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REVIEW

Enhancing Plant Resilience to Abiotic Stress: The Power of Biostimulants

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ABSTRACT

Abiotic stresses such as drought, heat, salinity, and heavy metal contamination severely affect global agricultural productivity. Between 2005 and 2015, droughts caused losses of approximately USD 29 billion in developing countries, and from 2008 to 2018, droughts accounted for over 34% of crop and livestock yield losses, totaling about USD 37 billion. To support the growing human population, agricultural output must increase substantially, necessitating a 60%–100% rise in crop productivity to meet the escalating demand. To address environmental challenges, organic, inorganic, and microbial biostimulants are increasingly employed to enhance plant resilience through various morphological, physiological, and biochemical modifications. Plant biostimulants enhance plant resilience under abiotic stress through mechanisms such as abscisic acid signaling modulation, which regulates stomatal closure to reduce water loss during drought and heat stress. Additionally, they aid in scavenging reactive oxygen species and stabilizing ion channels, mitigating oxidative damage, and maintaining ionic balance under stress conditions such as salinity. This review summarizes recent advancements in applying these biostimulants, focusing on their roles in triggering morphological, physiological, biochemical, and molecular changes that collectively enhance plant resilience under stress conditions. It also includes a bibliometric analysis of all articles published on biostimulants from 2019 to 2024 and explores future research directions. Emphasis was placed on optimizing biostimulant formulations and understanding their synergistic effects to maximize their efficacy under various stress conditions. By integrating biostimulants into agricultural practices, we can adopt a sustainable strategy to safeguard crop productivity in the face of climate change and environmental stressors.

KEYWORDS

Abiotic stress; crop improvement; microbial; plant growth promoting rhizobacteria; protein hydrolysate; seaweed

1 Introduction

Abiotic stresses like drought, heat stress, and salinity pose major challenges to global agriculture, contributing significantly to crop yield losses and global soil degradation. These stresses are particularly damaging as climate change accelerates, intensifying extreme weather patterns and altering precipitation and temperature regimes worldwide. Drought is one of the most devastating abiotic stressors responsible for billions of dollars in agricultural losses. Between 2005 and 2015, it caused losses of approximately USD 29 billion in developing countries [1]. Similarly, from 2008 to 2018, drought was the leading cause of crop and livestock yield losses, accounting for over 34% of the total losses, or about USD 37 billion [2]. For crops like soybeans, extreme heat conditions exceeding 30°C can reduce soybean yield by up to 6% under rainfed conditions in the USA [3]. Similarly, rising temperatures and shifting precipitation patterns in Malaysia are expected to reduce rice yield by 12% during the primary season and 31.3% during the off-season by 2030 [4]. Salinity stress, typically caused by high concentrations of Na^+ and Cl^- in soil, interferes with essential metabolic processes, such as seed germination and photosynthesis, potentially causing severe damage to plant tissues or the death of plants [5]. Additionally, heavy metals, such as iron (Fe), manganese (Mn), copper (Cu), nickel (Ni), cobalt (Co), cadmium (Cd), zinc (Zn), mercury (Hg), lead (Pb), and arsenic (As), can accumulate in soil due to industrial waste and sewage disposal. Although some of these metals are essential in small amounts for plant development, their excessive accumulation disrupts plant metabolism and impairs growth [6]. Together, these abiotic stresses impose significant challenges to crop production and necessitate adaptive strategies to secure food supplies in the face of environmental change.

One effective strategy to enhance food production under such challenging conditions is cultivating crops with enhanced resilience to environmental stress. Traditionally, improving crop resilience has relied on breeding programs. However, these programs often encounter difficulties due to the complex genetic basis of abiotic stress tolerance, which involves multiple genes with intricate interactions. This complexity makes identifying and incorporating these traits into new cultivars time-consuming and resource-intensive. Moreover, breeding programs require several generations to produce stable, high-yielding varieties, making them too slow to keep pace with the accelerating impact of climate-induced stresses. Given these constraints, plant biostimulants (PBs) have emerged as a promising alternative, attracting considerable interest from researchers for their ability to enhance plant growth, overall fitness, and resilience to abiotic stresses. PBs are formulated with diverse microorganisms or naturally occurring bioactive compounds and work by promoting nutrient uptake and supporting plant growth and development rather than directly supplying nutrients or targeting pests and pathogens.

Biostimulants, including both microbial and non-microbial formulations, enhance nutrient use efficiency, improve crop tolerance to stress, support soil health, and reduce the need for chemical fertilizers and pesticides [7]. For example, a case study on maize showed that *Kappaphycus alvarezii* seaweed extract allowed for a 50% reduction in fertilizer input without compromising yield, thereby decreasing reliance on chemical fertilizers [8]. Additionally, biostimulants have been shown to reduce the carbon footprint, saving approximately 2.06 kg CO_2 equivalent per ton of cane produced [9]. PBs growing market presence has made them a focal point in agricultural discussions and has been the subject of extensive reviews [7]. The availability and use of these products among growers have significantly increased, with the global market for PBs valued at approximately USD 2.6 billion in 2019 and projected to exceed USD 4 billion by 2025 [10]. This market growth reflects their practical potential, as demonstrated by Jiménez-Arias et al. [11], who conducted lab-to-field research using glycine betaine to cultivate maize under water-deprivation conditions. With an added cost of just 4.3 € per hectare, this treatment increased profits by 154.4 to 386.7 € per hectare under drought conditions. Such results highlight the effectiveness of biostimulants in mitigating drought-related losses and bridging the gap between research and practical solutions [11]. This review provides an overview of PBs and highlights recent advancements in applying PBs in agriculture, particularly their role in enhancing plant resilience under stress conditions.

2 Plant Biostimulants: Definition

The definition of PBs has been a subject of rigorous debate over the past decade, with various authors defining them based on product composition, source material, and mode of action. However, the complexity of PB efficacy, which arises from interactions between multiple compounds rather than a single active ingredient, complicates the understanding of their most active constituents and mechanisms. Recognizing this complexity, the European Commission identified the necessity to update existing fertilizer regulations to encompass a broader range of organic products, including PBs [12].

PBs, by definition, are claims-based according to the function of the product, encompass substances or microorganisms applied to plants to facilitate nutrient uptake, enhance environmental stress tolerance, and boost crop quality traits while ensuring good yields without being nutrients, soil improvers or pesticides [13]. Initially defined by Zhang et al. [14] as "materials that, in minute quantities, promote plant growth", PBs are distinguished from nutrients, soil improvers, and pesticides due to their minimal application quantities. Before the adoption of Regulation (EU) No 2019/1009 (European Parliament and European Council Regulation (EU) 2019/1009), PBs were defined by what they are not, differentiating them from fertilizers and pesticides.

The European Union Fertilizing Products Regulation (FPR) redefined PBs as "fertilizing products stimulating plant nutrition processes independently of the product's nutrient content with the sole aim of improving one or more of the following characteristics of the plant or the plant rhizosphere: nutrient use efficiency, tolerance to abiotic stress, quality traits, availability of confined nutrients in soil or rhizosphere" (European Parliament and European Council Regulation (EU) 2019/1009). This updated definition clarifies the categorization of PB products. Although PBs have been excluded from the Plant Protection Products Regulation, they remain within the purview of Regulation (EC) 1907/2006, also known as the Registration, Evaluation, Authorization, and Restriction of Chemicals (REACH) (European Parliament and European Council Commission Implementing Regulation (EU) No 354/2014). These new regulations are geared toward enhancing internal market operations for fertilizer products within the European Union, fostering investment, and promoting the development of effective and safe fertilizers [15].

PBs differ from direct nutrient supplements by improving nutrient use efficiency without directly supplying nutrients. PBs enhance root growth and modulate nutrient transporter activity, allowing plants to absorb and utilize available nutrients more effectively even in low-nutrient environments. The application of PBs leads to higher nutrient use efficiency than direct nutrient supplements, which provide nutrients but do not actively enhance plant nutrient uptake or stress tolerance. While nutrient supplements address specific deficiencies, biostimulants promote holistic plant metabolism, adaptability, and efficient nutrient use, reducing the risk of excess nutrient accumulation in the soil [16].

3 Non-Microbial Plant Biostimulants in Alleviating Abiotic Stresses

Non-microbial PBs, encompassing bioactive substances like seaweed extracts, humic substances, protein hydrolysates, chitosan, biopolymers, and inorganic compounds, play a significant role in the global biostimulant market. Seaweed extracts, the most dominant among these, accounted for 33.3% of the market in 2022, valued at approximately EUR 1.45 billion [17]. Their rich nutritional profile and historical use in enhancing nutrient efficiency, mitigating environmental stresses, and promoting root growth and microbial activity make them a favored choice. The biostimulant market is expected to grow to around EUR 2.66 billion, driven by the increasing demand for safe and sustainable agricultural products [18]. Organic PBs, such as seaweed extract, humic acids (HAs) derived from soil organic materials, chitosan, protein hydrolysate, and other plant-derived organic compounds, have attracted increasing attention from scientists. These substances have been shown to significantly enhance plant tolerance to abiotic stresses, thereby improving crop production and supporting plant physiological development. They help plants cope with major abiotic stressors, including drought, heat, and salinity [7,19]. The following examples illustrate the successful application of organic PBs in crop improvement.

3.1 Seaweed Extract

Seaweed, or macroalgae, are crucial to marine and coastal ecosystems, significantly enhancing their biodiversity and contributing to the broader biosphere. Rich in bioactive compounds, seaweeds contribute significantly to plant stress tolerance. These compounds, including alginate, laminarins, phlorotannins, betaines, and glycerol, play crucial roles in osmotic adjustment, ROS scavenging, and hormonal regulation. Seaweeds are classified into three main groups based on their color: (i) Phaeophyta (brown), (ii) Rhodophyta (red), and (iii) Chlorophyta (green) [20]. Each group has been commercially exploited for various agricultural applications, with each producing a distinct set of bioactive compounds that enhance plant stress resilience.

Brown algae, such as *Ascophyllum nodosum*, are well-known for their high content of laminarins and phlorotannins [21]. Laminarins, a type of β-glucan, act as osmoprotectants, stabilizing cellular structures and helping plants manage osmotic stress. Phlorotannins, a group of polyphenolic compounds, serve as potent antioxidants, scavenging reactive oxygen species (ROS) and thereby protecting plants from oxidative damage under stress conditions. These compounds also act as elicitors, priming plants for enhanced stress responses by activating plant defense pathways.

Red algae (e.g., *Kappaphycus alvarezii*) are rich in sulfated polysaccharides, which contribute to stress resilience by enhancing the plant's ability to manage oxidative stress and improve cellular water retention. These compounds, along with betaines such as γ-aminobutyric acid (GABA) (found in both brown and red algae), help regulate water balance and protect against osmotic stress.

Green algae, like *Ulva rigida*, contain high levels of glycerol and betaines, including glycine betaine (GB), which act as osmolytes, stabilizing proteins and cell membranes during stress [22]. GB is critical in enhancing plant tolerance to abiotic stresses like drought and salinity by maintaining cellular hydration and protecting against oxidative damage.

Seaweed is often used in foliar applications. For example, Trivedi et al. [8] applied an extract of the red algae *Kappaphycus alvarezii* to drought-stressed maize. Their study revealed significant improvements in plant growth, with enhancements of 4% in plant height, 16% in leaf length, 19% in green corn cob yield, and 17% in cob girth [8]. Similarly, the foliar application of brown algae (*Sargassum angustifolium*) extracts increased drought tolerance in canola, leading to greater shoot height and dry weight [23]. Additionally, the use of green algae (*Ulva rigida*) improved salinity tolerance in salinity-stressed wheat, resulting in increased plant growth compared with non-primed control plants [22]. These studies also reported a significant increase in photosynthetic activity. However, some studies suggest these treatments may induce stomatal closure under certain circumstances [24].

To further enhance plant tolerance and recovery from abiotic stresses, many PBs incorporate osmoprotectants such as proline, amides, GABA, and GB. These compounds, particularly betaines like GB, GABA, and proline, are abundant in marine algae. For instance, GB accounts for approximately 2% of the dry weight of green algae (*Chaetomorpha capillaris*), whereas other algae contain less than 1%. GABA, a primary betaine found in brown algae (*Ascophyllum nodosum*), is vital in stress resilience. Betaines function as osmolytes and ROS scavengers, protecting cellular structures by stabilizing molecules and membranes, thus aiding in the plant's ability to tolerate environmental stresses [25].

At the biochemical level, priming *Arabidopsis* seeds with Super Fifty (SF) PBs extracted from brown algae, *Ascophyllum nodosum*, alleviated drought stress by reducing ROS accumulation and ion leakage

[24]. Similarly, the drought-stressed tomato plants foliar-sprayed with *Ascophyllum nodosum* (brown algae) extract exhibited increased antioxidant enzyme activity and higher osmolyte levels, including proline and GB [26]. These treated plants also showed significantly greater plant height and total yield under reduced irrigation than control plants [26]. The beneficial effects of brown algae and GB in alleviating drought stress were further demonstrated in a field trial on grapevines [27]. Foliar application of *Ascophyllum nodosum* extract and GB improved the physiological and biochemical performance of grapevine cv. 'Touriga Franca' under summer stress in the Douro Demarcated Region, particularly within the 'Douro Superior' sub-region. These biostimulants, especially GB, showed significant potential in mitigating the adverse effects of summer stress, leading to increased levels of bioactive compounds, including total phenolics, flavonoids, and ortho-diphenols [27]. Under salinity conditions, wheat treated with *Ulva rigida* extract (a green algae) exhibited increased antioxidant enzyme activities, including superoxide dismutase (SOD), isocitrate dehydrogenase (ICDH), glutathione peroxidase (GPx), and glutathione reductase (GR) activities [22]. In addition to the increased activity of antioxidant enzymes, proline content was also elevated. This adaptive reaction is attributed to the upregulation of delta-1-pyrroline-5-carboxylate synthase, an enzyme involved in proline biosynthesis, and the downregulation of proline dehydrogenase, which catalyzes proline degradation [23]. Similarly, an extract from the green algae, *Ulva lactuca*, and its GB-rich fractions were found to significantly alleviate salinity stress in tomato plants [28]. At the highest GB concentration, the residual fraction acted as an osmoprotectant and ROS scavenger, reducing hydrogen peroxide (H_2O_2) levels and increasing tomato fresh weight under salinity stress conditions. These findings further support the crucial role of GB from seaweed extracts in mitigating salinity stress [28].

Brown algae extract priming alleviated drought-related damage in *Arabidopsis thaliana* through multiple genetically regulated mechanisms, underscoring its effectiveness as a drought-mitigation tool. Notably, *RESPONSIVE TO DESICCATION 26* (*RD26*), a drought-induced gene associated with abscisic acid (ABA) signaling and salinity response, was upregulated, whereas the cell cycle marker gene *HISTONE H4* (*HIS4*) was repressed. The brown algae extract priming also promotes stomatal closure during drought, minimizing water loss through the upregulation of *RCAR3* and *RBOHD*, which are key genes in the ABA-dependent signaling pathway for stomatal regulation [24]. Additionally, applying red algae (*Kappaphycus alvarezii*) to drought-stressed maize led to the upregulation of genes associated with photosynthesis, signal transduction, transmembrane transport, nitrogen assimilation, and carbohydrate metabolism. Simultaneously, genes involved in the catabolism of macromolecules, including starch, chitin, and protein degradation, are downregulated [8]. Overall, the seaweed extracts modulate the internal balance of plant hormones to maintain hormonal homeostasis, regulate the expression of key transporters to enhance nutrient uptake and assimilation, stimulate and protect photosynthesis, and reduce plant stress-induced responses [29].

In addition to seaweed extracts, certain medicinal plant extracts have shown effectiveness in enhancing plant tolerance to abiotic stress. For example, moringa seed extract has been shown to mitigate heat stress in cancer bushes (*Lessertia frutescens* L.), a medicinal and ornamental plant, by promoting growth, increasing carotenoid content, reducing electrolyte leakage, and preventing wilting. Plants treated with moringa seed extract also exhibit more branching and higher levels of ABA, jasmonic acid (JA), and indole-3-acetic acid (IAA), while showing reduced levels of superoxide and H_2O_2 levels [30]. Similarly, seven medicinal plant extracts, *Adathoda vasica*, *Cordia dichotoma*, *Asparagus racemosus*, *Saraca asoca*, *Kalanchoe pinnata*, *Andrographis paniculata*, and *Morus alba*, were evaluated for their effectiveness in alleviating drought stress in maize. Among these, *Adathoda vasica* leaf extract was the most effective. When combined with *Pseudomonas putida*, it significantly improved growth and reduced oxidative stress in drought-stressed maize by increasing chlorophyll, sugar, and phenolic levels, lowering proline, and upregulating defense gene expression (*ZmAPX*, *ZmSOD*, *ZmCAT*, *ZmNAC*, *ZmWRKY*, and *ZmMYB*) [31].

Overall, medicinal plant extracts, whether applied alone or synergistically with other biostimulants, offer a sustainable and eco-friendly approach to enhancing plant tolerance and productivity under abiotic stress.

3.2 Humic Acid

Humic and fulvic acids, derived from plant and animal wastes through biological or chemical processes, are vital to plant physiology. These substances enhance nutrient uptake and distribution, improving crop growth and increasing stress tolerance. Typically applied via soil drenching or foliar spraying depending on the crop's needs, humic substances offer several benefits: they improve soil structure, increase phosphorus availability, neutralize soil pH, promote lateral root growth, and stimulate nitrate assimilation in crops. Despite their well-documented advantages, the complex nature of humic substances and the varying responses they trigger in different plants make it challenging to elucidate their mechanisms of action [7,32].

HA-primed maize and sorghum seeds exhibited enhanced vegetative growth and physiological responses under varying levels of drought stress (100%, 80%, and 60% field capacity) [33]. In maize, biomass accumulation was reduced by 37.0% and 58.7% under moderate and severe drought conditions, respectively, while sorghum experienced 21.2% and 32.3% reduction under the same conditions compared to HA-treated seeds. HA priming significantly improved the photosynthesis rates, with increases of 29.2% in maize and 15.0% in sorghum under severe drought conditions [33]. This improvement was further reflected in higher levels of total chlorophyll, stomatal conductance, relative water content, and increased concentrations of sugars, proline, and soluble proteins in both maize and sorghum plants [33]. Another study showed similar findings, demonstrating that intermediate doses of HA (8 and 12 mL/L) enhanced drought tolerance in cowpeas [34]. This was achieved by reducing water potential and root nodule formation while increasing the fresh and dry weight of the shoots and roots, as well as total soluble protein content [34]. Like seaweed extracts, HA priming also exhibited enhanced enzymatic antioxidants such as catalase (CAT), ascorbate peroxidase (APX), peroxidase (POD), and polyphenol oxidase (PPO) enzymes, as well as non-enzymatic antioxidants (phenolic compounds) in maize and sorghum plants [33]. These findings suggest HA is a promising PB for enhancing crop drought tolerance. A 2023–2024 field trial on mango production also demonstrated the synergistic effects of combining wood vinegar, seaweed extract, and HA, resulting in significant improvements in chlorophyll content, leaf mineral levels, and fruit quality, with the 2 L/ha application of each showing the greatest impact by enhancing leaf nutrient uptake, antioxidant response, and sugar accumulation [35].

The role of humic substances in modulating ion transporters at the root-soil interface under salinity stress has been elucidated by Khaleda et al. [36] using *Arabidopsis*. Humic substances enhance salt stress tolerance by regulating ion transporters, specifically the sodium influx transporter HIGH-AFFINITY K^+ TRANSPORTER 1 (HKT1). The application of HA restored root growth and prevented the degradation of HKT1 protein in salt-stressed *HKT1*-overexpressing plants while also promoting sodium reabsorption in the roots [36]. Furthermore, HA can enhance plant nutrient uptake under stress by modulating critical processes at the root-soil interface. It may stimulate proton pump activity, exhibit auxin-like effects to promote lateral root emergence and improve nutrient availability, making essential nutrients more accessible to plants during abiotic stress conditions [37].

Overall, HAs are valuable additions to crop management strategies for enhancing plant resilience to drought, salinity, and nutrient stress. Their ability to improve soil health, nutrient uptake, and physiological responses makes them versatile tools for sustainable agriculture. As we explore further, the combination of humic substances with other biostimulants, such as seaweed extracts, may yield synergistic effects that amplify stress tolerance and improve crop quality and yield.

3.3 Protein Hydrolysates

Protein hydrolysates, derived from plant materials and animal by-products, consist of a mixture of free amino acids, oligo- and polypeptides. These substances are also commonly applied as foliar sprays or, occasionally, as substrate drenches or seed treatments. Protein hydrolysates are known for their biostimulatory effects, including the activation of key enzymes involved in nitrogen and carbon metabolism, as well as the enhancement of antioxidant enzyme activity and secondary metabolite production.

Applying protein hydrolysates, including brassinosteroid (BR), amino acids (AA), nitrophenolates (NP), and botanical extracts (BE), to heat-stressed rice genotypes 'F67' and 'F60' enhanced the heat tolerance by improving leaf gas exchange parameters. These improvements included an increase in net photosynthesis rate (P_N) (~14.5 μmol CO_2 m^{-2} s^{-1}), stomatal conductance (g_s) (~0.46 mmol m^{-2} s^{-1}), transpiration rate (*E*) (~43.9 H_2O day^{-1} $plant^{-1}$), leaf saturation (L_S), P_N/C_i ratio, and intrinsic water use efficiency (WUE_i) [38]. BR, AA, and NP protein hydrolysates enhance plant stress tolerance through various physiological mechanisms: BR promotes carbon metabolite accumulation and chlorophyll biosynthesis, AA supports nitrogen metabolism and glutamate receptor synthesis for stress response [39], and NP improves photosynthetic capacity by reducing stomatal resistance and enhancing chlorophyll stability [40]. Similarly, in Chinese cabbage, applying glutamic acid (Glu) and poly-γ-glutamic acid (γ-PGA) PBs improved heat stress tolerance by enhancing carotenoid biosynthesis, photosynthesis, and ROS signaling [41]. Together, protein hydrolysates act as effective biostimulants that support photosystem stability and enhance photosynthesis through multiple mechanisms, including stabilizing photosystem proteins and promoting chlorophyll biosynthesis or protecting it from degradation.

In addition, treatments with Glu and γ-PGA resulted in a notable increase in fresh weight (47.58% for Glu and 37.32% for γ-PGA) and dry weight (51.52% for Glu and 39.39% for γ-PGA) in Chinese cabbage compared to control plants [41]. Other morphological parameters, such as plant height, hypocotyl diameter, leaf length, and leaf width, also showed notable improvements following priming with Glu and γ-PGA [41]. In contrast, malondialdehyde (MDA) levels, electrolyte leakage, and superoxide radical content were significantly reduced, indicating a decrease in oxidative stress. These effects were accompanied by elevated activities of antioxidant enzymes, which help detoxify the ROS produced during heat stress, thereby reducing oxidative damage [41,42]. Transcriptomic analysis has revealed elevated expression levels of genes crucial for DNA repair, mitigating direct DNA damage caused by heat stress [43]. Notably, the *RPA1* gene, which encodes a 70 kDa DNA-binding replication protein, was differentially expressed. *RPA1* plays a vital role in DNA replication, repair, and recombination [44]. Similarly, in salt-stressed lettuce, priming with Graminaceae-derived PBs, including protein hydrolysates and their lighter molecular fraction F3 (<1 kDa), led to a significant reduction in proline, MDA levels, and osmolyte content, with a 35% decrease compared to control plants [45]. In protein hydrolysates-primed plants, genes involved in cell wall organization and biogenesis, carbohydrate catabolic processes, and polysaccharide metabolism, including putative linoleate 9S-lipoxygenase, were upregulated. Additionally, protein hydrolysates influence the structural components of chromatin and protein dimerization activity under salt stress. In contrast, F3 PBs affected a smaller set of genes, primarily affecting hormone-mediated signaling pathways, cellular responses to endogenous stimuli, and hormonal responses, notably through the upregulation of ethylene-responsive transcription factors. This study provides valuable insight into the molecular bioactivity of PBs, laying the groundwork for their application in agricultural practices to enhance plant stress resilience [45].

Hamedeh et al. [46] examined the use of EnNuVi® ALPAN®, a plant-derived biostimulant enriched with essential nutrients (Cu, Mg, Mn, and Zn) to mitigate drought stress in tomatoes, analyzing its effects at the phenomics and transcriptomics levels. From a photosynthetic perspective, ALPAN® treatment effectively maintained stable levels of photosynthetic pigments (chlorophyll *a*/*b* and carotenoids) across all time points (days 1, 7, and 8). In contrast, the untreated plants experienced significant fluctuations in pigment levels during water stress and recovery. ALPAN®-treated plants also exhibited lower electrolyte leakage and MDA and proline concentrations than the untreated controls, indicating reduced cellular damage. Transcriptomic analysis revealed that ALPAN® treatment upregulated the drought-responsive gene *SlTAS14*, which is associated with ABA and water-deficit responses, making it a key drought tolerance marker. Other genes such as *SlPDH1*, *SlFN1*, *SlTRX*, and *SlPAL1* were also expressed at higher levels in ALPAN®-treated plants, particularly on day 1 of water stress, supporting rapid adaptation and resilience in young seedlings under desiccation conditions [46].

Collectively, organic PBs have demonstrated significant potential for enhancing plant growth and development under abiotic stress. They improve nutrient uptake efficiency, increase photosynthetic pigments, and promote higher photosynthetic rates across various growth stages. Additionally, PBs promote the synthesis of non-enzymatic antioxidants like phenolic compounds, flavonoids, and ascorbic acid, leading to higher proline accumulation and reduced oxidative damage, as indicated by lower MDA levels. However, most studies have been conducted in controlled environments, highlighting the need for more field studies to understand PBs' effects in real-world conditions.

4 Inorganic Non-Microbial Plant Biostimulants

Several inorganic elements have been shown to benefit specific plant taxa. These include trace elements from the 16 essential nutrients required for plant growth and non-essential elements, often referred to as beneficial elements. Cobalt, sodium, silicon (Si), selenium (Se), and vanadium are some of the essential elements that can enhance physiological and biochemical activities, promote growth, and improve plants' adaptation to abiotic stress [47]. While an adequate supply of these trace elements can improve plant growth and development, excessive amounts may lead to toxicity and impair plant development [47,48]. Given the potential of inorganic PBs to enhance plant tolerance to abiotic stressors, research in this area is ongoing. Scientists are actively investigating how these inorganic PBs strengthen plants and optimize growth in an ever-changing environment.

The application of Se has shown promising results in mitigating the adverse effects of environmental stresses. For instance, applying Se at a rate of 60 g/ha to onions grown in semi-arid regions, where heat and drought stresses are prevalent, has been shown to increase total bulb yield and the Se content of the onions. This not only enhances the nutritional value for consumers, as Se is an essential element for human health, but also enhances crop resilience [49]. Similarly, the foliar application of Se at 20 mg/L significantly improved several growth parameters in drought-stressed rice, including plant height, number of tillers, filled grains/m^2, total grains/m^2, grain yield (kg/ha), and straw yield by 5.1%, 12.6%, 21.8%, 4.3%, 11.0%, and 10.1%, respectively, compared to the control [50]. Physiologically, Se application increased chlorophyll stability, membrane stability, proline content, and relative water content in drought-stressed rice.

Si, another well-known beneficial element for plants, plays a crucial role in enhancing drought stress tolerance. Once taken up by plants, Si accumulates primarily beneath the cuticles and within the cell walls as silica deposits, forming a physical barrier that strengthens the cell wall structure and helps plant cells mitigate the harmful effects of stress [51]. Si reinforcement reduces transpiration water loss by creating denser cell walls, limiting stomatal opening, and minimizing cuticular transpiration. This water retention is crucial under drought stress, as it maintains cellular turgor and prevents wilting [52]. Seed priming with Si has been shown to induce significant morpho-physiological and biochemical changes in drought-stressed maize plants, leading to notable improvements in growth parameters, such as shoot length, root length, and both fresh and dry weights of shoots and roots [53]. Additionally, higher stomatal conductance was observed in Si-primed drought-stressed tomato plants [54]. At the biochemical level, Si priming significantly reduces the accumulation of ROS, as evidenced by lower levels of H_2O_2, MDA, and proline [53]. It also decreases the concentration of phenolic compounds, glycine betaine, and total soluble sugars in maize plants. This reduction in ROS is coupled with an enhanced activity of antioxidant enzymes [53].

Advances such as nano-encapsulation have introduced unique physicochemical properties such as high reactivity, precise surface structures, and large surface-area-to-volume ratios, which differentiate them from traditional molecular formulations [55]. In biostimulant applications, nano-encapsulation enhances bioavailability, stability, and uptake efficiency by enabling the controlled and targeted release of active compounds into plant tissues. This approach not only boosts nutrient-use efficiency but also reduces the need for frequent applications, thereby promoting more sustainable crop practices [56]. Additionally, the transition from conventional to green synthesis in nanoparticle development offers an eco-friendly alternative that relies on natural agents, such as plant extracts, microbes, or biomolecules. This approach minimizes the use of toxic chemicals and reduces energy consumption. Green-synthesized nanoparticles further support sustainable agriculture by improving nutrient delivery, enabling controlled release, and enhancing pest resistance, all while reducing environmental impact [57]. For instance, silicon nanoparticles (Si-NPs) have been shown to enhance plant growth and photosynthesis while reducing Cd and lead (Pb) concentrations in wheat [58] and maize [59], respectively. Si-NPs treatment has also been shown to alleviate oxidative stress in these plants, evidenced by lower levels of H_2O_2, electrolyte leakage, and MDA content [58,59]. The potential of Si-NPs in mitigating heavy metal stress is increasingly recognized, as demonstrated by Hussain et al. [60], who explored the synergistic effects of combining different nanoparticles (SiNPs, ZnONPs, and FeNPs) in wheat grown in Cd-contaminated fields. Their study demonstrated that the combination of these three NPs significantly reduced Cd uptake in wheat straw and grains by 84% and 99%, respectively, while increasing Zn and Fe levels in the grains. In line with other research, this study also found improvements in chlorophyll and carotenoid contents, increased antioxidant enzyme activities, and reduced electrolyte leakage compared to the control [60]. Similarly, Khan et al. [61] showed that applying Si-NPs to wheat under combined heavy metal and drought stress conditions improved growth, enhanced photosynthesis, and lowered Cd levels in plant tissues, especially in grains. Si-NPs also reduce oxidative stress by decreasing H_2O_2, electrolyte leakage, and MDA, while boosting antioxidant enzyme activity. These findings underscore the potential of nano-encapsulation biostimulants as powerful tools for enhancing plant resilience to multiple abiotic stresses, supporting productivity under challenging conditions [61].

Conversely, the application of calcium-silicon nanoparticles (Ca-SiNPs) has been shown to mitigate salinity stress in Lilium plants, leading to enhanced flower quality, as evidenced by increased flower size and fresh biomass [62]. Moreover, Ca-SiNP treatment boosted chlorophyll content, ascorbic acid levels, and antioxidant capacity, as measured by DPPH (1,1-diphenyl-2-picrylhydrazyl) assays in the leaves, despite an observed increase in MDA levels under salinity stress [62]. These findings highlight the potential of combining different NPs to mitigate heavy metal stress and improve plant resilience.

In addition to Se and Si, silver (Ag) also plays a vital role in salinity stress, a common stressor that can negatively impair plants' growth and crop productivity. Barley seed primed with polyvinylpyrrolidone-coated silver nanoparticles (PVP-AgNPs) exhibited a 100% germination rate [63]. Similarly, applying AgNPs to lily plants improved flowering, plant height, petal width, fresh bulb weight, bulb diameter, number of scales in a bulb, and enhanced the levels of essential nutrients in the plant tissue (N, K, Ca, Cu, Mn, and Zn), compared to control under salt stress conditions [64]. Other nanoparticles, such as carbon nanotubes and graphene, have also demonstrated significant benefits. Research indicates that carbon nanoparticles improved tomato plant growth under salt stress [65]. The treated tomato plants showed an increase in chlorophyll, ascorbic acid, glutathione, protein, and phenolic compounds while also boosting the activity of antioxidant enzymes, such as CAT, APX, and GPx. These treatments also improved tomato fruit quality, characterized by higher total soluble solids, phenolic compounds, flavonoids, ascorbic acid, and lycopene [65].

Interestingly, the combination of various inorganic substances, such as HA, Si, and biochar, has been shown to significantly reduce ABA levels while increasing salicylic acid (SA) concentration and enhancing antioxidant activity, particularly polyphenol production, in rice [66]. The synergistic interaction between HAs, biochar, and Si highlights the complex relationship between phytohormones, particularly ABA and SA, and antioxidant responses in rice plants under heavy metal, drought, and salinity stress. In rice, ABA activation is facilitated by a Ca^{2+}/calmodulin-dependent kinase, which triggers the activation of antioxidant enzymes such as SOD and CAT. These enzymes manage oxidative stress by converting harmful O_2 to H_2O_2, which is further detoxified, thereby reducing cellular damage [67,68]. SA production in plants is often induced under stress conditions and works synergistically with ABA. Under stress, the production of phenolic compounds not only contributes to SA biosynthesis but also facilitates the scavenging of ROS. These compounds are critical in metal ion chelation, activate phytohormones, and improve nutrient uptake [69]. Together, these mechanisms highlight the potential of HA, biochar, and Si to bolster plant resilience against environmental stress.

An example of a commercial product that enhances plant resilience is Quantis™, a PB derived from sugar cane by-products fermented with yeast and enriched with potassium and calcium [70]. In potato plants, the application of the PB Quantis™ significantly improved heat tolerance compared to untreated plants. Quantis™ enhanced Photosystem II photochemical efficiency and reduced thermal dissipation in heat-stressed potatoes, leading to a 4% increase in tuber weight and a 40% increase in tuber size compared with the control. Furthermore, the Quantis™ application upregulated the gene *StFKF1*, which promotes tuberization, resulting in larger tubers. It also increased the expression of heat-defense genes, such as *PEN1*, *PR4*, and *MEE59*, contributing to leaf photoprotection and thermal protection in roots. Additionally, Quantis™ treatment was linked to increased cytokinin signaling in roots and reduced levels of endogenous ABA and cytokinin in leaves, essential factors in mitigating stress responses [70].

The success of inorganic PBs in alleviating abiotic stresses presents a promising strategy for enhancing plant resilience under challenging environmental conditions. By improving plant growth, photosynthesis, and stress tolerance, these biostimulants can contribute significantly to sustainable agricultural practices. Continued research and application of inorganic PBs may be key to addressing the challenges of feeding a growing global population in the face of climate change and environmental degradation.

5 Role of Microbial Plant Biostimulants in Alleviating Abiotic Stresses

Plant growth-promoting rhizobacteria (PGPR), such as *Salinispora arenicola* [71], *Burkholderia* sp. BK01 [72], and *B. velezensis* HY23 [73], have been reported to alleviate salt stress in various plants, including tomatoes [71], *Arabidopsis* [71], and soybeans [73]. These PGPR enhance germination and shoot and root growth under saline conditions. They also increase chlorophyll content and activities of SOD, POD and CAT in *Arabidopsis* under salinity stress while reducing MDA levels [72]. Notably, *Burkholderia* sp. BK01 produces polysaccharides that could serve as biostimulants to further enhance plant growth and salt tolerance. Both *Burkholderia* sp. BK01 [72] and *B. velezensis* HY23 [73] produce exopolysaccharides that improve salt tolerance in soybeans and *Arabidopsis* by modulating the antioxidant defense system and regulating the expression of ion transporters. Moreover, *Pseudomonas thivervalensis* SC5, which produces 1-aminocyclopropane-1-carboxylate deaminase, increases osmolyte and polyamine production, which are essential for improving osmotic stress tolerance in cucumber plants [74].

Acinetobacter calcoaceticus AC06 and *Bacillus amyloliquefaciens* BA01 [75] have been identified as effective osmolyte-producing microbial biostimulants under drought stress. These microbes significantly increase proline, SA, trehalose, and glycine betaine levels, thereby enhancing drought tolerance in groundnut plants. Their presence leads to improved plant biomass, higher concentrations of photosynthetic pigments, increased relative water content, and elevated levels of proline and soluble sugars compared to control plants. Additionally, *A. calcoaceticus* AC06 and *B. amyloliquefaciens* BA01 reduce the electrolyte leakage and MDA content in drought-stressed groundnut while enhancing antioxidant enzyme activities, such as CAT, APX, and SOD [75].

Other studies have highlighted the benefits of different PGPR strains in stress tolerance. For example, *B. butanolivorans* KJ40 and *B. siamensis* H30-3, when used to prime soybean seeds, promote osmotic stress tolerance during germination and mitigate cellular damage from secondary oxidative stress by increasing enzyme activities [76]. Similarly, Lozo et al. [77] explored the effects of drought-tolerant *Bacillus* strains (*B. safensis* SS-2.7 and *B. thuringiensis* SS-29.2) on four sweet pepper genotypes. While genotype 274 exhibited the best establishment under normal conditions, it was the most drought-sensitive. In contrast, Matica, though slower to establish under normal conditions, along with CalW, demonstrated superior drought tolerance. The authors found that antioxidant enzyme activity varied by genotype and treatment, with CalW showing the best bacterial response, while genotype 133 declined more rapidly under drought, even with treatment. These results highlight the potential of *Bacillus* strains in breeding programs to select biostimulant-compatible, drought-resilient pepper genotypes and other crops [77].

Several studies suggest that the beneficial effects of microbial PBs may result from the unique metabolites they produce, such as IAA, siderophores, and other compounds. For example, a comparison of 15 PGPR isolates for alleviating drought stress in oilseed crops revealed that *A. calcoaceticus* AC06 exhibited the highest IAA production (128.82 μg ml^{-1}) and siderophore production (84.87%), along with significant osmotic resistance to −0.73 MPa [75]. In osmotically stressed wheat, *A. brasilense* produced approximately twice the phytohormone levels (IAA, GA, and ABA) than *B. subtilis*. IAA promotes cell division, elongation, and differentiation, whereas GA and ABA serve as signaling molecules in plants that enhance plant stress tolerance under adverse conditions [78,79]. Additionally, siderophore production facilitates iron uptake by chelating ferric ions, which is particularly beneficial in nutrient-poor soils and improving drought tolerance [80]. Altogether, these findings suggest that *Azospirillum* sp. confer greater drought stress tolerance than *Bacillus* sp. The natural symbiotic relationship between arbuscular mycorrhizal fungi (AMF) and many plant species positively affects plant water relations, especially under water deficit conditions. AMF improves soil-plant hydraulic conductance and enhances the water status of tomato plants in drying soil by increasing the effective root radius [81]. This expansion reduces water flow at the root-soil boundary and eases the decrease in water potential in the surrounding soil, thereby promoting drought tolerance in tomato plants [81]. Similarly, *Serendipita indica*, a culturable endophytic fungus that can colonize various host roots, including citrus plants, has been shown to enhance plant drought tolerance. It achieves this by reducing growth inhibition, increasing the photosynthetic rate, chlorophyll index, and water use efficiency, and boosting antioxidant enzyme activities in citrus plants [82]. Moreover, the endosymbiosis of *Piriformospora indica* with *Andrographis paniculata* not only promotes the production of andrographolide, but also enhances antioxidant enzyme activities and proline content, thereby improving drought tolerance in *A. paniculata* [83].

Building on the success of single-strain microbial biostimulants, researchers are now exploring the use of multistrain biostimulants to enhance their effectiveness in promoting abiotic stress tolerance. For example, a combination of multistrain microbial biostimulants, including *Claroideoglomus claroideum* BEG96, *Funneliformis caledonium* BEG97 and *F. geosporum* BEG199, along with a mix of *Glomus* spp. and rhizospheric bacteria has been shown to improve drought tolerance in tomato plants [84]. These plants showed higher IAA production, chlorophylls, and polyphenols under drought stress [84]. Similarly, combining *Glomus* spp., *Bacillus* spp., *Streptomyces* spp., *Pseudomonas* spp., and *Trichoderma* spp. significantly increased the total phenolic compound content in drought-stressed green beans compared to control plants [85]. Furthermore, a study on the synergistic effects of microbial and non-microbial biostimulants demonstrated that a combination of AMF and protein hydrolysates could alleviate heavy metal stress caused by iodine fortification in eggplants [86]. This combination enhances nutrient uptake through root system expansion, increases proline content, and boosts ROS-scavenging enzyme activity, thereby reducing oxidative damage caused by iodine [86]. Among non-microbial biostimulants, HAs are particularly effective in improving soil fertility [87]. They can act as carriers for introducing beneficial microorganisms into the soil as they are resistant to microbial degradation [88]. A synergistic effect was observed with the combined application of HA and endophytic bacteria in tomato plants [89]. These bacterial strains demonstrated active root colonization in tomato seedlings, supported by their biofilm-forming capability, which helps them survive in challenging environments and improves their persistence [90]. These mechanistic insights provide valuable guidance for developing innovative formulation strategies, leading to the development of more effective and resilient biostimulant products.

In summary, the use of PGPR and AMF as biostimulants has demonstrated significant potential in enhancing plant tolerance to abiotic stresses, such as drought and salinity. These beneficial microbes improve plant growth, stress resilience, and overall productivity through the production of various metabolites and the modulation of plant defense mechanisms. When combined with non-microbial biostimulants, the benefits are further amplified, offering new avenues for developing more robust agricultural practices to address environmental challenges. Notably, some bioactive compounds and natural plant hormones, such as melatonin, fall within the broader category of PBs. Although it is not traditionally grouped with common biostimulant types like HA, amino acids, seaweed extracts, or microbial inoculants, melatonin functions similarly by enhancing abiotic stress tolerance in horticultural crops, strengthening resilience to cold, drought, heat, salinity, and heavy metal stress. As a potent antioxidant, melatonin regulates stress-responsive genes, promotes water-use and photosynthetic efficiency, and interacts synergistically with other plant hormones to support growth under adverse environmental conditions [91]. Examples of the non-microbial and microbial PBs that have been reported to alleviate abiotic stresses are listed in Table 1.

Table 1: List of organic, inorganic and microbial biostimulants used to alleviate abiotic stresses

Plant species	Type of stress	Biostimulants	Mode of application	Concentration range	Effect	Reference
Organic plant biostimulants						
Oryza sativa	Heat	Brassinosteroid (BR), amino acids (AA), nitrophenolates (NP), botanical extracts (BE)	Foliar spray at 54th, 65th, and 75th days after sowing	1 mL/L BR, 30 mL/L AA, 15 mL/L NP, 15 mL/L BE	Increased photosynthesis rate (46%), stomatal conductance (48%), transpiration value (61%), higher chlorophyll content (32%) with lower malondialdehyde (MDA) (15%), and proline production (15%).	[38]
Solanum tuberosum	Heat	Quantis (sugarcane by-product enriched with potassium and calcium)	Foliar spray at potato tuber initiation stage	0.2 mL/m^2	Enhanced photosystem II photochemical efficiency, tuber weight (4%) and size (40%); increased cytokinin and abscisic acid level (55%); decreased thermal dissipation.	[70]
	Heat		Foliar spray daily for		Increased vegetative growth in terms of fresh weight (48% for Glu, and	[41]

(Continued)

Table 1 (continued)

Plant species	Type of stress	Biostimulants	Mode of application	Concentration range	Effect	Reference
Brassica rapa L. ssp. *pekinensis*		Glutamic acid (Glu), and Poly-γ-glutamic acid (γ-PGA)	5 days prior to heat stress	2.0 mM/L Glu, or 20 mg/L γ-PGA	37% for γ-PGA), dry weight (52% for Glu, and 39% for γ-PGA), height (28% for Glu, and 26% for γ-PGA), hypocotyl diameter (14% for Glu, and 9% for γ-PGA), leaf length (36% for Glu, and 33% for γ-PGA) and leaf width (43% for Glu, and 31% for γ-PGA); enhanced level of total chlorophyll (42% for Glu, and 23% for γ-PGA), and carotenoid (32% for Glu, and 24% for γ-PGA) along with inhibited levels of MDA (50% for Glu, and 36% for γ-PGA), electrolyte leakage (42% for Glu, and 24% for γ-PGA), and superoxide anion radical by higher antioxidant enzyme activity (increment ranging from 13% to 45%).	
Cucumis sativus L.	Heat	Lignin derivatives with plant derived amino acids and molybdenum	Seed coating	20% KIEM®	Increased seed germination (7%), seedling biomass (13%); decreased H_2O_2 content (70%); higher accumulation of antioxidant gene: *CuZnSOD* (1.8-fold), *MnSOD* (1.8-fold), and *CAT* (3.4-fold); downregulation of *FeSOD* (0.2-fold): increased isocitrate lyase activity (37%).	[92]
Lycopersicon esculentum cv. Micro Tom	Heat	*Ascophyllum nodosum* (brown seaweed extract)	Foliar spray to 105-day-old plants at the early pollen development stage (3 days before heat treatment) and again 14 days after the onset of heat stress	0.106%	Improved reproductive stage including flower development, pollen viability (3.2 to 4.4 folds compared to control) and fruit production (22% to 33%).	[93]
Agrostis stolonifera cv. Penncross	Heat	β-carotene	Foliar spray every 7 days for 28 days	1 mM	Suppressed leaf senescence, higher antioxidant enzyme activity (SOD: 10%, 20%, and 24% on 14-, 21-, and 28-day), POX: (11%, 19%, 43% on 14-, 21-, and 28-day), CAT: 47%, 172%, 227% on 14-, 21-, and 28-day), and APX: 55% and 224% on 21- and 28-day)], and lower MDA content (15%, 17%, and 19% on 14-, 21-, and 28-day).	[94]
Zea mays L. (hybrid Knezha 307)	Heat	Protein hydrolysate	Foliar spray or root drench	10^{-3}, 10^{-6}, 10^{-9}, 10^{-12} dilution	Enhanced shoot and root growth, stabilized chlorophyll *a*/*b* ratio, starch content restored, reduced MDA level, increased proline content, and higher	[95]

(Continued)

Table 1 (continued)

Plant species	Type of stress	Biostimulants	Mode of application	Concentration range	Effect	Reference
					expression of heat shock protein, dehydrins, and protease-coding genes.	
Zea mays L. SC 131 and *Sorghum bicolor* L. H 306	Drought	Humic acid	Seed coating for 12 h	100 mg/L	Increased plant biomass (11% to 30% in maize and 16% to 36% in sorghum), chlorophyll (42% in maize and 27% in sorghum) and carotenoid content (24.5% in maize and 24.1% in sorghum), photosynthesis rate (29% in maize and 15% in sorghum), stomatal conductance (30% in maize and 14% in sorghum), CO_2 assimilation (40% in maize and 35% in sorghum), sucrose (24% in maize and 10% in sorghum), total soluble sugar (13% in maize and 6% in sorghum), total carbohydrate (8% in maize and 9% in sorghum), proline content (14% in maize and 11% in sorghum), total soluble protein (10% in maize and 5% in sorghum), and antioxidant enzyme activities; reduced electrolyte leakage (9% in maize and 10% in sorghum), H_2O_2 (12% in maize and 12% in sorghum), and MDA level (14% in maize and 12% in sorghum).	[33]
Lycopersicon esculentum cv. Rio grande	Drought	Magnesium based plant-derived pool of polyphenol	Foliar spray at 1 day before drought, and at day 7 after recovery from drought stress	0.1%	Increased chlorophyll *a*, chlorophyll *b*, and carotenoid level, reduced cell damage and cellular membrane.	[46]
Arabidopsis thaliana	Drought	Super fifty (*Ascophyllum nodosum* extracts)	Foliar spray (25th and 27th day-after-germination)	0.2%	Reduces reactive oxygen species (ROS) accumulation and ion leakage; increased relative water content.	[24]
Brassica napus L.	Drought	*Sargassum angustifolium* (brown algae extract)	Foliar spray at 3-leaf stage	0.001% (7 mL for each plant)	Increased shoot height (~25% to 27%), dry weight (~44% to 56%), photosynthetic pigments level, free radical scavenging, SOD antioxidant enzyme activity, and proline accumulation.	[23]
Lycopersicon esculentum cv. Micro Tom	Drought	Chitosan from mushroom	Foliar spray on 46-day-old plant (3 days before drought stress)	0.01%	Increased the number (32%) and weight of fruits (3%), relative water content (3%), chlorophyll content (3%); reduced lipid peroxidation (2%).	[96]
Lactuca sativa L.	Salinity	Graminacear-derived protein hydrolysate and its lighter fraction (F3)	Foliar spray on 10th day, followed by weekly application	3 mL/L solution	Reduction of proline (34%), MDA (12%), and osmolyte level (35%).	[45]
Lycopersicon esculentum	Salinity	*Crataegus oxyacantha* Extract	Root drench	20, 30, 70 mg/L of diluted extracts	Increased plant height (1% to 17%), photosynthetic pigment level (75%), soluble sugar (23%), free amino acid	[97]

(Continued)

Table 1 (continued)

Plant species	Type of stress	Biostimulants	Mode of application	Concentration range	Effect	Reference
					(37%), antioxidant enzyme activity (SOD: 44%, GPx: 45%, GST: 47%, and GR: 100%); reduced MDA level (45%).	
Triticum turgidum L. var. Durum	Salinity	*Rosmarinus ofcinalis* L. essential oil	Seed coating for 12 h	1, 2.5, and 5 ppm	Increased germination rate (36%), seedling length (~1.7-fold), fresh weight (~2.6-fold), total leaf area (~1.5-fold), proline content (~1.5-fold), carbohydrates content (~1.3-fold), antioxidant activity (CAT: 2-fold, SOD: 1.7-fold, and POD: 5.2-fold),; reduced membrane deterioration and electrolyte leakage (~1.5-fold).	[98]
Brassica rapa	Salinity	Thymol	Root drench	5, 10, 20, 40 µM contained in Hoagland solution	Promotion of seedling growth (71% of seedling fresh weight) with reduced level of ROS accumulation (10%), cell membrane destruction (34% of lipid peroxidation), and cell death (21% reduction in PI fluorescence); reduced the ROS via increased activity of antioxidant enzyme, ascorbic acid/ dehydroascorbic acid ration, and level of phenolic compound (72%).	[99]
Lycopersicon esculentum	Salinity	Tannin based biostimulant	Root drench	1 mL/L	Improved root development: increased root weight (24%) and length (23%).	[100]
Triticum durum L. var Karim	Salinity	*Ulva rigida* seaweed water extracts	Foliar application from 2nd to 8th week	12.5%, 25% and 50%	Increased overall growth and photosynthetic pigment content (197% of chlorophyll *a* and 64% of chlorophyll *b*) accompanied by enhanced antioxidant enzyme activity leading to reduction in ROS accumulation.	[22]
Olea europaea L. cv. Arbequina	Salinity	Formulation containing vitamins, amino acids, proteins, betaines and growth factors	Root drench	150 mL of 2.5 mL/L of biostimulant	Increased potassium accumulation in leaf (44%), restoring a higher K^+/Na^+ ratio; recovery of higher H_2O_2 level and MDA by increased level of SOD antioxidant enzyme activity (10%). The pollen grains showed Ca^{2+} chelating activity, which mitigate negative impact of H_2O_2 on Ca^{2+} metabolism.	[101]
Inorganic plant biostimulants						
Allium cepa L.	Drought	Selenium	Foliar application	15, 30, 45, and 60 g ha^{-1}	Increased plant growth (10% in height) and yield (26%), higher dry mass (26%) in the onion plant and higher Se content in the bulb.	[49]
Oryza sativa L.	Drought	Selenium	Foliar spray 2 times after drought stress	10, 20 mg/L	Increased plant growth, number of tillers (13%), filled grains (22%), and grain yield (11%) associated with	[50]

(Continued)

Table 1 (continued)

Plant species	Type of stress	Biostimulants	Mode of application	Concentration range	Effect	Reference
			in 1 day interval		increased chlorophyll stability (20%), membrane stability (14%), proline content (18%), and relative water content (14%).	
Cucumis sativus L. Cultivar dar	Drought	Selenium	Root drench	1, 5, 10 µM	Reduced severity of oxidative stress [H_2O_2: 40%, O_2^- radical, and $OH^·$ radical accumulation: 2.4-fold via enhanced activity of antioxidant enzymes (APX: 104%, POX: 44%, CAT: 45%, SOD: 63%)].	[102]
Lactuca sativa L.	Drought	MgO and $MgCO_3$ nanoparticle	Foliar spray	Mixture of 10 mg/L nMgO, 10 mg/L $nMgCO_3$	Improved plant growth, water content, total soluble sugar and starch, photosynthetic pigment content, and higher photosynthetic rate.	[103]
Zea mays L.	Drought	Silicon	Seed coating for 16 h	4, 6 mM of sodium metasilicate	Increased shoot length (54%), root length (69%), and fresh and dry weight of shoot (83%) and root (88%); higher chlorophyll *a* (85%), chlorophyll *b* (76%), and carotene levels; reduced level of proline, glycine betaine, and total soluble sugar; reduced H_2O_2, MDA, and phenolic compounds level with an elevated activity of antioxidant enzymes.	[53]
Solanum lycopersicum L. "Jinpeng 1#"	Drought	Silicon	Root drench	0.6 mM of sodium metasilicate in Hoagland solution	Stabilizing mitochondrial structure, upregulation of the *RuBisCO* involved in carbon fixation, and proton gradient regulation 5 that increase non-photochemical quenching; optimized energy dissipation in chloroplast by alteration of oxidase, and malate/oxaloacetate shuttle.	[54]
Zea mays L.	Heavy metal (lead)	Silicon nanoparticles	Foliar spray at 3 weeks after sowing, followed by 3 sprays at one week interval	200, 400 mg/L of SiNPs	Reduced electrolyte leakage and H_2O_2 level (20% to 26%); increased photosynthetic pigment level (39% to 79%), antioxidant enzyme activities, plant height (19% to 106%), shoot (20% to 88%) and root dry weight, silicon accumulation; lower lead concentration in plant tissues (24% to 51%).	[59]
Triticum aestivum L.	Heavy metal (Cadmium)	Silicon nanoparticles	Root drench and foliar spray	300, 600, 900, and 1200 mg/kg soil as soil mixture; foliar spray (first at thinning stage, and 3 more times on 4th, 6th, and 8th week)	Increased shoot (9% to 43% via root drench and 20% to 54% via foliar spray), root (26%), spike (45%), and grain dry biomass (57%); enhanced leaf gas exchange (105% via root drench and 110% via foliar spray) and chlorophyll *a* (53% via root drench and 60% via foliar spray), chlorophyll *b* concentration (130% via root drench and 140% via foliar spray) and Si accumulation; reduction of oxidative	[58]

(Continued)

Table 1 (continued)

Plant species	Type of stress	Biostimulants	Mode of application	Concentration range	Effect	Reference
					stress by reduced electrolyte leakage (27% via root drench and 26% via foliar spray), higher level of antioxidant enzyme activities (35% to 51%); reduced cadmium (Cd) accumulation (19% to 65%).	
Triticum aestivum L.	Heavy metal (Cadmium)	Zinc oxide (ZnONPs), iron (FeNPs), and silicon nanoparticles (SiNPs)	Foliar spray at 4th, 6th, and 8th week	300 mg/L SiNPs, 5 mg/L FeNPs, 25 mg/L ZnONPs, 25 mg/L ZnONPs + 5 mg/L FeNPs, 25 mg/L ZnONPs + 300 mg/L SiNPs, 5 mg/L FeNPs + 300 mg/L SiNPs, and 25 mg/L ZnONP + 5 mg/L FeNPs + 300 mg/L SiNPs	Increased chlorophyll and carotene content (28% to 66%), enzymatic antioxidant activity (SOD: 227%, POD: 80%); reduced electrolyte leakage (42%) and reduction of Cd uptake in plants (88% in wheat straw and 98% in grains) with increased zinc and iron accumulation in wheat grains.	[60]
Triticum aestivum L.	Heavy metal (Cadmium) and drought	Silicon nanoparticles	Root drench	25, 50, and 100 mg/kg as soil mix	Improved plant growth: plant height (5%, 18% and 25% for 25, 50, and 100 mg/kg, respectively), spike length (18%, 22% and 34% for 25, 50, and 100 mg/kg, respectively), shoot (70% at 100 mg/kg), root (54% at 100 mg/kg), and grain dry weight (75% at 100 mg/kg), along with a higher concentration of chlorophyll *a* and chlorophyll *b*; reduced ROS (H_2O_2: 46% at 100 mg/kg) and MDA: 45% at 100 mg/kg)) accumulation and electrolyte leakage (43% at 100 mg/kg) via higher SOD (40%, 52% and 71% for 25, 50, and 100 mg/kg, respectively) and POX content (13%, 35% and 52% for 25, 50, and 100 mg/kg, respectively); reduced Cd (17%, 35% and 47% for 25, 50, and 100 mg/kg, respectively) but elevated Si levels in shoot and root (3 to 51 mg/kg).	[61]
Hordeum vulgare L.	Salinity	Polyvinylpyrrolidone-coated silver nanoparticles (AgNPs)	Seed coating for 2 h	1, 20, 40 mg/L	Increased seed germination (100% with application of 40 mg/L AgNPs) and antioxidant enzymes (SOD: 1.7 to 2.6-fold, CAT: 2.7 to 3.5-fold).	[63]
Lilium sp.	Salinity	Colloidal silver nanoparticles	Bulb coating for 1 h	25, 50, 100, 150 ppm	Improved plant growth and flowering via higher plant height (8% in flower height), petal width (14%), fresh bulb weight (36% to 64%), bulb diameter	[64]

(Continued)

Table 1 (continued)

Plant species	Type of stress	Biostimulants	Mode of application	Concentration range	Effect	Reference
					(20% to 22%), number of scales (12%), and nutrients content in plant.	
Solanum lycopersicum L.	Salinity	Carbon nanotubes and graphene	Seed coating for 24 h	50, 250, 500 mg/L	Increased chlorophyll content (9% to 22%), ascorbic acid (20%), glutathione (13%), protein (10% to 12%), phenolic compounds (14%) and antioxidant enzyme activities in the leaf (APX: 25%, CAT: 48%, SOD: 11% to 13%); elevated total soluble solid (26%), phenolic compounds (145%), flavonoids (38%), ascorbic acid (28%), and lycopene levels in the fruit (12% to 36%).	[65]
Hybrid of *Lilium auratum* and *Lilium speciosum*	Salinity	Calcium-Silicon nanoparticles	Foliar spray	500 and 750 mg/L	Improved flower quality via an increase in flower size (4% to 5%) and fresh biomass (38% to 58%); increased chlorophyll content (38%), ascorbic acid (9%), and antioxidant capacity (19% to 24%) with an increased MDA level (23% to 51%).	[62]
Fragaria × *anansa* plants 'cv; Camarosa'	Salinity	Silicon dioxide nanoparticles	Root drench	50, 100 mg/L of SiO_2 in Hoagland solution until begin flowering; 50 mg/L during reproductive stage	Increased epicuticular wax layer stability, chlorophyll, and carotene content; lower proline accumulation level with thicker wax crystal deposition and increased canopy temperature.	[104]
Solanum lycopersicum L "El Cid F1"	Salinity	Selenium nanoparticles (SeNPs)	Root drench	1, 5, 10, 20 mg/L	Improved chlorophyll *a* (166% with 20 mg/L SeNPs), and chlorophyll *b* content (224% with 20 mg/L SeNPs); higher phenol content in leaf (17% to 21%); higher flavonoids, phenolic compounds, lycopene (172% to 322%), and β-carotene in the fruits (109% to 114%); improved antioxidant enzyme activities in leaf and fruit (APX: 486%, CAT: 312% to 345%, and SOD: 91%) with also elevated levels of glutathione peroxidase (GPx) in fruit (28%).	[105]
Microbial plant biostimulants						
Solanum lycopersicum L.	Salinity	*Salinispora arenicola*	Seed coating for 2 h and inoculate root in suspension for 3 min	1 mg/mL of bacteria suspension	Increased osmolyte (30%) and antioxidant production (9%); increased expression of selective transport channel gene *SIHKT1,2* (2.4-fold)	[71]
Cucumis sativus	Salinity	*Pseudomonas thivervalensis* SC5	Seed coating for 1 h and application at root-shoot junction	3 mL of direct bacterial suspension with OD_{600} = 0.3	Increased production of ACC Deaminase, osmolytes, and polyamines.	[74]
	Salinity	*Burkholderia* sp. BK01	Root drench			[72]

(Continued)

Table 1 (continued)

Plant species	Type of stress	Biostimulants	Mode of application	Concentration range	Effect	Reference
Arabidopsis thaliana				100 ppm of BK01	Increased plant growth (170% of fresh weight, 40% of root length, 79% of shoot length), chlorophyll content (110%), proline production; enhanced antioxidant enzyme activities (SOD: 43%, POD: 71%, and CAT: 37%); decreased MDA content (53%).	
Glycine max cv Daewon	Salinity	*Bacillus butanolivorans* KJ40 and *B. siamensis* H30-3	Seed coating for 1 h	1, 10, and 100 μg/mL	Increased antioxidant enzyme activity.	[76]
Glycine max	Salinity	*Bacillus velezensis*	Root drench	10 mL of direct bacterial suspension with OD_{600} = 0.8	Regulation of the antioxidant pool and ion transporter expression.	[73]
Solanum lycopersicum L.	Drought	Arbuscular Mycorrhiza Fungi	Root drench	50 spore/kg in the soil	Increased root surface active in water uptake; enhanced soil-plant hydraulic conductance.	[81]
Phaseolus vulgaris L.	Drought	*Glomus* spp., *Bacillus* spp., *Streptomyces* spp., *Pseudomonas* spp., and *Trichoderma* spp.	Root drench	5 L/ha Nomoren, 500 g/100L Twin-Antistress, 500 g/100L Veramin Ca, and 1 kg/ha EKOprop at 10, 20, and 30 days after sowing with irrigation	Increased total phenolic compounds content (86% to 102%).	[85]
Arachis hypogaea L.	Drought	*Acinetobacter calcoaceticus* AC06 and *Bacillus amyloliquefaciens* BA01	Root drench	10 mL of 108 CFU/mL inoculum as soil drench at time of sowing and 14 days after first inoculation	Increased osmolyte production (proline, salicylic acid, trehalose, and glycine betaine); increased plant biomass, photosynthetic pigments, relative water content, and soluble sugar; reduced plant sensitivity indexes such as electrolyte leakage and MDA contents; increased antioxidant enzyme activities (CAT, APX), and SOD).	[75]
Capsicum annuum L.	Drought	*Bacillus safensus* SS-2.7 and *B. thuringiensis* SS-29.2	Seed coating for 1 h	Direct bacterial suspension with OD_{600} = 1	Showed a plant growth-promoting effect, increased antioxidant enzyme activities (APX: 198%, POD: 128%).	[77]
Andrographis paniculata (Burm. f.) Wall. ex Nees	Drought	*Piriformospora indica*	Root drench	500,000 spores/mL suspension as dipping agent	Promote andrographolide (198%) and biomass production (2.3-fold).	[83]
Ponsirus trifoliata L. Raf.	Drought	*Serendipita indica*	Root drench	12.5 mL of 5.0 × 10^8 CFU/mL spore suspension and 14.5 mL of 0.018 g/mL mycelial suspension inoculate	Increased plant biomass (10% to 22%), shoot/root ratio (22% to 25%), net photosynthetic rate (106%), water use efficiency (115%), chlorophyll index (55%), and nitrogen balance index (64%); reduced ROS levels resulting in lower membrane lipid peroxidation (MDA) (15% to 17%); increased ascorbate (65%) and glutathione, and antioxidant enzyme	[82]

(Continued)

Table 1 (continued)

Plant species	Type of stress	Biostimulants	Mode of application	Concentration range	Effect	Reference
					activities (CAT: 38%, POD: 87%, and GPx).	
Solanum lycopersicum 'cv; San Marzano Nano'	Drought	*Claroideoglomus claroideum* BEG96, *Funneliformis caledonium* BEG97 and *F. geosporum* BEG199 *Glomus* spp. and rhizospheric bacteria	Root drench	15 g/pot of arbuscular mycorrhizal product placed in the planting hole with contact at the root	Increased IAA, chlorophyll and polyphenols production.	[84]
Solanum melongena L.	Iodine	Arbuscular Mycorrhiza Fungi and protein hydrolysates	Root drench by dipping the root for 15 min at 24 h prior of planting	400 spores/ plant repeated with 150 mL/ plant of solution	Enhanced growth (31% in plant height) and yield (78%), fruit dry matter content (0.8%), total chlorophyll (59%), total anthocyanins (3%) and chlorogenic acid.	[86]

Note: Abbreviations: APX: ascorbate peroxidase; CAT: catalase: Cd: cadmium; GPx: glutathione peroxidase; GST: glutathione S-transferase; H_2O_2: hydrogen peroxide; MDA: malondialdehyde; PI: propidium iodide; POX: peroxidase; ROS: reactive oxygen species; SOD: superoxide dismutase.

6 Bibliometric Analysis

More than 260 scientific papers on PBs and abiotic stresses have been published in the last five years (2019–2024) from a single database (www.scopus.com) (accessed on 12 December 2024). A list of relevant publications from 2019–2024 with the co-occurrence of terms in titles and abstracts from journal articles and conference proceedings from the database were compiled. The strings of keywords used when searching were: "Plant" AND "Biostimulant" AND "Abiotic stress" AND "Microbial" OR "Microbes" OR "Plant growth-promoting bacteria" OR "Plant growth-promoting rhizobacteria" OR "Mycorrhizal fungi" OR "Humic" OR "Seaweed" OR "Organic" OR "protein hydrolysate" OR "inorganic". Bibliographic maps and networks were generated using VOSviewer, version 1.6.18. The eligibility criteria were set as follows: the terms repeated at least five times were selected, singular and plural forms were standardized to singular forms to avoid redundancies, and full names and abbreviations were standardized to full names.

Based on Fig. 1, the central role of "biostimulant" is expected, given its widespread application and interest in improving plant growth and stress tolerance. However, the network also highlights specific biostimulant types and their benefits, indicating targeted research efforts. The keyword "drought" having a high link strength (98) with "biostimulant" suggests a significant research focus on developing drought-tolerance crops through biostimulant application (Table 2). This aligns with global agricultural challenges, where water scarcity necessitates innovative solutions for crop sustainability. Additionally, "protein hydrolysate" with a notable link strength (84), indicates substantial research into how these substances can enhance nutrient uptake and soil fertility, reflecting a trend towards sustainable agriculture practices that reduce dependency on synthetic fertilizers.

The presence of "antioxidant" and "humic substance" as key terms with strong link strengths (72 and 55, respectively) highlights the dual focus on improving plant resilience and soil health. Antioxidants are crucial in mitigating oxidative stress in plants, while humic substances are known for their soil conditioning properties, enhancing nutrient availability and microbial activity. This suggests an integrated approach in biostimulant research, targeting plant and soil health for overall ecosystem benefits. Moreover, the inclusion of "microbiome" and "rhizosphere" with considerable link strengths (35 each) indicates an emerging interest in the role of microbial communities in plant health. This reflects a broader shift towards understanding and leveraging plant-microbe interactions to boost plant growth and stress resistance. The keyword "plant growth promoting rhizobacteria (PGPR)" with a link strength of 25, further supports this trend, showcasing the potential of beneficial microbes as biostimulants.

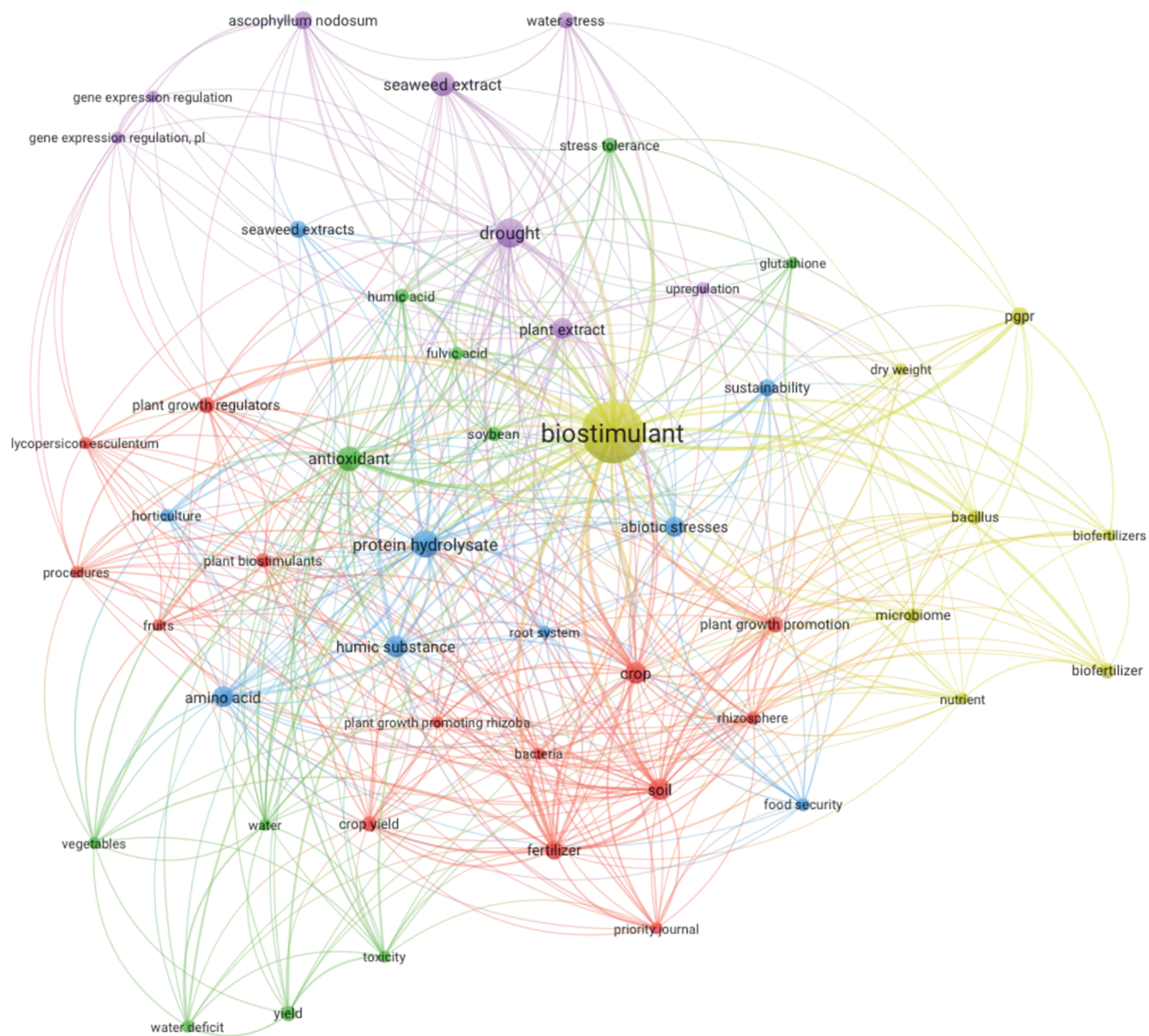

Figure 1: Network map in biostimulant research. The node (circle) size represents the occurrence frequency of the keyword in the dataset, with larger nodes indicating higher frequency. Line thickness represents the link strength between keywords, with thicker edges indicating stronger connections. Node and line colors represent clusters of related keywords, with different colors indicating clusters or thematic groups within the research network. The map contains six distinct colors: yellow for core biostimulant research and general plant growth promotion, purple for drought resistance and stress tolerance, blue for protein hydrolysates and related soil health topics, green for antioxidants and nutrient management, red for soil health, microbiome interactions, and crop yield, and light blue for specific biostimulants like amino acids and humic substances

Table 2: Keyword occurrence and link strength in biostimulant research

Rank	Keyword	Occurrence	Link strength
1	Biostimulant	134	293
2	Drought	30	98
3	Crop	16	95
4	Protein hydrolysate	26	84
5	Soil	16	84
6	Fertilizer	12	78
7	Antioxidant	21	72
8	Plant extract	15	58
9	Humic substance	16	55
10	Amino acid	15	48
11	Seaweed extract	20	43
12	Crop yield	8	39
13	Plant growth promotion	9	39
14	Abiotic stresses	14	38
15	Microbiome	8	35
16	Rhizosphere	6	35
17	Bacteria	5	34
18	Plant growth regulators	9	33
19	Humic acid	7	31
20	*Ascophyllum nodosum*	11	30
21	*Bacillus*	7	29
22	Priority journal	5	29
23	Root system	5	29
24	Procedures	5	27
25	Fulvic acid	6	26
26	Plant growth promoting rhizobacteria	5	26
27	Horticulture	6	25
28	*Lycopersicon esculentum*	5	25
29	Pgpr	11	25
30	Fruits	5	24
31	Food security	6	23
32	Nutrient	5	21
33	Biofertilizer	8	20
34	Gene expression regulation	5	20
35	Gene expression regulation, plant	5	20

(Continued)

Table 2 (continued)

Rank	Keyword	Occurrence	Link strength
36	Dry weight	5	17
37	Abiotic stress tolerance	9	16
38	Glutathione	5	16
39	*Arabidopsis*	5	15
40	Crop protection	5	15
41	Growth	5	15
42	Nutrient use efficiency	6	14
43	Protein	5	14
44	Plant biostimulant	6	13
45	Endophytes	5	12
46	Fruit quality	5	12
47	Microbial biostimulant	7	11
48	Osmolytes	5	11
49	Secondary metabolism	5	9
50	*Cyanobacteria*	5	5

Overall, the network map reveals a comprehensive and multifaceted research landscape. It indicates a synergistic approach where biostimulants are applied directly to plants, soil, and microbial environments to optimize plant growth and resilience. This holistic strategy underscores the complexity and interconnectedness of modern agricultural research, aiming for sustainable and resilient crop production systems. Limitations of this approach include the reliance on Scopus alone, which may omit relevant articles indexed in other databases like Web of Science or PubMed. Additionally, our strategy might have excluded some niche studies due to the specificity of the keywords used, potentially overlooking articles that discuss PBs indirectly or under different terminologies. Despite these limitations, the selected approach offers a comprehensive view of recent PB research.

7 Limitations and Concerns

Organic, inorganic, and microbial biostimulants each offer unique advantages in enhancing crop resilience under drought, heat, salinity, and heavy metal stresses, but they also present notable challenges. Organic biostimulants are limited by variability in composition, potential contamination, and slower response times, whereas inorganic biostimulants can lead to environmental pollution, nutrient imbalances, and short-lived efficacy. Microbial biostimulants, although promising, face issues related to specificity, survivability under stress, and biosafety concerns. In addition, formulating effective biostimulants using nano-enabled methods across diverse soil types and plant species is challenging. Key issues include enabling nanoparticles to penetrate cell membranes and walls and understanding the growth-enhancing effects of specific nanomaterials, such as carbon nanotubes. Despite the potential of PBs, conducting field trials with PBs presents several challenges, including environmental variability, complex plant-microbe-soil interactions, and difficulties in optimizing application methods and dosages. Most PBs showed no phytotoxic effects on treated plants. However, applying more than 10 μM of Se led to phytotoxicity in cucumber plants [69], and protein hydrolysate at dilutions of 10^{-3} or higher inhibited maize germination

[58]. The lack of standardized protocols for assessing PB efficacy and the need for long-term studies add to its complexity. Additionally, regulatory issues, economic constraints, and the challenge of ensuring reproducibility across diverse conditions must be considered. Addressing these challenges requires careful experimental design, standardized methods, and a deep understanding of environmental and biological factors influencing PB effectiveness.

8 Conclusions

In conclusion, the use of various PBs, including seaweed extracts, HAs, organic and inorganic PBs, PGPR, and mycorrhizal fungi, offers significant promise in enhancing plant resilience to abiotic stresses, such as drought, salinity, and nutrient limitations. These biostimulants function through various mechanisms and support osmoregulation, antioxidant activity, hormonal balance, and nutrient uptake efficiency, ultimately improving growth, yield, and stress tolerance in crops such as maize, wheat, and tomatoes (Fig. 2). Organic PBs, such as seaweed extracts and HAs, have proven effective in promoting photosynthesis, enhancing antioxidant defenses, and reducing oxidative damage, whereas inorganic PBs contribute to stress resilience and plant productivity. Furthermore, the integration of microbial biostimulants, such as PGPR and mycorrhizal fungi, enhances plant defence systems, further improving stress tolerance. Synergy between microbial and non-microbial biostimulants offers an exciting pathway for the development of sustainable agricultural strategies. However, further field studies are necessary to validate these findings under real-world conditions, making the continued exploration of biostimulants crucial to addressing the challenges posed by climate change and ensuring food security for the future.

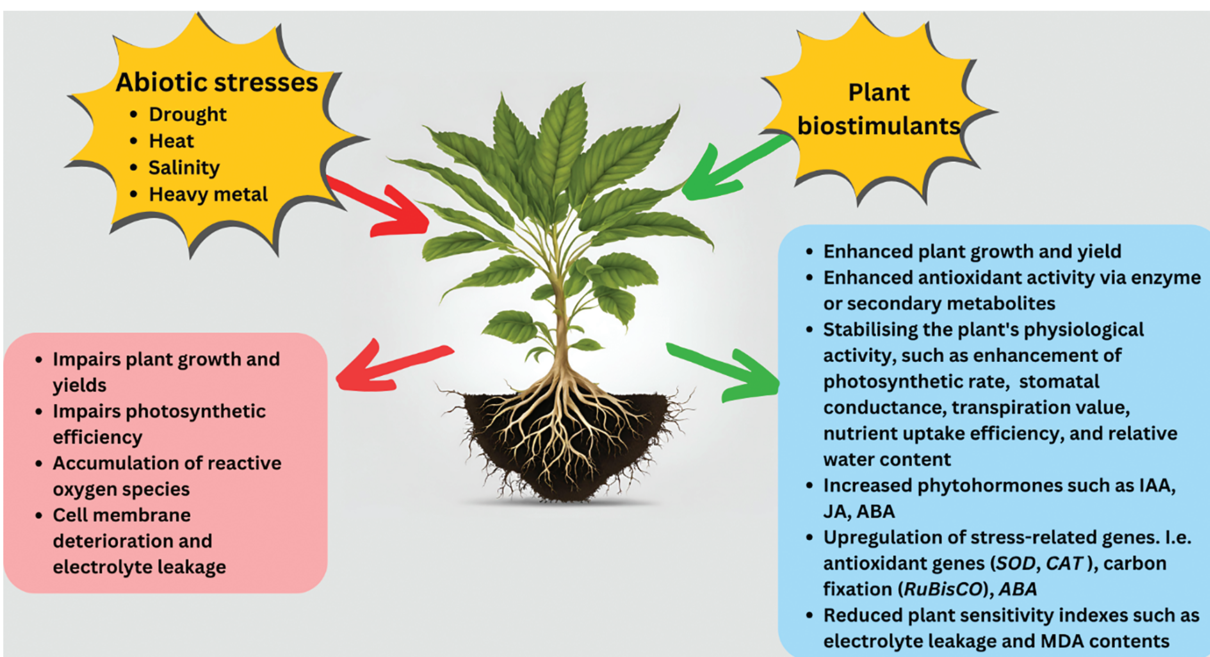

Figure 2: Overview of the role of plant biostimulants in modulating plant responses to abiotic stress. Abbreviations: ABA: Abscisic acid; CAT: Catalase; IAA: Indole-3-acetic acid; JA: Jasmonic acid; MDA: Malondialdehyde; SOD: Superoxide dismutase

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