



REVIEW ARTICLE

Enhancing salt stress tolerance in tomato plants (*Solanum lycopersicum* L.) through biostimulants

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Abstract

Biostimulants are substances or microorganisms applied in small quantities, improve plant growth and productivity by modulating their natural biological processes, distinct from fertilisers and pesticides. Derived from natural sources such as plant extracts, algae or beneficial microorganisms, they enhance nutrient uptake and tolerance to abiotic stress. In tomato (*Solanum lycopersicum* L.) exposed to salt stress, the application of biostimulants, including a combination of 70 % biofertiliser and 30 % biocompost (Bf70/Bc30), improved vegetative growth, photosynthesis and membrane stability while reducing malondialdehyde and excessive proline accumulation. These treatments also regulate the expression of genes related to proline biosynthesis and antioxidant activity, enhancing tolerance to salt stress. Thus, biostimulants constitute a sustainable approach to improve yield, quality and resilience of tomatoes, while reducing dependence on chemical inputs.

Keywords: algae; biostimulants; humic substances; plant extracts; protein hydrolysates

Introduction

Biostimulants play a vital role in promoting plant growth and productivity by modulating natural biological processes. Unlike fertilisers, which primarily supply nutrients to plants, biostimulants are designed to enhance or stimulate the natural mechanisms of plants, improving nutrient uptake and adaptation to environmental challenges. As noted in earlier studies, this distinction is critical since biostimulants promote growth through mechanisms distinct from those of fertilisers and pesticides (1).

Over time, their scope has expanded to include a wider range of substances and mechanisms of action (2, 3). These products are often contrasted with other agricultural inputs, such as nutrients, pesticides or soil amendments. Biostimulants are known for improving nutrient efficiency, boosting resilience to abiotic stresses such as drought, salinity and extreme temperatures and enhancing overall plant quality, regardless of their nutritional content (4). They are typically derived from natural sources, including plant extracts, algae and microorganisms, aligning with the increasing demand for sustainable agricultural practices (5).

By modulating internal physiological functions, biostimulants encourage growth, strengthen disease resistance and enhance plants' ability to cope with unfavourable environmental conditions (6). Their effectiveness is linked to complex physiological processes, such as the activation of hormonal signalling pathways and the reinforcement of cellular structures (7). Furthermore, it was categorised into three

primary groups: humic substances, products containing active plant hormones (such as auxins and cytokinins) and those based on amino acids (8). The diversity in their composition and modes of action highlights their growing importance in modern agricultural systems. This article seeks to enhance the understanding of biostimulants, with a particular emphasis on their role in mitigating the effects of salt stress in tomato (*Solanum lycopersicum*) cultivation. By examining various types of biostimulants, their mechanisms of action and their influence on abiotic stress tolerance, the article aims to underscore their potential as a sustainable solution for farmers dealing with environmental challenges, particularly salinity (9).

The discussion will delve into the main categories of biostimulants utilised in agriculture and horticulture, shedding light on their specific mechanisms and modes of action that contribute to improved stress resilience. By integrating theoretical frameworks with practical applications, this work aspires to provide a comprehensive understanding of biostimulants and their capacity to bolster crop resilience against environmental pressures. Through this analysis, the article will highlight their growing significance in promoting sustainable agricultural practices, showcasing their potential to enhance productivity while addressing the challenges posed by abiotic stressors.

Definition of biostimulants

Biostimulants are defined as substances or microorganisms applied in low but biologically active concentrations that promote plant growth and productivity by influencing natural biological processes.

Unlike fertilisers, which primarily supply nutrients, biostimulants do not serve as direct nutrient sources. Instead, they enhance plants' natural mechanisms for nutrient utilisation and adaptation to environmental conditions—mechanisms fundamentally different from those of fertilisers and pesticides (1). Biostimulants play a crucial role in enhancing nutrient use efficiency, improving tolerance to abiotic stresses such as drought, salinity and extreme temperatures and promoting overall plant quality—even in the absence of significant nutrient content (4). These effects are largely achieved by stimulating targeted physiological mechanisms that optimise nutrient uptake and root absorption. Moreover, their natural origin—often from plant extracts, macroalgae or microorganisms meets the growing demand for sustainable agricultural solutions (5). Biostimulants, such as protein hydrolysates, promote both the improvement of root system architecture (density, length and number of lateral branches) and the efficiency of nutrient uptake, thereby contributing to enhanced plant nutrition (10). Unlike conventional fertilisers or pesticides that focus on nutrition or protection, biostimulants act by modulating internal physiological processes, thereby enhancing plant growth, resistance to diseases and resilience to adverse environmental conditions (6). The effectiveness of biostimulants stems from complex physiological mechanisms, including the activation of hormonal signalling pathways, improvements in cell wall integrity and the strengthening of plants' defence responses (7).

Biostimulants can be broadly classified into three categories: humic substances, products containing active plant hormones such as auxins and cytokinins and those based on amino acids. This diversity in composition and mechanisms of action highlights their growing importance in modern agriculture (8). Plant growth-promoting rhizobacteria (PGPR) are key microbial biostimulants; in symbiosis with plant roots, they enhance nutrient uptake, increase tolerance to abiotic stresses and promote plant growth, supporting their inclusion in the modern definition of biostimulants (1, 11). As their application becomes more widespread, regulatory frameworks aim to ensure their effectiveness, safety and environmental sustainability.

Evolution of the concept

The concept of "biostimulants" has evolved significantly over time, expanding its scope to include a progressively broader spectrum of substances and mechanisms of action (3, 8). Initially, the term 'biostimulant' was limited to seaweed extracts and humic acids, but it has gradually extended to new compounds such as protein hydrolysates, complex organic substances and beneficial microorganisms, including mycorrhizal fungi, nitrogen-fixing bacteria and pathogen-antagonistic fungi (3, 8). Modern definitions of biostimulants emphasise their ability to enhance plant performance while distinguishing them from traditional agricultural inputs such as fertilisers, pesticides and soil amendments (2). For instance, biostimulants do not directly supply essential nutrients but instead promote their assimilation and efficient use by plants (9). This distinction has been highlighted by the European Biostimulants Industry Council (EBIC), which defines biostimulants as substances that improve abiotic stress tolerance, nutrient absorption and crop quality without directly affecting pathogens (2). The broadening of the biostimulant concept is driven by advances in scientific research and analytical techniques, particularly through "omics" approaches such as transcriptomics, proteomics and metabolomics, providing high-resolution insights into the signalling pathways and metabolic networks influenced by biostimulants, which have begun to

elucidate their molecular mechanisms of action (8, 9). Studies have shown that certain biostimulants regulate gene expression linked to water stress tolerance, photosynthesis and ion homeostasis. Research indicates that a protein-hydrolysate-based biostimulant modulated the expression of genes encoding proteases, dehydrins (DHNs) and heat-shock proteins (HSPs) in maize, illustrating specific molecular pathways through which biostimulants enhance heat-stress tolerance (12).

At the same time, growing environmental concerns and the transition toward sustainable agriculture have positioned biostimulants as promising alternatives to chemical inputs, helping to reduce reliance on synthetic fertilisers and pesticides (8, 9). For instance, protein hydrolysates and seaweed extracts are being investigated for their ability to enhance plant resistance to drought and extreme temperatures, thus lowering the need for irrigation and chemical protection. In conclusion, the concept of biostimulants is rapidly evolving, encompassing an ever-expanding range of natural substances and innovative formulations. This evolution is driven by the need to improve agricultural productivity while minimising environmental impact, as well as by scientific advances that provide a deeper understanding of their mechanisms of action and effectiveness in diverse agronomic contexts and is expected to further expand with emerging trends such as microbial consortia and nanotechnology-based biostimulants.

Characteristics and composition

Plant biostimulants, derived from organic or inorganic substances and microorganisms, enhance plant growth, productivity and resilience to abiotic stress through mechanisms that go beyond simple nutrient supply (1, 10). They include humic and fulvic acids, protein hydrolysates, seaweed extracts rich in bioactive polysaccharides such as alginates and fucoidans and microbial inoculants such as mycorrhizal fungi and nitrogen-fixing bacteria (1, 2). These biostimulants influence plant physiology and biochemical pathways, enhance vegetative growth and yield stability, root architecture, metabolism and hormone signalling (10). Their diverse composition includes minerals, vitamins and amino acids, as well as polysaccharides and natural phytohormones. These components contribute to improved nutrient solubilization, enhanced nutrient use efficiency and increased stress tolerance. For instance, humic substances stimulate root development and nutrient uptake, protein hydrolysates regulate nitrogen and carbon metabolism, while microbial biostimulants promote root expansion, water relations and resistance to abiotic stress. Overall, biostimulants represent a sustainable agronomic tool that boosts plant productivity and quality through complex interactions with plant metabolism, offering a promising alternative to traditional fertilisers (1, 10).

Modes of action of biostimulants

Biostimulants enhance plant physiology and metabolism by improving soil conditions and increasing nutrient availability (13, 14). They interact with plant metabolic pathways, promoting growth and resilience to stress by modifying the soil microbiome, e.g., promoting beneficial rhizobacteria that enhance phosphorus availability and boosting nutrient bioavailability (13, 6). At the molecular level, biostimulants have been shown to regulate the expression of specific genes and activate key enzymes and signalling cascades associated with stress tolerance. For example, genes involved in proline biosynthesis (*P5CS*), antioxidant defence (*SOD*, *CAT*, *APX*, *GPX*) and osmolyte regulation (*P5CS*, *BADH* for glycine

betaine) are upregulated in response to biostimulant application. These changes enhance reactive oxygen species (ROS) scavenging, maintain redox homeostasis and promote osmotic adjustment, while hormonal signalling pathways such as auxin, cytokinin, abscisic acid (ABA) and jasmonic acid (JA) are modulated to optimise growth and stress adaptation (6, 15). By specifically targeting these molecular components, biostimulants not only improve physiological performance but also enhance tolerance to abiotic stresses like drought, salinity and extreme temperatures. At the molecular level, biostimulants optimize water and nutrient use efficiency, influence hormone production such as auxins and cytokinins, enhance antioxidant defenses through ROS scavenging and activation of antioxidant enzymes, and promote osmolyte accumulation (e.g., proline, glycine betaine), thereby increasing tolerance to abiotic stresses like drought, salinity and extreme temperatures, and regulating stress adaptation and growth (6, 15). Biostimulants activate both primary and secondary metabolic pathways, enhancing essential processes like photosynthesis and respiration while also stimulating the production of bioactive compounds that improve plant defence and crop quality (14, 16).

Additionally, they contribute to soil health by promoting organic matter degradation and microbial activity, leading to better nutrient absorption and plant development (13, 14). Microbial biostimulants further aid nitrogen fixation and phosphorus solubilization, reinforcing plant health (15). In particular, beneficial microbial groups such as *Rhizobium* and *Azotobacter* play a key role in biological nitrogen fixation, while mycorrhizal hyphal networks contribute to soil aggregation and enhance nutrient foraging, further strengthening the definition and functional scope of biostimulants (1, 2, 15). Overall, biostimulants play a crucial role in sustainable agriculture, improving plant growth, stress resistance and crop quality while reducing reliance on chemical fertilisers (13–16).

Main categories of plant biostimulants

Although both the European Union and the United States have their own legal definitions of biostimulants, there is currently no single, internationally harmonised definition recognised worldwide. This

lack of standardisation poses challenges in precisely classifying the substances and microorganisms that fall under this category. Nevertheless, some key categories of biostimulants are widely acknowledged by researchers, policymakers and agricultural stakeholders (2, 3, 9). One significant group of biostimulants includes beneficial microorganisms, particularly PGPR such as *Azospirillum*, *Bacillus* and *Pseudomonas*. These bacteria establish mutually beneficial interactions with plant roots, enhancing nutrient uptake, producing phytohormones like auxins and cytokinins, inducing systemic resistance and offering protection against pathogens (1, 2, 17, 18). PGPR also contribute to stress tolerance, including mitigation of salinity and other abiotic stresses, thereby improving plant growth, health and overall crop productivity (5, 6, 19).

Another important group of biostimulants is fungi, which can be free-living in the soil, associated with the rhizosphere or endosymbiotic within plant tissues. Arbuscular mycorrhizal fungi (AMF), for instance, form mutualistic associations with plant roots, enhancing nutrient uptake—particularly phosphorus, improving soil structure, optimising water relations and increasing plant tolerance to abiotic stresses such as drought and salinity (20). Additionally, fungal biostimulants may include beneficial species like *Trichoderma* spp., which contribute to nutrient solubilization and stress resilience, further supporting plant growth and health (1, 2, 19, 21, 22). These categories provide an overview of biostimulants and their specific mechanisms and practical applications will be explored in greater depth in other articles within this special issue, which examines the potential of biostimulants in horticulture.

Classification of biostimulants

Biostimulants can be broadly classified into three main categories: humic substances (HS), hormone-containing products (HCP) such as seaweed extracts rich in auxins and cytokinins and amino acid-containing products (AACP) (8) (Fig. 1). Over time, this definition has expanded to include beneficial microorganisms, particularly PGPR, which are distinct from fertilisers, pesticides and soil amendments (1, 2, 5, 6). PGPR, including representative genera such as *Azospirillum*, *Bacillus* and *Pseudomonas*, form mutually beneficial associations

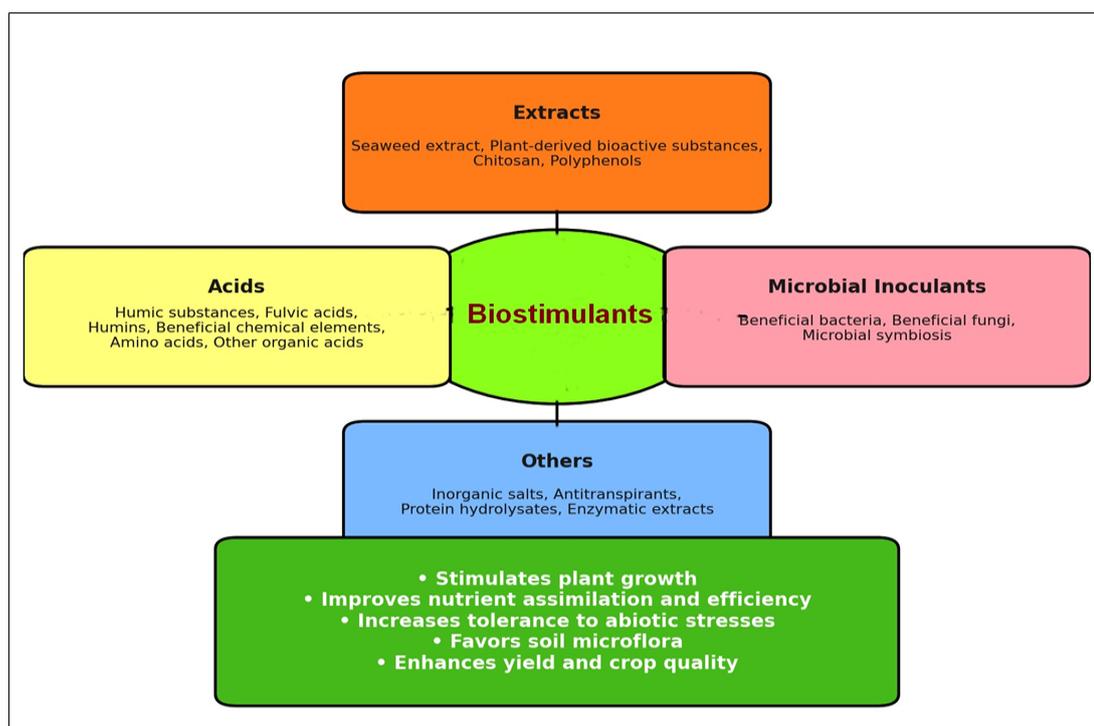


Fig. 1. Types and effects of plant biostimulants on crop growth and soil health.

with plant roots, enhancing nutrient uptake, producing phytohormones and inducing systemic resistance, thereby improving plant growth, stress tolerance and productivity under abiotic stress conditions like salinity and drought (17, 18, 21-23). Sometimes referred to as “biofertilisers” or “biocontrol agents,” PGPR provide significant agronomic benefits, reinforcing the functional scope of modern biostimulants and contributing to sustainable agriculture (1, 2, 6, 17, 18).

Humic and fulvic acids

Humic Substances (HS) are naturally derived compounds formed through the decomposition of organic matter, such as plant, animal and microbial residues, as well as the metabolic by-products of soil microorganisms. They are categorised into humic acids, fulvic acids and humins based on their solubility and molecular weight. These compounds form colloidal structures that interact with plant roots and soil microorganisms, improving nutrient absorption and overall plant growth. The effectiveness of HS depends on factors such as the source material (e.g., peat, compost, Leonardite), environmental conditions, target plant species and application methods (3) (Table 1).

Research indicates that HS treatments can lead to average increases in shoot dry weight by $22 \pm 4\%$ and root dry weight by $21 \pm 6\%$ (24). Additionally, “pseudo-humic” substances, synthesised from agricultural by-products through chemical processes, serve as an alternative to natural humic substances; however, their relative efficacy and cost-effectiveness compared to natural HS remain to be fully established (25). Humic substances significantly contribute to soil fertility by enhancing its physical, chemical and biological properties. They facilitate root nutrition by increasing the soil’s cation exchange capacity and improving phosphorus availability. Moreover, HS activate plasma membrane H^+ -ATPases, which promote nutrient uptake, cell expansion and organ growth (26). These substances also affect enzymatic and respiratory activities and may exhibit hormonal-like effects, although the underlying mechanisms are not fully understood. Furthermore, HS help plants cope with stress by modulating certain metabolic pathways, such as the synthesis of phenolic compounds (27, 28). The application of HS has shown positive effects, including improved root development, increased water and nutrient uptake and enhanced tolerance to abiotic stresses. However, their complex molecular structure makes

it difficult to fully elucidate their mechanisms of action (29, 30).

Protein hydrolysates and nitrogen-containing compounds

Protein hydrolysates are produced through the enzymatic or chemical hydrolysis of proteins sourced from agro-industrial by-products. These can be derived from plant materials (e.g., crop residues) or animal sources (e.g., collagen or other tissues) (2, 3, 9). Protein hydrolysates exhibit direct biostimulant effects by enhancing nitrogen uptake and assimilation. They influence the expression and activity of enzymes involved in nitrogen metabolism, improving nutrient acquisition in roots. Additionally, these compounds regulate carbon-nitrogen interactions by modulating the activity of Krebs cycle enzymes, which ensures a balanced supply of essential nutrients for plant development. Certain molecules, such as proline, function as chelators, protecting plants from heavy metal toxicity and improving the mobility and absorption of micronutrients (31). They contain amino acids, peptides and polypeptides, along with nitrogenous compounds such as betaines and polyamines, which play various roles in plant physiology. Glycine betaine, for instance, is well-documented for its ability to mitigate plant stress (32).

In addition to their direct effects, protein hydrolysates possess antioxidant properties that help plants combat oxidative stress by neutralising free radicals (33). Indirectly, their application improves soil fertility by stimulating microbial biomass and activity, which enhances nutrient availability to plants. Commercial protein hydrolysate products, sourced from both plant and animal origins, have been shown to improve crop yield and quality in various agricultural systems (2). Safety assessments of animal-derived hydrolysates have found no evidence of genotoxic, ecotoxic or phytotoxic effects. However, concerns regarding the use of animal by-products in the food chain have led to regulatory restrictions in certain regions. For example, the European Union prohibits the use of animal-derived protein hydrolysates on the edible parts of organic crops, as stipulated in Implementing Regulation (EU) No 354/2014. Despite their benefits, limited knowledge about the precise composition of protein hydrolysates poses challenges to understanding their molecular and biochemical mechanisms of action (34).

Algae and plant extracts

Table 1. Classification of humic substances (HS): solubility, molecular weight and main functional roles.

Types of humic substances (HS):	Solubility	Molecular weight	Main functional roles
Humins	Insoluble in water at all pH	Very high (≥ 100 kDa)	Improvement of soil structure, water and nutrient retention, support of microorganisms (3, 16)
Humic acids	Soluble in alkaline conditions (pH > 7), insoluble in acidic conditions	High (10–100 kDa)	Chelation of minerals, stimulation of root growth, improvement of nutrient uptake, hormonal modulation (3, 16, 24, 29)
Fulvic acids	Soluble at all pH values	Low (≤ 10 kDa)	Rapid transport of nutrients, stimulation of plant metabolism, antioxidant effect, improvement of stress tolerance (3, 16, 24, 29)
Intermediate humin-like substances	Partially soluble depending on the fraction	Variable	Transition between humins and humic acids, buffering role and nutrient reservoir (3, 16)

Algae and plant extracts have become integral components in modern agriculture, particularly as biostimulants. Although the use of fresh algae as organic matter and fertiliser dates back centuries, their biostimulant properties have only recently been thoroughly explored. Marine algae, especially brown algae (e.g., *Ascophyllum*, *Fucus* and *Laminaria*) and red algae, are highly valued for their polysaccharides, such as laminarin, alginates and carrageenans. These compounds enhance soil structure by improving water retention, promoting aeration and facilitating the fixation of cations and heavy metals (35, 36). Algal extracts are rich in bioactive compounds, including sterols, betaines and essential nutrients, which support plant growth. They enhance soil health by stimulating beneficial microflora and improving fertility, while directly promoting plant development through hormonal modulation (37, 38). Importantly, these extracts also improve plant tolerance to abiotic stresses by activating stress-response regulators, such as HSPs and antioxidant enzymes like superoxide dismutase (SOD) and catalase (CAT), which help mitigate oxidative damage (2, 36).

As biostimulants, these extracts not only improve crop growth, yield and quality but also modulate plant hormone activity, particularly cytokinins and auxins (30, 39). Additionally, algae-derived complex polysaccharides, such as fucoidan and alginates, have been shown to increase the efficacy of foliar treatments. Certain plants rich in secondary metabolites, such as Borage (*Borago officinalis*) and *Withania somnifera*, also exhibit biostimulant properties due to their bioactive compounds (40, 10). Both plant and algal extracts represent a natural and effective strategy for enhancing agricultural productivity and reducing crop vulnerability to environmental stresses (40).

Inorganic compounds

Botanicals or plant-derived substances, are used across multiple sectors including pharmaceuticals, cosmetics, food and plant protection (41). Although their potential as biostimulants has been less extensively studied compared to algal extracts, these compounds, often containing allelochemicals, are increasingly recognised for their sustainable applications in crop management and the development of new biostimulants (42). Allelopathic interactions, where plants chemically influence each other, are already exploited in agricultural practices such as crop rotation and intercropping. Including this discussion here, before inorganic compounds, highlights the role of naturally derived plant substances as a bridge between organic biostimulants like algae and mineral-based inputs.

Inorganic compounds, defined as elements that enhance plant growth but are not universally essential, play an important role in strengthening plant resilience. For instance, selenium contributes to antioxidant defence by limiting oxidative damage, cobalt supports nitrogen fixation in legumes and may indirectly benefit tomato in crop rotation systems, while sodium can aid osmotic adjustment under salinity stress (43, 44). Although their effects are often crop-dependent, studies suggest that the application of these beneficial elements could improve tomato tolerance to abiotic stresses, thereby aligning with the focus of this work. These elements can have long-term effects, such as strengthening cell walls through silica deposition, or short-term impacts, such as improving stress tolerance under adverse conditions. The influence of these beneficial elements on plant resilience and development depends on environmental factors and their bioavailability in the soil (1, 45).

Beneficial microorganisms

Beneficial microorganisms, including bacteria, yeasts, fungi and microalgae inhabiting soil, plants and aquatic environments, play a pivotal role in improving agricultural productivity. These organisms enhance nutrient uptake, stimulate the production of plant hormones and strengthen stress resistance while producing beneficial volatile organic compounds. Among them, rhizosphere-associated bacteria, commonly referred to as PGPR, are particularly notable for their ability to form protective biofilms around roots, facilitating efficient water and nutrient absorption (46, 47). For example, several PGPR strains, such as *Pseudomonas* and *Bacillus* species, have been reported to enhance tomato growth and stress tolerance by improving nutrient acquisition and activating plant antioxidant defence mechanisms (46, 47).

Beneficial microorganisms can be broadly categorised into bacteria, fungi and actinobacteria, each exerting its effects through distinct mechanisms. Bacteria such as *Rhizobium*, which fixes nitrogen, *Azospirillum*, which stimulates root development and certain species of *Pseudomonas* that release growth-enhancing compounds support plant growth through hormone production, nitrogen fixation and stress mitigation (48). Fungi also play a key role; for example, mycorrhizal species like *Glomus intraradices* form symbiotic associations with roots that improve water and phosphorus uptake while enhancing stress tolerance (20). In tomato, *G. intraradices* has been reported to improve K⁺/Na⁺ balance under salinity, thereby strengthening resilience, while *Trichoderma* species further contribute by stimulating growth and protecting against pathogens (49). Actinobacteria such as *Streptomyces* complement these functions by decomposing organic matter, recycling nutrients and producing bioactive metabolites that promote plant health.

Biological non-microbial biostimulants marine algae and agro-industrial by-products marine macroalgae (e.g., *Ascophyllum nodosum*) are widely used as sources of bioactive compounds (sterols, betaines, polysaccharides and phytohormone modulators) that improve plant establishment, growth and stress tolerance (35, 36, 38). Likewise, biostimulants derived from agro-industrial by-products (composts, aquaculture residues) have been shown to stimulate enzymes of phenylpropanoid metabolism such as phenylalanine ammonia-lyase (PAL) and to promote synthesis of secondary metabolites that reinforce plant defences and quality (25, 26, 30). These product streams align with circular-economy principles by valorising waste into value-added inputs for sustainable crop management, although the heterogeneity of raw materials complicates mechanistic attribution and standardisation (25, 26, 30). Emerging abiotic biostimulants—Nanoparticles and nanomaterials. Nanoparticles represent an emerging class of abiotic biostimulants with distinctive physico-chemical properties that can modify ion and metabolite transport and thereby enhance crop quality and abiotic stress tolerance (50). For example, zinc oxide nanoparticles (ZnO-NPs) applied to tomato have been reported to increase chlorophyll content and soluble protein, improve photosynthetic performance and upregulate antioxidant enzyme activities (e.g., SOD, CAT), which collectively mitigate oxidative stress and support growth under challenging conditions (51, 49). However, alongside these promising effects, there are environmental and safety considerations: nanoparticles may exert dose-dependent phytotoxicity, alter soil microbial communities, persist or accumulate in soils and food chains and thus require thorough risk

assessment and regulatory oversight before widespread agronomic use (50, 51).

Biostimulants and tolerance to abiotic stress

The ability of biostimulants to alleviate abiotic stress in plants remains an area of active research due to the complexity of their mechanisms of action. Current hypotheses suggest that bioactive molecules in biostimulants modulate plant metabolism by targeting specific pathways. Under stress conditions, biostimulants may activate or enhance certain metabolic processes, enabling plants to better adapt and survive during critical periods (52). Plants treated with biostimulants often exhibit increased levels of antioxidant molecules, which play a vital role in mitigating damage caused by ROS that accumulate during stress (52, 53).

Salinity stress

Salinity stress is a major factor limiting plant growth, causing cellular damage and reducing overall vitality and productivity (54). High salinity levels induce osmotic stress, restricting water uptake by roots and mimicking drought-like symptoms. Biostimulants have demonstrated potential in mitigating these effects by enhancing plant tolerance to salinity (55). Biostimulants promote the accumulation of protective compounds such as proline, simple sugars, alcohols, abscisic acid and antioxidants, which help counteract the damage caused by ROS (56). For instance, plant-derived protein hydrolysates have been effective in improving salinity tolerance in horticultural crops like lettuce by increasing yield and dry matter accumulation (57, 58). Microbial biostimulants have shown similar benefits. For example, treatments with *Azospirillum brasilense* have enhanced the growth and resilience of crops such as lettuce (*Lactuca sativa*), peppers (*Capsicum annum*), chickpeas (*Cicer arietinum*) and fava beans (*Vicia faba*) under high salinity conditions (46, 59). In tomato, salinity stress often results in reduced fruit size, lower soluble solids and chlorophyll degradation.

Plant defence mechanisms

Plants respond to biotic and abiotic stresses through a combination of biochemical, physiological and microbial-mediated mechanisms. Under stress, ROS accumulate, triggering oxidative bursts that, in excess, damage membranes, proteins and nucleic acids (60, 61). To maintain cellular homeostasis, plants produce osmolytes, stress-related proteins and antioxidant metabolites such as flavonoids, carotenoids, glucosinolates and ascorbic acid (62-66).

Microbial biostimulants further enhance plant resilience. In tomato, inoculation with AMF such as *G. intraradices* improves K^+/Na^+ homeostasis under salinity stress, promoting biomass accumulation and yield (67). Similarly, *A. brasilense* enhances salinity tolerance by stimulating root growth and producing exopolysaccharides that limit Na^+ uptake (59, 18). The combined action of microbial biostimulants, plant-derived compounds and humic substances supports antioxidant defences, osmotic adjustment and nutrient acquisition, providing an integrated strategy to mitigate abiotic stress and sustain tomato productivity (1, 2, 6, 27, 28).

Hormonal signalling pathways, particularly those involving jasmonates, play a crucial role in coordinating these defence responses (68, 69). Among antioxidants, ascorbic acid is particularly significant due to its potent ability to neutralise ROS, a function maintained through recycling by specific enzymatic systems (70). In response to abiotic stress, plants activate a sophisticated antioxidant network composed of enzymatic (e.g., SOD, CAT), ascorbate

peroxidase (APX) and glutathione peroxidase (GPX) and non-enzymatic (e.g., ascorbate, glutathione) components. These mechanisms work together to maintain redox homeostasis and protect cellular integrity. Additionally, redox signalling mechanisms involving interactions between ROS and phytohormones such as ABA and JA regulate key stress responses including stomatal closure, metabolic adjustments and defence activation, thereby enhancing plant resilience (71, 72).

While some biostimulants, such as essential oils, have shown limited impact on improving drought stress tolerance, others, like alfalfa-derived protein hydrolysates, have demonstrated their ability to enhance plant growth under salinity stress (73). These hydrolysates strengthen antioxidant defences and improve nitrogen metabolism, contributing to increased stress resilience (42). Additionally, polysaccharides like laminarin, derived from the brown algae *Laminaria digitata*, have been found to activate plant defence mechanisms by stimulating resistance-related enzymes, genes and signalling molecules such as salicylic acid (74). Seaweed extracts have also been effective in improving drought tolerance in crops like oranges and grapes (74, 75). Similarly, biostimulants derived from algae and peat have promoted growth in crops such as canola by enhancing chloroplast division and improving the absorption of essential minerals (76). These studies underscore the potential of biostimulants to enhance plant resilience and adaptation to challenging environmental conditions.

Biostimulants and salt stress tolerance

Salt stress poses a significant challenge to plant growth and metabolism, largely due to the osmotic effects of salts such as sodium chloride (NaCl), which can become toxic at high concentrations. This issue is particularly prevalent in coastal areas where saline water is frequently used for irrigation, potentially reducing crop yields by up to 50% in certain species like lettuce (77). Salinity leads to reduced fresh weight and chlorophyll content, negatively affecting crops such as spinach, beans and other vegetables (78-80). Chlorophyll, vital for photosynthesis and plant health, is also critical for the marketability of leafy vegetables, as consumers often prefer visually appealing products. Moreover, salt stress disrupts nutrient uptake, compromising the nutritional quality of horticultural crops. High salinity interferes with the availability and absorption of essential ions such as calcium (Ca^{2+}), phosphorus (P) and potassium (K), while also reducing their mobility within the plant and lowering water potential (81). It additionally decreases the solubility of micronutrients, including copper (Cu), iron (Fe), manganese (Mn), molybdenum (Mo) and zinc (Zn). Research has indicated that salt stress significantly reduces phenolic compound levels, soluble protein content and enzymatic activity in carrots (82). These disruptions affect essential metabolic functions, such as photosynthesis, respiration and nitrogen assimilation, ultimately leading to decreased crop yields and quality. Studies on lettuce have shown that biostimulants like plant protein hydrolysates and Retrosal® can enhance salt stress tolerance by increasing yield, dry weight and photosynthetic performance.

Additionally, metabolomic analysis has revealed that biostimulants contribute to oxidative stress mitigation, increase osmolyte accumulation and alter sterol and terpene composition, which play crucial roles in plant adaptation to salinity (83). PGPR can enhance plant tolerance to salinity through specific mechanistic traits. Inoculation with *A. brasilense* has been shown to improve growth and physiological parameters in lettuce, sweet pepper,

chickpea and fava bean (59, 84, 85, 86). These benefits are mediated by ACC deaminase activity, which reduces stress-induced ethylene, IAA production that promotes root elongation and exopolysaccharide secretion that enhances soil water retention (18, 22, 87). Sweet pepper, particularly sensitive to salinity, exhibited increased dry weight, chlorophyll content and ascorbic acid accumulation under NaCl stress when inoculated. Similarly, tomato plants inoculated with *Bacillus subtilis* showed improved root architecture, ion homeostasis and antioxidant activity under saline conditions (27, 55). In legumes, PGPR promoted both root and shoot growth, mitigating salt-induced biomass reductions. These results highlight that PGPR benefits are mechanistically linked to hormonal regulation, stress alleviation and improved nutrient and water uptake.

Marine algae-derived biostimulants, such as *A. nodosum* products (e.g., Super Fifty® and Acadian), have also proven effective in enhancing salt stress tolerance in lettuce, improving root yield and dry weight even under unfavourable conditions (88). Additionally, sulfated exopolysaccharides extracted from *Dunaliella salina* improved growth and antioxidant enzyme activity in tomato seedlings while activating metabolic pathways related to jasmonic acid, mitigating salinity-induced damage (89). Extracts from algae such as *Sargassum muticum* and *Jania rubens* have been found to reduce the adverse effects of salinity on chickpea seedlings by regulating amino acid metabolism, restoring ion balance and enhancing antioxidant defence systems. Specific amino acids, including serine, threonine, proline and aspartic acid, have been identified as contributing to improved salt stress tolerance in plant roots (90).

Plant-derived biostimulants represent a promising strategy to mitigate salinity stress across a wide range of horticultural crops. Rather than being crop-specific, their beneficial effects often rely on the presence of bioactive molecules. For example, extracts from *Moringa oleifera* leaves, rich in phytohormones such as cytokinins and liquorice root which contains flavonoids and phenolic

compounds have been shown to enhance germination, stabilise membranes and maintain water potential under saline conditions (91, 92). These bioactive metabolites directly contribute to antioxidant defence, limiting lipid peroxidation and electrolyte leakage, while promoting chlorophyll and carotenoid accumulation and improving photosynthetic efficiency (92–94). Although much of the experimental work has focused on beans, similar mechanisms are relevant for other salt-sensitive crops. In tomato, for instance, tannin-based biostimulants and seaweed extracts have been reported to improve ion balance, antioxidant enzyme activities and biomass under NaCl stress (55, 89). Such evidence suggests that the efficacy of plant-based biostimulants is linked to their metabolite composition, particularly flavonoids, phytohormones and phenolic antioxidants, which modulate stress signalling pathways and support osmotic adjustment across diverse horticultural species (1, 5, 9, 10).

Honey-based biostimulant demonstrated the ability to improve salt stress tolerance in onion plants by increasing biomass, bulb yield and photosynthetic pigment content. Honey contains reducing sugars and phenolic compounds that can act as osmoprotectants and ROS scavengers. This treatment also enhanced osmoprotectant levels, such as proline and soluble sugars and improved the membrane stability index alongside enzymatic and non-enzymatic antioxidant activity (90) (Fig. 2). These diverse plant-, microbe- and algae-derived biostimulants demonstrate multiple, complementary mechanisms from osmolyte accumulation to hormonal modulation that can be leveraged to enhance crop resilience to salinity.

Role of biostimulants in enhancing tomato production quality under salt stress

Recent studies have highlighted the effectiveness of biostimulants in improving tomato (*S. lycopersicum*) performance under saline conditions. The application of Tecamin Flower® (TF) and Tecamin Brix® (TB) not only enhanced flowering and fruit quality but also contributed to yield stability by modulating hormonal balance and

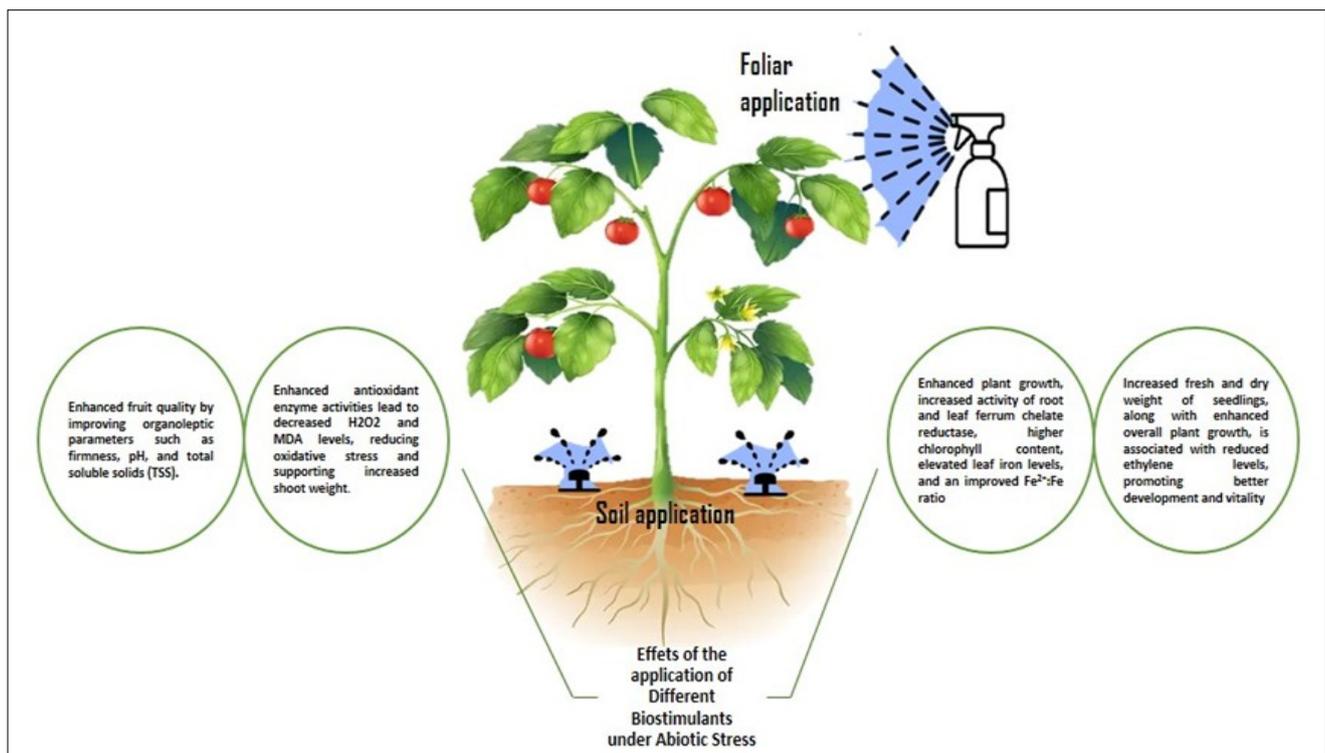


Fig. 2. Different applications of biostimulants and their effects on plants under saline stress.

stimulating nutrient uptake efficiency. These mechanisms, particularly relevant under salt stress, reduced the reliance on chemical fertilisers while supporting physiological resilience and productivity (95, 96). These improvements are largely attributed to the stimulation of natural plant growth mechanisms (97). The combined use of TF and TB emerges as an effective strategy to enhance tomato productivity and quality in saline environments (96). As such, these biostimulants represent a sustainable solution for farmers facing environmental constraints, contributing to both agricultural performance and reduced ecological impact (95).

Building on recent research, the application of a seaweed-derived biostimulant (*Chaetomorpha antennina* extract, sea weed extract) has been shown to enhance tomato (*S. lycopersicum*) performance under saline stress (98). Sea weed extract treatments, applied as foliar sprays, improved key growth parameters, including germination rates, plant height and root/shoot length, indicating enhanced vegetative vigour (99-101). In terms of biochemical defences, sea weed extract increased the activity of antioxidant enzymes and promoted the accumulation of proteins and phenolic compounds, strengthening the plants' resilience to oxidative stress induced by salinity (102). Regarding nutritional quality, fruits from sea weed extract-treated plants exhibited higher levels of photosynthetic pigments, vitamin C and lycopene, thus improving both their nutritional and sensory attributes (103). GC-MS analyses revealed elevated siloxane and phenolic content in the fruits, suggesting that sea weed extract may contribute to fruit protection and quality enhancement by modulating secondary metabolites (104). Complementary research investigated the effects of salinity and biostimulants on cherry tomato yield and quality. Soil salinisation, often linked to low-quality irrigation water and climate change, is a growing concern in many irrigated regions, especially in the Mediterranean (105, 106). Saline irrigation raises soil EC, leading to osmotic stress and ionic toxicity that reduce plant growth and marketable yields (107, 108). Although the effectiveness of biostimulants, such as seaweed extracts and protein hydrolysates, decreases under severe salinity (EC9, 12.82 dS/m) due to irreversible ionic toxicity that overwhelms their protective mechanisms, they have proven very effective at mitigating the effects of moderate stress. Under moderate salinity (EC3, ~3 dS/m), these products increased average yields by 41.7 % and improved fruit quality, notably firmness and lycopene content (+34.4 %) (109, 110, 111). Therefore, for practical field application, it is recommended to strategically target crops suffering from low to moderate salt stress, where the return on investment will be optimal, rather than using them as a rescue treatment in severely degraded soils.

Recent studies have further highlighted the effectiveness of biostimulants in supporting tomato growth under both saline and non-saline conditions (112). Among the tested formulations, the combination of 70 % biofertiliser and 30 % biocompost (Bf70/Bc30) produced the most consistent benefits, resulting in taller plants with improved vigour (113). The biofertilizer contained a consortium of beneficial microorganisms, including nitrogen-fixing and phosphate-solubilising bacteria, while the biocompost was derived from decomposed plant residues enriched with organic matter. Interestingly, this treatment significantly reduced malondialdehyde (MDA) and proline levels in stressed plants. Although proline is commonly recognised as a protective osmolyte, its excessive accumulation generally reflects severe cellular stress. Therefore, lower proline levels in Bf70/Bc30-treated plants indicate that they

experienced less oxidative and osmotic damage, demonstrating more effective stress tolerance and improved membrane stability.

Moreover, studies have shown that salt stress negatively affects tomato plant development, leading to reduced root elongation, shoot height and chlorophyll content due to osmotic imbalance and ion toxicity (114). However, some biostimulants and microbial inoculants have demonstrated their ability to counteract these effects by enhancing water use efficiency, improving root architecture and stabilising photosynthetic activity under salinity stress (115). Additionally, recent findings highlight that plant growth and defence responses are intricately linked, requiring a dynamic balance in resource allocation to optimise productivity under stress conditions (116, 117). At the molecular level, biostimulants were found to modulate the expression of specific stress-responsive genes, such as P5CS (involved in proline biosynthesis) and antioxidant-related genes, including SOD and CAT (118). The upregulation of these genes enhanced the antioxidant defence system and contributed to a more balanced proline metabolism, which in turn mitigated oxidative damage and osmotic stress under saline conditions. These molecular adjustments were reflected in practical outcomes, including improved plant vigour, fruit yield and overall tomato quality under salinity stress. Furthermore, such molecular regulation is consistent with previous findings showing that salinity significantly alters photosynthetic efficiency and chlorophyll fluorescence kinetics in tomato leaves, highlighting the importance of maintaining both molecular and physiological homeostasis under stress (119) (Table 2).

Conclusion

The increasing challenge of soil salinisation poses a major threat to agricultural productivity, requiring sustainable solutions to mitigate its negative effects. Biostimulants, with their ability to enhance nutrient uptake, regulate osmotic balance and activate plant defence mechanisms, have emerged as a promising alternative. This study highlights the effectiveness of biostimulants such as protein hydrolysates, humic substances, microbial inoculants and seaweed extracts in improving salt stress tolerance in tomatoes (*S. lycopersicum*). By strengthening the physiological and biochemical responses of plants, biostimulants promote growth, yield and fruit quality under saline conditions, particularly by stimulating antioxidant activity, regulating osmoprotectants and optimising photosynthesis. Integrating biostimulants into tomato cultivation offers a sustainable approach to reducing the reliance on chemical inputs while maintaining crop productivity. However, further research is needed to refine the most effective formulations, application methods and combinations based on different environmental conditions. A deeper understanding of the molecular interactions between biostimulants and plant signalling pathways could lead to the development of more targeted and efficient products. As agriculture transitions towards more sustainable practices, the adoption of biostimulants represents a key solution to enhancing crop resilience against climate change and soil degradation, ensuring a more stable and environmentally friendly agricultural production.

Table 2: Illustrations of biostimulant products and substances used on horticultural crops (*Solanum lycopersicum*) to alleviate the effects of abiotic stress.

Abiotic stress	Biostimulant substances and products	Dose	Methods of application and treatment frequency	Beneficial effects	Reference
Heat stress	Siliforce	1.5–3 mL/L	Foliar spray or fertigation	Enhances the plant's tolerance to drought stress and accelerates recovery post-stress	(30)
Salt stress	Nano-TiO ₂	5, 10, 20 and 40 mg/L	Foliar spray	Enhances key enzymatic activities (carbonic anhydrase, nitrate reductase, SOD and POX), increases proline and glycine betaine levels, boosting growth and yield	(49)
Salt stress	<i>Dunaliella salina</i> exopolysaccharides	0.1 g/L	Foliar spray (2×)	Improves chlorophyll and protein content while reducing proline levels, contributing to stress mitigation and plant development	(91)
Salt stress	Tecamin Brix® and Tecamin Flower®	3 mL/L	Foliar spray	Enhances fruit quality by improving parameters such as firmness, pH, and TSS, ensuring better marketable produce	(97)
Salt stress	Tecamin Brix® version 2	3 mL/L	Foliar spray	Mitigates root nutrient deficiencies induced by salt stress, significantly increasing tomato yield and improving fruit quality	(98)
Salt stress	<i>Achromobacter piechaudii</i>	-	Seedling inoculation	Promotes growth by increasing fresh and dry weights of seedlings, reducing ethylene production and enhancing uptake of phosphorus and potassium, improving water use efficiency	(120)
Heat stress	<i>Achromobacter piechaudii</i> (ARV8)	-	Seedling inoculation	Increases seedling growth (fresh and dry weight), lowers ethylene levels, and promotes vitality for better drought resistance	(120)
Iron deficiency	Amino acids	0.1, 0.2 mL/L / 0.2, 0.7 mL/L	Root application/foliar spray (4×)	Stimulates plant growth, increases chlorophyll levels, enhances root and leaf ferrum chelate reductase activity and improves iron assimilation in plants	(121)
Iron deficiency	VIVA®	10.5 mL/plant	Foliar spray	Enhances yield and improves chlorophyll, carotenoid and lycopene content, along with higher levels of ascorbic acid	(122)
Heat stress	Nano-TiO ₂	0.05, 0.1, 0.2 g/L	Foliar spray (1×)	Enhances photosynthesis and increases transpiration rates, contributing to better stress management	(123)
Heat stress	Brassinosteroids	0.01, 0.1 and 1.0 mg/L	Foliar spray (1×)	Boosts antioxidant enzyme activities, reduces oxidative stress by lowering H ₂ O ₂ and MDA levels and supports shoot weight improvement	(124)

Heat stress	Siliforce	1.5–3 mL/L	Foliar spray	Strengthens cell walls, increases resistance to environmental fluctuations, and promotes drought tolerance	(126)
Heat stress	VIVA®	-	Foliar spray	Stimulates both plant and root biomass growth, leading to an overall improvement in plant health and productivity	(127)
Salt stress	Arbuscular Mycorrhizal Fungi (AMF)	10 g/plant	Soil inoculation	Boosts root growth, enhances water absorption, and strengthens the plant's overall stress tolerance	(128)
Heat stress	Salicylic acid, humic acid and fulvic acid	50 mg/L (salicylic acid)	Foliar spray	Increases antioxidant activity, decreases oxidative damage and improves protein levels associated with stress response	(129)
Heat stress	Seaweed extract (<i>Ascophyllum nodosum</i>)	2–3 % solution	Foliar spray	Improves chlorophyll content, enhances water use efficiency and strengthens tolerance to high temperatures	(130)
Heat stress	Mycorrhizal fungi (AMF) inoculation	10 g/plant	Soil inoculation at planting and during early fruit set	Optimises nutrient uptake, improves root structure and increases resilience under stress	(131)
Heat stress	Seaweed extract (<i>Ascophyllum nodosum</i>)	2–3 % solution	Foliar spray	Enhances chlorophyll production, reduces leaf wilting and improves fruit yield under drought stress conditions	(132)
Heat stress	Protein hydrolysates (Plant-derived)	3 mL/L	Soil drench	Activates enzymatic defences, reduces stress markers and improves water-use efficiency during drought periods	(133)

Authors' contributions

MM proposed the idea and wrote this research article. MB, MA revised the manuscript. HAH and SEM read and edited the manuscript. All authors read and approved the Manuscript.

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