth of blueberry plants under low temperature conditions by improving the P and K uptake by the stems and foliage of blueberries.[114]

According to Botta,[115] compared with untreated plants, lettuce plants subjected to an enzymatic protein hydrolysate obtained from animals showed increased shoot and root fresh weights and stomatal conductance under low temperatures. Commercial *A. nodosum* extracts improve lettuce seedlings and seed germination performance when exposed to heat. Wheat was bacterized with the highly heat-resistant *Pseudomonas putida* strain AKMP7, which greatly improved heat tolerance. According to Ali *et al*.,[81] treated plants showed improved shoot, root, and seed biomass. Botta[115] performed heat stress experiments on ryegrass plants using an animal-based protein hydrolysate. Treated plants exhibited higher photosynthetic efficiency, chlorophylls and carotenoids content in leaves compared to untreated plants grown at 36°C. Proline-treated chickpea seedlings under heat stress had increased antioxidant activity, more chlorophyll, and better carbon fixation and sucrose metabolism enzyme activities.[116]

Microbial biostimulants improve adverse hydrogen ion concentration (pH) tolerance in fruit

One of the most significant abiotic stressors affecting plant development, growth, crop quality, and yield in the era of climate change is adverse soil pH. Several studies indicate that alkaline stress poses a greater risk than saline stress[117-120] Excessive alkalinity inhibits germination, damages root cells, disrupts nutrient uptake, and hinders crop growth.[121,122] Rufyikiri *et al*.,[123] studied the bacterization capacity of *R. intraradices* (MUCL 41833) on cultivated banana to enhance its tolerance to aluminum (Al) toxicity. The results showed that AMF improved shoot biomass and reduced Al concentrations in the roots and branches. Consistent with prior investigations, Rouphael *et al*.,[124] confirmed that AMF (*R. irregularis* and *F. mosseae*)could counteract the sensitivity of zucchini and squash to acidity and Al toxicity. The inoculated plants maintained greater plant biomass under both Al stress and acidity than non-inoculated plants. The enhanced nutritional status of Ca, K, and Mg, which is typically rare in acidic soils, has been attributed to these favorable reactions,[125] the limited movement of Al to the aerial part, and the ability to maintain the stability and integrity of the cell membrane.[124] The effects of AMF on zucchini, squash, and cucumber under alkaline conditions have been the subject of numerous studies. Varying morphological, physiological, and biochemical responses were observed between the inoculated and non-inoculated plants. By preserving higher chlorophyll levels and a higher rate of net CO_2 assimilation, AMF lessened the detrimental effects of alkalinity on plants. Another reason may be the enhanced nutritional status, particularly the contents of Fe, P, K, Mn, and Zn in the leaf tissue. The primary mechanism for reducing the negative effect of iron shortage due to alkalinity on yield appears to be the translocation and build-up of iron in the inoculated plants.[33]

Cartmill *et al*.,[126,127] evaluated the efficacy of co-inoculation with a mixture of *Glomus* species isolate ZAC-19 (*G. albidum, C. claroideum, and G. diaphanum*) to improve the growth of ornamental plants (Rosa multi-flora 'Burr' and vinca [*Catharantus roseus*] G. Don) under high alkaline conditions in irrigation water. The authors reported that ZAC19 enhanced the tolerance of *Rosa multiflora* due to its capacity to increase nutrient absorption and translocation, leaf photosynthetic rate, and simultaneously reduce iron reductase and soluble alkaline and phosphate activities. Plant growth parameters of vinca were also improved under adverse pH stress by AMF inoculation. The tolerance of the inoculated plants appeared to be mediated by improved uptake and translocation of P as well as improved activity of antioxidant enzymes.

Seed priming with Si is an important technique employed to mitigate abiotic stresses in plants.[90] Researchers have investigated the effects of Si (Na_2SiO_3) on maize plants cultivated in alkaline salt-irrigated soils. The study included an evaluation of antioxidant enzyme activities, osmoprotectants, photosynthetic pigments, total phenols, Na^+ and K^+ ion concentrations, MDA levels, and maize growth parameters. The findings demonstrated that Si treatment enhanced plant growth under alkaline stress conditions. Increases in photosynthetic pigments, osmoprotectants, relative leaf water content, and antioxidant enzyme activities were observed, underscoring the role of Si in enhancing tolerance to alkaline stress.

Limitation of biostimulants application on fruit

Plant biostimulants do not uniformly enhance all crop types; their effectiveness can vary significantly. For example, compared to other crops grown in greenhouse conditions, the stimulatory effects of plant biostimulants may not consistently translate to improved outcomes in the fruit industry. This variability could be attributed to higher application rates and favorable climatic conditions in controlled environments, which potentially enhance leaf permeability and thereby biostimulant effectiveness.[128] Additionally, the efficacy of biostimulants may be hindered by the carryover effects from previous seasons on the organic and inorganic compound reserves in plants, affecting their metabolic activities. Varied meteorological conditions further contribute to this inconsistency.

Research outcomes indicate that crop responses are not universally predictable. Therefore, it is crucial to conduct further experiments to elucidate the mechanisms underlying biostimulant-induced growth promotion. These findings underscore the key considerations in developing new biostimulants. Significant progress has been made in understanding the molecular and physiological mechanisms of both microbial and non-microbial biostimulants. However, several unresolved issues necessitate further investigation, including optimal application methods (foliar or soil drench), timing of application (pre-stress, during stress, or post-stress and phenological stages), application rates,[129] environmental factors, crop management practices, and species-specific responses.

To enhance plant nutrient uptake and utilization efficiency, first-generation plant biostimulants have been developed using microorganisms and bioactive substances to stimulate physiological and molecular processes in plants. Recent advancements in chemistry, biology, and omics sciences have spurred the formulation of a second generation of biostimulants. However, the significance of issues related to agricultural and horticultural management remains underappreciated. Understanding the molecular mechanisms that regulate plant physiology, as well as the synergistic effects of microbial and non-microbial biostimulants, is crucial for the strategic development of third-generation biostimulants. A deeper understanding of these mechanisms will enable the selection of the most suitable biostimulant for specific crops and growing conditions. Moreover, comprehending these molecular mechanisms will aid in determining the optimal dosage and the ideal stage of plant development and growth for applying a particular biostimulant.[130]

Ultimately, developing novel microbial biostimulants presents certain challenges. The process of registering such products can be intricate, and there is currently a lack of standardized global regulations.[131] Further hindrances to product development include the high costs associated with microbial biostimulant registration and manufacturing,[132] which limits the number of commercialized products and restricts their adoption in horticulture.

CONCLUSION

Crops are frequently subjected to abiotic stresses during their life cycle, which can act individually or in combination to drastically lower product quality and yield. Global food security faces a serious threat from abiotic stressors. Emerging as novel, eco-friendly, and promising products, biostimulants aim to enhance the overall sustainability of crop production systems. This review discusses the potential effects of biostimulants on plants, with a focus on enhancing plant tolerance to abiotic stresses in fruit crops. The main benefits of biostimulants include improved soil properties, increased biodiversity of beneficial microorganisms, no adverse effects on people, animals, or the environment, and positive effects on crop quality and performance. Nevertheless, additional molecular research is required to completely comprehend the mode of action and mechanism by which biostimulants confer stress tolerance. Therefore, in order to address the problems with global food security, more research into the production of even more stress-tolerant biostimulants and their application under field conditions is essential.

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The authors declare that there is no conflict of interest.

AUTHORS' CONTRIBUTION

All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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