

Review

Biostimulants for Sustainable and Resilient Agriculture

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Abstract

The growing pressure exerted by global food demand, combined with the excessive use of chemical and synthetic inputs, is prompting the agricultural sector to seek innovative and sustainable solutions to improve, or at least maintain, crop yields in a context of increased abiotic stress linked to climate change. Among the promising approaches, biostimulants are attracting growing interest, particularly those derived from natural sources such as seaweed extracts, humic acids, and beneficial microorganisms. These products work through various mechanisms, including osmotic regulation, activation of antioxidant systems, stimulation of root growth, and improvement of nutrient absorption. Many recent research and review articles have explored the optimal combinations of raw materials, formulation processes, target crops, and environmental conditions to maximize beneficial effects on plant growth, soil health, and tolerance to abiotic stresses. As a result, a growing range of commercial products is emerging, with diverse chemical compositions, formulations, and modes of application. However, the precise relationships between the biochemical composition of biostimulants and their physiological effects remain poorly understood, suggesting a key role for molecular synergies. This review provides a concise overview of recent advances in biostimulant research and their potential to enhance food security by improving crop resilience in the context of climate change.

Keywords: biostimulants; food security; climate change; chemical inputs; environmental stress; sustainability



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1. Introduction

In the current situation, the agriculture industry must simultaneously raise crop yields to feed the growing population and optimize resource use efficiency (RUE) while reducing the negative impacts on the environment and human health [1,2]. To do this, it is essential to integrate bio-based opportunities and innovative practices in order to boost crop productivity, improve RUE, and ensure both food security and soil health [3–5]. Using bioproducts like biostimulants could offer a sustainable and effective strategy for promoting bioagriculture [6,7]. Plant biostimulants, as defined by the European Biostimulants Industry Council (EBIC) and subject to regulation (EU) 2019/1009, include substances or micro-organisms

that stimulate natural plant processes to improve nutrient use efficiency, abiotic stress tolerance, crop quality, and nutrient availability in the rhizosphere, without directly resorting to fertilizers or plant protection treatments [6,8]. Plant biostimulants include a wide range of natural or derived substances (humic substances (HSs), protein hydrolysates (PHs), and seaweed extracts (SWEs)), as well as beneficial microorganisms such as arbuscular mycorrhizal fungi (AMF) and plant growth-promoting bacteria (PGPB) [9–12]. Administered by foliar spraying or soil application, in liquid, granular or soluble form, they are considered environmentally safe inputs with low or no toxicity [13–15]. The biostimulants market, which is growing rapidly (10–12% per year), was valued at USD 4.2 billion in 2024 and is expected to grow at a compound annual growth rate (CAGR) of 12.8% between 2030 and 2034 [16]. This review provides a comprehensive analysis of plant biostimulants, categorizing traditional microbial and non-microbial sources while highlighting the critical paradigm shift toward the next generation of biostimulants (NGBs) rooted in precision molecular engineering, nanotechnology, AI-assisted synthetic consortia (SynComs), and RNAi-based applications. The primary objective is to decode the intricate physiological, biochemical, and molecular mechanisms underpinning their action, such as hormonal signaling, nutrient transport, gene regulation, and stress responses. Furthermore, this review evaluates their practical roles in sustainable agronomy, including bio-priming, biofortification, and climate change resilience, while critically addressing current scientific, regulatory, and economic bottlenecks, thereby establishing a strategic roadmap for bio-based precision agriculture.

2. Review Methodology

This narrative review was developed from a systematic search of peer-reviewed scientific literature, covering the period from January 2018 to April 2026. To do this, three international bibliographic databases were surveyed: Scopus, Web of Science Core Collection, and PubMed. Search strategies combined controlled vocabulary (such as MeSH/EMTREE) and free text terms, rigorously organized around four main conceptual axes: biostimulants, their physiological and molecular modes of action, their effects on the rhizosphere and soil microbiota, and crop tolerance to abiotic stresses.

Regarding the inclusion criteria, articles were selected if they met all of the following conditions: they had to be a peer-reviewed primary article, a systematic review, or a reference review. In addition, the subject of the study had to strictly fall within the regulatory definition of a biostimulant as set forth in EU Regulation 2019/1009. The studies also had to report at least one relevant finding related to nutrient use efficiency, abiotic stress tolerance, soil health, crop quality, rhizosphere modulation, or molecular modes of action. Finally, inclusion was restricted to published articles that provided extractable data or conclusions.

Conversely, several strict exclusion criteria were applied to ensure the quality and reliability of the selected sources. We thus discarded preprints not validated by peers, book chapters lacking a DOI, and congress summaries without full text availability, as well as studies exclusively on mineral fertilizers or synthetic pesticides without biostimulant components. Similarly, expert opinions not based on primary data were excluded, as well as duplicates detected by systematic cross-checking between different databases.

For the synthesis of data, the selected literature showed a strong heterogeneity, both in its experimental devices (in vitro, greenhouse, field or meta-analysis) and in the modes of presentation of its results. A narrative synthesis approach was favored. It was structured around eight major thematic areas: typology, mechanisms of action, soil-plant microbiota, bio-priming, biofortification, yield and quality, climate resilience, and finally the reduction in chemical inputs.

Finally, the preparation of the figures was based on the use of dedicated graphic tools. The schematic illustration detailing the action mechanism was generated using

BioRender.com (accessed in February 2026), under an institutional license. The summary figure illustrating the constraints and limits of these technologies was designed using Microsoft PowerPoint (Microsoft 365, version 2402). It should be stressed that all the figures presented in this manuscript are entirely original and do not incorporate any element subject to third party rights.

3. Typology and Biostimulants Classification

3.1. Microbial Biostimulants

Few PGPB are used in a range of formulations, despite their considerable biodiversity [17]. Free-living bacteria from the soil and rhizobacteria, which colonize the rhizosphere, are classified as PGPB and include *Arthrobacter* spp., *Pseudomonas* spp., *Rhodococcus* spp., *Enterobacter* spp., *Ochrobactrum* spp., *Acinetobacter* spp., *Bacillus* spp., *Rhizobium* spp., and *Streptomyces* spp. [18]. Numerous studies have proposed a number of beneficial impacts on plant performance, including enhanced plant nutrition, resistance to (a)biotic stress, and enhanced growth and yield [19–21]. In order to create an environment that is conducive to their growth, they are either used directly on the seed and plant or combined with a carrier material like peat or compost [22,23].

AMF are the most widely used biostimulants and have the ability to form a symbiotic association with plants [24]. *Rhizophagus* species, *Septoglycyus viscosum*, *Claroideoglomus etunicatum*, and *Claroideoglomus claroideum* are examples of this type of biostimulant [25]. The colonization by AMF of the root cortex is responsible for the symbiotic relationship that promotes crop growth [26–28]. While the plant provides the fungi with carbohydrates, the fungi produce hyphae that branch into intraradical hyphae with formations such as arbuscules (exchange platforms) and vesicles (storage units), and extraradical hyphae that attach to the root and enable plant nutrition acquisition [29]. More soil contact for the root is made possible by this hyphae expansion, which is crucial for the uptake of non-mobile nutrients like phosphorus (P) [29]. Also, it has been discovered that several AMF are effective P solubilizers [30]. Future crop output will be significantly impacted by the finding that AMF can work in concert with soil bacteria to optimize the performance of biostimulants to enhance plant growth and restore soil health. Furthermore, fungi of the genus *Trichoderma* are among the most studied and widely used microbial biostimulants in sustainable agriculture. Initially recognized for their biocontrol properties against soil-borne plant pathogens, these filamentous fungi also act as powerful regulators of plant growth. It is important to note that while *Trichoderma* spp. possess dual capabilities, their biocontrol activities against pathogens fall under the regulatory framework of plant protection products in the EU, whereas only their nutritional and abiotic stress tolerance functions are classified as biostimulatory. Their effectiveness is based on active colonization of the rhizosphere, facilitated by the secretion of lytic enzymes and secondary metabolites that modulate root architecture, thereby increasing the exchange surface area for water and nutrients [31]. At the physiological level, inoculation with *Trichoderma* induces metabolic reprogramming in the host plant, including the activation of hormonal signaling pathways (auxins and gibberellins) and the strengthening of antioxidant defense systems. These mechanisms not only improve crop vigor but also increase their resilience to abiotic stresses such as salinity or drought by maintaining cellular homeostasis [31].

3.2. Non-Microbial Biostimulants

3.2.1. Plant Extracts

The most researched and marketed biostimulants are those derived from seaweeds [32]. These macroscopic and multicellular marine algae, belonging to different taxonomic groups such as red (*Rhodophyta*), green (*Chlorophyta*), and brown (*Phaeophyceae*) algae, are rich in

biologically active compounds, including polysaccharides, polyphenols, and various micronutrients [13,18,33]. Recent studies have shown that their beneficial effects on plants are primarily linked to these non-hormonal compounds, which influence plant gene expression, metabolism, and stress tolerance, rather than their hormone content [34].

Besides algae, a growing number of plant-based biostimulants come from terrestrial species, particularly aromatic and medicinal plants (AMP) [35]. Ethanolic extracts derived from *Salvia rosmarinus* L. distillation residues have been shown to combine antifungal, antioxidant, and metal-chelating abilities with biostimulating effects on adventitious rooting [36]. Foliar application of *Rosmarinus officinalis* L. has also been reported to improve shoot and root growth, as well as nutrient content, in *Solanum lycopersicum* L. [35]. Furthermore, foliar applications of *Salvia officinalis* L., and other biostimulants, have shown contrasting responses regarding yield and essential oil composition in organic culture [37].

Extracts of many plant parts such as *Linum usitatissimum* L. and *Artemisia absinthium* L. can be used to obtain some biostimulants [38–40]. These extracts are full of bioactive chemicals that may help plants perform better and be more resilient to environmental stressors [10]. The high concentrations of minerals, carbs, proteins, hormones, amino acids, and antioxidant molecules are linked to this advantageous effect [10,41].

3.2.2. Organic Acids

A major family of bioactive molecules present in plant extracts are the phenolic compounds and tannins [42]. Previous studies have demonstrated that the exogenous application of gallic acid (GA) induces an increase in root length compared to the control and could exert an auxinic-like function [43,44]. In classical rooting studies, GA synergized with naphthalene acetic acid (NAA) and indole-3-butyric acid (IBA) to increase root number in cuttings of *Eranthemum tricolor* L. [45], while ferulic acid significantly increased the formation of adventitious roots in apple micro-cuttings [46]. On a more applied scale, chestnut tannin extracts—rich in gallic and ellagic acids—such as HyTan, have been validated as effective biostimulants for the nursery production of high-quality vine planting material. [47]. In addition, tannin hydrolysates in general showed a biostimulating effect with a low concentration of GA [42].

Humic substances are another type of biostimulant. They are the primary organic constituents of soil, lignites and peat, and consist of humic and fulvic acids [33,48]. These substances are macromolecules that have hydrophilic and hydrophobic parts. They are produced when small molecules associate during plant or animal decomposition or when soil microbes engage in metabolic activity [38,49].

Proteins from various matrices, such as plant or animal, can be hydrolyzed chemically, thermally or enzymatically to produce a combination of amino acids, polypeptides, and oligopeptides [32]. Protein hydrolysates made from industrial and agricultural waste are becoming more and more appreciated since they are an environmentally responsible and alternative choice to deal with a variety of wastes and support a circular economy [3]. Animal-derived proteins make up the majority of commercially available PH biostimulants [50].

3.2.3. Inorganic Substances

Inorganic substances can be combined with one another or with organic biostimulants to produce synergistic effects, particularly in cases of abiotic stress. The combined application of silicon (Si) and selenium (Se) illustrates this synergy: Si improves root architecture and salinity tolerance, while Se, at low doses, enhances antioxidant defense, with both elements acting on complementary pathways of the stress response [51,52]. Similarly, the co-application of titanium dioxide (TiO₂) nanoparticles with plant extracts (e.g., PH)

potentiates the stimulation of photosynthesis and nitrogen use efficiency (NUE), giving a higher response than that of each component applied alone [53]. These combinatorial strategies pave the way for multi-component formulation protocols, in which the overall biostimulating effect exceeds the sum of individual effects, a phenomenon documented for several pairs of inorganic and organic elements [54].

Besides TiO₂, zinc oxide (ZnO) nanoparticles are an emerging category of inorganic nano-biostimulants, with particular interest due to the dual role of Zn as an essential nutrient (structural component of more than 300 enzymes, including superoxide dismutase Cu/Zn-SOD) and as a stress modulator. A comparative study in tomatoes (*Solanum lycopersicum* L.) showed that ZnO nanoparticles exert marked biostimulatory effects on germination, biomass accumulation, and physiological parameters, however with a narrow concentration window between the promoter effect and phytotoxicity—a hormetic effect shared with TiO₂ [55]. For instance, ZnO nanoparticles at 10–20 mg.L^{−1} stimulated root growth and biomass accumulation, while ≥100 mg.L^{−1} concentrations induced measurable oxidative stress and reduced elongation [55]. These data position ZnO as a second-generation nano-inorganic biostimulant, with significant potential for Zn biofortification in cereal crops [53,56].

The increasing use of inorganic substances as biostimulants raises several methodological and regulatory questions that structure research perspectives. First, the hormetic principle requires a rigorous characterization of the dose-response window for each species and each pedo-climatic condition, because the same substance can be biostimulating or phytotoxic depending on variations in concentration of an order of magnitude [53]. Secondly, the European regulatory framework remains evolving: Regulation EU 2019/1009 now integrates microbial and non-microbial biostimulants into a single functional category (stimulation of nutrition processes), but the nano-biostimulants are not yet explicitly treated, which creates an area of legal uncertainty for marketing [56]. Thirdly, field-scale data remain limited compared to data in controlled conditions, and the extrapolation of laboratory results to commercial agriculture requires multi-local and multi-annual trials [52]. Finally, the life cycle analysis of nano-formulations (production, application, environmental fate) should be integrated into future assessments to ensure that the development of these biostimulants is part of an effectively sustainable trajectory [56].

3.3. Next Generation of Biostimulants

The transition to the next generation of biostimulants (NGBs) marks the shift from an approach based on raw natural extracts to high-precision molecular engineering [57]. Unlike conventional formulations whose composition is subject to seasonal variability, NGBs rely on the isolation of pure signal molecules, such as bioactive polyamines which act at micromolar concentrations [58,59]. These elicitors target highly specific membrane receptors (notably LysM domain receptors), triggering phosphorylation cascades that prepare the plant for stress without inducing significant energy “fitness cost” [60,61]. Transcriptomic analysis confirms today that these molecules activate regulatory gene networks dedicated to hydric resilience, rather than a simple disordered metabolic stimulation [62].

The integration of nanotechnology constitutes one of the major pillars of this evolution via nano-biostimulants [59]. These systems employ bio-based nanocarriers, such as mesoporous silica, nano-chitosan or nanoliposomes, to protect the active ingredients against photodegradation and premature leaching [63–65]. Thanks to their small size, these vectors penetrate the hydrophobic barriers of the leaf cuticle more effectively, ensuring rapid systemic translocation to the sink organs (or targets) via the phloem [66]. New “smart” release devices now allow releasing compounds only in response to specific environmental stimuli,

such as a change in rhizospheric pH or an increase in the concentration of free radicals in tissues [67].

Another breakthrough innovation is the design of synthetic microbial consortia (SynComs) from the *Brachypodium distachyon* L. rhizosphere assisted by artificial intelligence (AI) [68]. Unlike traditional single-strain inoculants, SynComs are assembled to maximize functional complementarity and ecological stability within the rhizosphere [69]. AI here is mobilized to model metabolic fluxes and quorum sensing between species, ensuring that the consortium resists competition from indigenous microflora [68]. These precision communities coordinate the secretion of siderophores and 1-aminocyclopropane-1-carboxylate (ACC)-deaminase, thus neutralizing the deleterious ethylene (ET) peaks produced by the plant under abiotic stress conditions [70].

Finally, the emergence of interfering RNA (RNAi)-based biostimulants represents the ultimate frontier of biotechnological specificity [68]. Applied by spraying, these short-acting biostimulants allow temporary gene silencing of specific targets, such as genes from the NAC or MYB family involved in early senescence or salt sensitivity [71]. By acting on phenotypic plasticity without permanently altering the genome, they offer a flexible solution to adapt crops to climate fluctuations in real time [72]. This synergy between chemical elicitors and epigenetic regulation tools now defines the new standard of precision agriculture [62]. The MYB family is one of the largest transcription-factor (TF) families in plants, characterized by a conserved N-terminal MYB domain consisting of imperfect amino acid repeats of approximately 52 residues; based on the number and position of these repeats, MYB proteins are subdivided into four subfamilies (1R-, R2R3-, 3R-, and 4R-MYB), of which the R2R3-MYB group is the most expansive and functionally diverse [73,74]. MYB proteins generate diverse stress responses through several interconnected pathways and have emerged as central regulators of plant defense against bacterial, viral, and fungal pathogens, as well as against insect herbivores [73,74]. Within this family, the *Chrysanthemum* R2R3-MYB (CmMYB15) is induced by aphids (a model insect pest system) and binds directly to AC cis-elements that typify the promoters of lignin-biosynthesis genes; overexpression of CmMYB15 in *Chrysanthemum morifolium* L. enhances aphid resistance with simultaneous increases in lignin content and expression of several lignin-biosynthesis genes [75]. Multiple monocot and dicot orthologues extend this MYB15-defense module across evolutionary distances: in soybean, the related TF GsMYB15 enhances resistance to *Helicoverpa armigera* L. in transgenic Arabidopsis; in rice, OsMYB30 regulates the expression of OsPALs (phenylalanine ammonia-lyases) to confer brown planthopper resistance; and transcriptome analysis of the related ornamental *Camellia sasanqua* L. in response to scale insect infestation reveals activation of a MYB15-like flavonoid biosynthetic module, supporting the conservation of a MYB15-pest-defense hub across Asteridae and Theaceae [75,76]. The historical link between MYB TFs and salicylate-mediated defense was established with the isolation of the tobacco *myb1* gene, identified as a signaling component downstream of salicylic acid (SA) that participates in transcriptional activation of PR genes and consequently plant disease resistance, establishing MYB as part of the canonical SA-MYB-PR defense axis in plants [77]. For RNAi-based next generation biostimulants, MYB family members and especially MYB15-like orthologues constitute a complementary actionable target to NAC: transient silencing of MYB repressors of lignin biosynthesis amplifies cell wall reinforcement (anti-pest priming), while transient silencing of MYB repressors of abiotic stress tolerance (in conjunction with NAC silencing) supports a coordinated, dual-axis resilience strategy without the energetic cost of constitutive transgene expression.

4. Mechanisms Underlying Biostimulant Action

Biostimulants act through a variety of physiological, biochemical and molecular changes that give plants better growth, efficient use of resources and increased resilience to environmental stresses (Figure 1). Unlike conventional fertilizers, which directly supply nutrients, biostimulants modulate plant metabolism and stimulate beneficial interactions with the soil and rhizosphere. Microorganisms that solubilize nutrients, such as *Bacillus*, *Pseudomonas*, *Aspergillus*, *Rhizobium*, *Azotobacter*, *Azospirillum*, and AMF, mobilize phosphorus, nitrogen, and iron through the secretion of organic acids, phosphatases and siderophores, or through symbiotic fixation, improving crop development, such as in alfalfa, corn, rice, wheat, and oilseeds [11,30,78–80]. Non-microbial biostimulants induce positive regulation of photosynthesis, carbon metabolism, and water absorption by activating Rubisco, aquaporins, and antioxidant enzymes and regulating hormone genes, while regulating abscisic acid (ABA), auxin, cytokinin, and jasmonate pathways, which induces the synthesis of stress proteins such as heat stress proteins (HSPs) and thereby enhances tolerance to abiotic stress [81,82]. Others act as ‘primers’ by preparing the plant to respond more quickly and effectively to future abiotic stresses, reinforcing the concept of resilience [83]. In short, the functional diversity of biostimulants stems from the complementary nature of their modes of action. Non-microbial substances, such as algal extracts and composts, provide mineral elements, organic matter, and essential signaling molecules (notably betaines and polysaccharides), while microbial inoculants—including PGPB and AMF—act as true biological catalysts. The latter stimulate plants’ intrinsic ability to access soil resources, optimize nutrient use efficiency, and enhance tolerance to biotic and abiotic stresses. Harnessing these synergies serves as a strategic lever for the transition to sustainable agriculture, ensuring stable yields while streamlining the use of synthetic inputs.

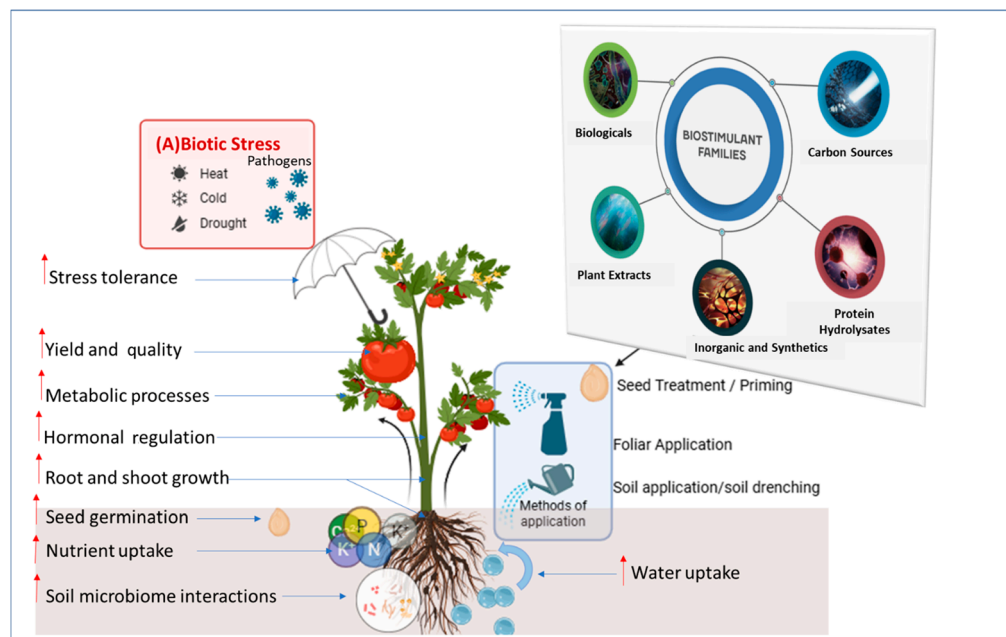


Figure 1. Conceptual diagram of the mechanisms of biostimulant actions.

5. Roles of Biostimulants in Sustainable Agriculture

5.1. Restoring and Maintaining Soil Structure and Quality

The effectiveness of microbial biostimulants relies on complex bidirectional molecular communication within the rhizosphere, transforming the physiology of the host plant through precise biochemical and genetic levers.

PGPB, such as strains of *Bacillus velezensis* and *Pseudomonas fluorescens*, act primarily by modulating the hormone balance of the plant. They secrete exogenous indole-3-acetic acid (IAA), which interferes with the root's auxin transporters (PIN proteins), causing inhibition of the primary root in favor of a massive proliferation of lateral roots and root hairs [69,84]. This mechanism, coupled with the production of ACC-deaminase, reduces ethylene (ET) levels induced by stress in the plant, thus preventing premature cessation of root growth under drought or salinity conditions [85]. A recent transcriptomic study confirmed that this microbial signaling activates the *expansin* (*EXP*) and *xyloglucan endotransglucosylase hydrolase* (*XTH*) genes, increasing the extensibility of root cell walls [86].

AMF create a symbiosis where extra-matrix hyphae explore a volume of soil greater than that accessible by roots alone [87]. Beyond this physical extension, the key molecular mechanism lies in the induction of high-affinity phosphate transporters (*PT* genes) and ammonium transporters (*AMT* genes) specifically expressed in the peri-arbuscular interface [88]. Indeed, it has been demonstrated that this symbiosis also regulates the genes of the *aquaporin* family (*TIP* and *PIP*), optimizing the hydraulic flow between the fungus and the plant cell, which allows the host to maintain stable stomatal conductance even under very low soil water potential [89,90].

A crucial mechanism of action of microbial biostimulants is induced systemic resistance (ISR). However, from a regulatory standpoint in the EU and many other countries, when microorganisms trigger ISR to protect against pathogens (biotic stress), they are considered plant protection products or plant strengtheners rather than biostimulants, as the latter are legally restricted to abiotic stress tolerance. Nevertheless, from a biological perspective, PGPB prepare the plant ("priming") by modulating signaling pathways of ET and jasmonic acid (JA) [91]. This molecular "priming" results in an increased accumulation of antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT), and ascorbate peroxidase (APX) under salt stress [92]. Omics studies show that this process is mediated by epigenetic changes, notably histone acetylation at promoter sites of defense genes, allowing a faster and more robust transcriptional response during environmental attacks [93,94].

Microbial species act chemically in the rhizospheric zone through the excretion of organic acids (citric acid, gluconic acid) that lower the local pH, thereby releasing complexed P and Fe [95]. The production of high-affinity siderophores by SynComs bacteria (synthetic consortia) ensures exclusive bioavailability of Fe for the host plant, limiting the growth of competitive microorganisms [96]. In addition, the secretion of volatile organic compounds (VOCs), such as 2,3-butanediol, acts as a long-range gaseous signal capable of stimulating stomata closure through the ABA pathway during a thermal shock [62,84].

5.2. Enhancing Root Growth and Nutrient Uptake

Biostimulants play a fundamental role in the optimization of the root–soil interface, acting both on the physical structure of the plant and on its physiological assimilation capacities [97,98]. One of the most documented effects is the modification of the root system architecture, characterized by an increase in root length, density and branching [4,99]. For example, extracts of brown algae, such as *Ascophyllum nodosum* and *Duvallea potatorum*, have demonstrated their ability to significantly increase root mass and root hair density, enabling a broader exploration of soil volume [4]. In the same way, abundant HSs are linked to increased radical system volume, favoring thus better water and nutrient collecting [100].

The improvement of nutrient absorption by biostimulants is not limited to a simple physical extension of the roots; it also relies on complex molecular and biochemical mechanisms [101]. Biostimulants, notably humic acids, can induce positive regulation of genes involved in nutrient transport. These substances have been shown to activate mineral nitrogen transport genes (such as *BnNRT1.1* and *BnNRT2.1*) in species like oilseed rape

(*Brassica napus*) [101]. The application of PHs and algae extracts stimulates the activity of key metabolism enzymes, such as nitrate reductase, which accelerates nitrogen assimilation once absorbed [102]. Some biostimulants improve nutrient availability by altering the physico-chemical properties of soil, for example, by increasing cation exchange capacity (CEC) or forming chelated complexes with trace elements (such as Fe), thus making them available to the plant [102,103]. Microbial biostimulants, such as fungi of the genus *Trichoderma*, promote root growth through the secretion of auxin-like compounds, increasing root biomass by up to 35% under optimal conditions and 43% under drought conditions [101].

By promoting a “nutrient acquisition response”, these biostimulants improve RUE, which is crucial for maintaining high yields while reducing dependency on synthetic mineral fertilizers [4,97]. This synergy between increasing the root exchange surface and activating molecular transport pathways allows for more vigorous and resilient crops in the face of nutritional deficiencies [98].

5.3. Enhancing Soil and Plant Microbiomes

The application of biostimulants induces profound changes in the agroecosystem by restoring the overall health of the soil and finely modulating the rhizospheric microbiome [104,105]. These products act as elicitors of biological and physical fertility through three complementary levers: the conditioning of the organic matrix, the prebiotic effect, and the activation of ecosystem functions.

5.3.1. Restoration of the Physical and Chemical Properties of Soil

Non-microbial biostimulants, such as HSs and algae extracts, function as true soil conditioners. HSs promote primary particle aggregation by optimizing porosity and structural stability [97,106]. At the same time, sulfated polysaccharide carrageenan from algae act as hydrophilic colloids capable of absorbing and retaining moisture [107]. This improvement in water retention capacity is crucial for maintaining the enzyme activity and functional diversity of microorganisms, particularly during severe water stress [108,109]. On the chemical level, the increase in CEC and pH regulation induced by humic acids facilitate P solubilization and prevent leaching of essential trace elements. [97,104].

5.3.2. Prebiotic Effect and Selective Recruitment of the Microbiome

A major advance in research highlights that some biostimulants function as “prebiotics”, providing specific carbon sources that selectively stimulate beneficial indigenous populations [104,110]. The contribution of these compounds can improve the carbonated microbial biomass [111]. Kinetic studies show that after seven weeks of application, the taxonomic richness of active fungi and saprophytic bacteria significantly increases, promoting effective decomposition of organic matter [107,111]. This recruitment targets pivot genera such as *Bacillus* and *Pseudomonas* [112]; algae extracts have been shown to increase the colonial counts of *B. subtilis* and *B. licheniformis*, which enhances the systemic protection of the host [113]. Furthermore, the increase in the ratio of fungi/bacteria induced by certain commercial prebiotics signals increased ecological stability and optimized mineralization of crop residues [104,110].

5.3.3. Enzyme Activation and Ecosystem Services

Beyond taxonomic restructuring, biostimulants exacerbate soil functional activity. They act on biogeochemical cycles by boosting the enzymatic activities related to carbon, nitrogen, and phosphorus [110]. This preferential recruitment of decomposing microorganisms accelerates the transformation of organic matter into nutrients directly assimilable by the plant, thus reducing dependency on synthetic inputs [107,111]. In conclusion, by transforming the rhizosphere into a dynamic and resilient environment, biostimulants sus-

tainably support plant productivity while preserving the physical and biological integrity of the soil [105,106].

5.4. Bio-Priming

Seed priming is a crucial pre-seeding strategy, consisting of controlled hydration that activates germinal metabolism without inducing the emergence of radicles [114]. The integration of biostimulants into this protocol, referred to as ‘bio-priming’, catalyzes plantlet vigor and emergence uniformity, particularly under severe environmental constraints [115,116].

5.4.1. Physiological Mechanisms and Biochemical Rearrangements

The effectiveness of bio-priming relies on an orchestration of fundamental cellular transformations. At the structural level, biostimulant-assisted imbibition facilitates the transition of cell membranes from a hexagonal state (characteristic of dry seed) to a stable lamellar state, an essential reorganization to secure the membrane integrity and accelerate post-seeding emergence [117]. Metabolically, these agents restore oxidative homeostasis and trigger the expression of genes encoding key enzymes, notably, isocitrate lyase, a pivotal enzyme in the glyoxylate cycle, essential for the mobilization of lipid reserves supporting initial heterotrophic growth [118]. This dynamic is finely regulated by a hormonal modulation where biostimulants rebalance the ABA/gibberellin ratio, thus lifting dormancy signals to the benefit of growth pathways [116,118].

5.4.2. Increasing Resilience and ‘Boot Memory’ Concept

One of the major contributions of biostimulants is the establishment of a ‘priming memory’, a pre-activated physiological state allowing the seed to recruit its defense mechanisms with increased kinetics during subsequent exposures to abiotic stresses [115]. This phenomenon of molecular preparation is particularly effective for salt stress tolerance: the application of flavonoids or algae extracts during priming strengthens resilience to salinity via optimized regulation of ion transporters and drastic mitigation of oxidative damage [115,118]. At the same time, microbial biopriming, using PGPB, combines intrinsic physiological seed improvement with early rhizospheric colonization. This synergy establishes sustainable biological protection from the early stages of development, securing the ecological niche of the seedling [116].

Bio-priming transforms the seed into a high-performance biological unit, capable of dynamically adapting to climate fluctuations. This technique now constitutes a pillar of productivity in sustainable agriculture, ensuring robust cultivation in physically or chemically hostile soils [114,117].

5.5. Biofortification

Biofortification, defined as the improvement of the nutritional quality of crops through agronomic practices, selection and/or biotechnology [119], finds in the use of biostimulants a particularly promising agronomic approach. These agents increase the content and bioavailability of essential minerals in edible parts, thus addressing public health challenges related to micronutrient deficiencies [120,121]. The effectiveness of this strategy is based on a synergy between physiological levers, notably an increased translocation of microelements such as Fe and Zn to grains, stimulated by compounds derived from amino acids [121]. At the same time, HSs and algae extracts operate as natural chelating agents, keeping metals in a soluble and assimilable form, even in constraining limestone soils [102,122]. Moreover, the combined application of biostimulants with mineral fertilizers, such as Zn sulfate associated with inositol, generates synergistic effects that maximize the final mineral concentration compared to isolated fertilization [123].

Beyond mineral enrichment, biostimulants modulate the secondary metabolism of plants, generating foods with high nutritional and functional added value [123,124]. Their application is correlated with a significant increase in the contents of vitamin C, phenolic compounds, and antioxidants, while favorably influencing the profile of amino acids and sugars, which optimizes the organoleptic properties of crops [121,125]. Microbial biostimulants, such as AMF, also play a pivotal role in extending the root absorption surface and activating Zn-specific transporters [120]. Moreover, the integration of these agents into technical practices allows target nutrient levels to be increased by up to 15 times for Se while optimizing the efficiency of exogenous inputs, making biofortification assisted by biostimulants a pillar of nutritional security and sustainable agriculture [121,124].

5.6. Increasing Crop Yield and Quality

One of the main advantages of biostimulants resides in their ability to simultaneously increase the quantitative yield and qualitative value of crops, thus forming part of a sustainable agriculture approach [97,98]. Unlike conventional fertilizers that mainly target biomass, these agents act on physiological processes to optimize the genetic potential of the plant [4]. This increase in productivity does not result from a simple vegetative growth, but from better resource use efficiency and better stimulation of flowering and fruit-setting [98,103]. For instance, a study on cherry tomatoes has shown that the application of animal PHs stimulates flowering and root development, leading to a direct increase in marketable yield [103]. In arboriculture, particularly for organic apples, the use of biostimulants leads to stabilizing the annual yield by improving the tree's vigor and optimizing fruit abundance, thus reducing production fluctuations from one year to another [102].

Alongside yield, the quality of harvested products is a determining factor of their commercial value and of consumer health [98]. Biostimulants positively influence organoleptic and biochemical characteristics by increasing the total soluble solids content (Brix degrees), titratable acidity, and concentration of antioxidant compounds such as polyphenols and flavonoids [98,102]. These modifications improve not only the taste but also the nutritional value of the products [125]. In addition, these treatments prolong the post-harvest shelf life by strengthening the cell wall structure and delaying senescence processes, maintaining for example, a better firmness of apple pulp during storage [102].

The sustainable nature of this kind of productivity is based on a synergy between the plant and its environment. By improving nutritional efficiency, biostimulants help maintain high yields while reducing mineral fertilizer inputs, thus limiting the environmental footprint of chemical inputs [4,97]. This systemic resilience, often coupled with better resistance to abiotic stresses, ensures production security in the face of increasing climatic hazards [97,99]. In summary, the integration of biostimulants into fertilization programs allows for optimal productivity, characterized by more nutritious and homogeneous harvests, while sustainably preserving the integrity of natural resources [97,98].

5.7. Improving Resilience to Climate Change

Climate change increases the frequency and severity of abiotic stresses, such as drought, salinity and extreme temperatures, threatening to reduce global yields by nearly 50% [99,126]. In this context, biostimulants act as proactive protective agents. Unlike curative chemical interventions, they activate intrinsic plant defensive mechanisms before stress becomes irreversible [127].

One of the key mechanisms lies in the modulation of oxidative homeostasis. Under thermal or water stress, plants accumulate reactive oxygen species (ROS) that damage ADN, proteins, and membranes [99]. The application of biostimulants, such as algae extracts and humic acids, stimulates the production of anti-ROS enzymes such as SOD, CAT, and

APX [127,128]. At the same time, these substances promote the accumulation of protective osmolytes such as proline and soluble sugars, which maintains the turgor potential and water use efficiency under conditions of severe water deficit [127].

At the physiological level, biostimulants optimize stomatic regulation through the ABA pathway, by limiting losses via transpiration while preserving photosynthetic activity [127]. It has been demonstrated that brown algae extracts (e.g., *Ascophyllum nodosum*) help the plant to “memorize” stress episodes (priming phenomenon), allowing it to react more quickly and robustly during subsequent exposures to heat or drought [127]. This increased resilience is essential to stabilize agricultural production in vulnerable areas [127].

5.8. Reducing Dependence on Chemical Inputs

The transition to sustainable agriculture requires a drastic reduction in the chemical footprint, both in fertilizers and in pesticides [129]. Biostimulants offer a strategic solution by improving the nutrient use efficiency of macro- and microelements [130,131]. By optimizing the root architecture, specifically by increasing the density of lateral roots and root hairs, a larger volume of soil is being explored and nutrients that are otherwise immobile, such as P, are being captured [4,128]. Biochemically, some biostimulants such as HSs stimulate the activity of plasma membrane H^+ -ATPases, a process that generates an electrochemical gradient that facilitates the active transport of nitrates and other ions into plant cells [132]. This allows yields to be maintained while reducing the nitrogen and phosphorus doses applied, limiting nitrate leaching towards groundwater and decreasing greenhouse gas emissions [129,130]. With regard to crop protection, biostimulants act analogously to “probiotics” or “vitamins” for plants [133].

5.9. Biostimulants in Hydroponic Cultivation Systems

Conventional soil-based agriculture is increasingly exposed to compound pressures such as opportunistic soil-borne pathogens, climate-driven shifts in precipitation and temperature regimes, progressive land degradation, water scarcity, and disruptions to fertilizer and agrochemical supply chains linked to geopolitical instability and trade restrictions [13,99,134]. Hydroponic cultivation systems (including various forms like floating rafts, the nutrient film technique (NFT), deep flow technique (DFT), and drip systems, as well as aeroponics and aquaponics) have undergone rapid expansion worldwide as a response to these challenges [135]. Different biostimulant categories have been actively deployed in these cultivation systems [57,100,136,137]. Because hydroponic systems isolate the plant from native soil microbiota and from soil chemical buffering, they offer an idealized experimental framework for biostimulant testing while simultaneously emerging as a fast-growing commercial application segment. Projected to have an annual growth rate of 12–12.4%, the global biostimulant market counts the hydroponic segment among its most dynamic frontiers, with SWEs, PHs, and microbial inoculants representing the dominant sub-categories [136–138]. Conversely, hydroponic systems also constrain the modes of action available: products that act through soil aggregation, cation bridging, or soil-microbe recruitment (notably HSs when applied as soil conditioners and whole-soil microbial products) have a structurally reduced role in inert substrates, while foliar uptake and direct root-zone signaling become dominant pathways [99,139].

Among non-microbial biostimulants applied in hydroponics, PHs are by far the most documented category. In hydroponic *Lactuca sativa* L. supplied at four nitrogen levels (2, 5, 10, and 15 mM), weekly root drench application of a plant-derived PHs (3 g.L^{−1}) markedly enhanced shoot dry weight, marketable yield, chlorophyll content, antioxidant activities, and nitrogen-use efficiency, regardless of nitrogen level, with root application outperforming foliar spray [140]. In NFT-grown lettuce, fish-derived PHs applied as a substrate drench

significantly increased leaf number, stem diameter, shoot fresh and dry weight, root dry weight, relative water content, chlorophyll content, photosynthetic rate, stomatal conductance, and transpiration rate, without altering chlorophyll fluorescence [141]. In floating raft *Ocimum basilicum* L. ‘Genovese’, biostimulatory action of vegetal PHs compensated for reduced nutrient strength [142], while in *Diplotaxis* (rocket), trialed under NaCl-induced salt stress, a PH root-promoting biostimulant restored yield in both wild and cultivated genotypes [143]. Beyond mineral nutrition, PHs characterized by a high concentration of free amino acids dramatically limited phloem loading of organic nitrogen, thus preventing excessive root NO_3^- uptake and accumulation [144–146]. Counter-evidence in baby-leaf spinach shows that the same PH produces qualitatively opposite effects depending on nitrogen dose and source, and in glasshouse soilless strawberry under 50% deficit irrigation, *Hicure* and *Vitalnova TriBoost*® significantly improved stomatal conductance but yielded significant fruit-weight gains only in ‘Malwina’, not in ‘Loren’. Both sets of findings emphasize cultivar $\times$ dose $\times$ system specificity as the rule rather than the exception [146–148]. A complementary study on hempseed press-cake-derived PHs applied foliarly to red oak lettuce confirmed source dependence [147].

Three other biostimulant categories have documented activity in soilless systems. SWE from brown macroalgae (*Ascophyllum nodosum*, *Ecklonia maxima*, *Laminaria* spp.), supplying polysaccharides, polyphenols, and phytohormones, improved biomass accumulation, leaf expansion, stomatal conductance and water/nitrogen use efficiency in hydroponic leaf lettuce, with preharvest *E. maxima* at 2 mL.L⁻¹ delaying senescence of fresh-cut leaves during 21 days of cold storage; the same *E. maxima* combined with Se biofortification improved growth, soluble solids, and drought stress tolerance in soilless chicory [136,148,149]. However, two different commercial *A. nodosum* products dysregulated 4.47% vs. 0.87% of the Arabidopsis transcriptome, respectively, demonstrating that choice of commercial product may have a significant effect on plant responses [150,151]. Microbial inoculants (PGPR: *Bacillus*, *Pseudomonas*, *Azospirillum*; AMF: *Trichoderma* spp.) function in soilless systems through direct root-colonization, biofilm formation, and production of soluble secondary metabolites in the recirculating nutrient solution. In hydroponic lettuce under NaCl-induced alkaline/saline stress, simultaneous supply of a microbial-based biostimulant (*Rhizophagus irregularis* BEG72 + *Trichoderma atroviride* MUCL45632) and a plant-derived PH reduced the Na⁺ hyperaccumulation (+290% in stressed controls) and restored N, P, K and Fe homeostasis [152,153]; the synergistic effect is consistent across multiple vegetable crops under salinity stress [13,154,155]. In *Trichoderma* spp.-supplemented hydroponic Pac Choi, *Bacillus amyloliquefaciens* showed promise in NFT and deep water culture (DWC) systems, whereas *Trichoderma* negatively affected NUE, establishing that *Trichoderma* may not be recommended for hydroponic production [156]. In floating-root lettuce, *Trichoderma asperellum* strains significantly increased plant height (+19%), root length (+25.7%), total fresh biomass (+76.4%), and dry biomass (+82.63%), while reducing nitrate content by 24.94% [157]; in DWC spinach, *T. asperellum* TaMFP1 improved yield, leaf area, and P/Ca uptake [157]. HSs and chitosan complete the picture: in hydroponic lettuce, HSs combined with a microbial inoculum improved productivity, nutrient uptake, and primary/secondary metabolism through H⁺-ATPase and NADPH-oxidase activation [158,159], and humic acid improved growth and nutrient uptake in hydroponic *Cannabis sativa* L. [160]; chitosan treatment (0.01–1%) significantly increased phenolic and terpenic compound accumulation in sweet basil (rosmarinic acid and eugenol increased 2.5 $\times$ and 2 $\times$, respectively; DPPH antioxidant activity was at least 3.5-fold higher, CAT increased 32-fold at 0.5% chitosan; plant height and weight increased 17% and 12%, respectively) [161]; chitosan nanoparticles increased lettuce yield by 24.6%, total phenols by 31.2%, and antioxidant capacity by 34.6% [162]; chitosan increased antiradical activity of rocket by 12.7% at 300 ppm [163],

and chitosan at 0.6% was optimal for basil microgreens [164]. Silicon supplementation represents a final emerging category: although omission of Si from solution cultures may lead to distorted results in inorganic plant nutrition studies [165], Si remains functionally comparable to a biostimulant under stress, where it accumulates beneath the cuticle, potentiates phenylpropanoid/terpenoid pathways, and modulates hormonal networks and osmotic balance [166–169].

6. Molecular Modes of Action of Biostimulants

6.1. Improvement of the Structure and Activity of Soil and Plant Microbiomes

Biostimulants exert a multidimensional influence on the agroecosystem, with effects that critically depend on the mode of application. When applied directly to the soil matrix (soil drench, fertigation, or incorporation), certain biostimulant categories, namely humic and fulvic acids, microbial inoculants producing exopolysaccharides, and PHs, can contribute to improving soil porosity, filtration, and water retention capacity by modifying soil physical properties and orchestrating molecular communication within the rhizosphere [109]. This action begins with an optimization of the soil structure: the application of these agents improves porosity, filtration and water retention capacity, thus creating a physical environment favorable to biological activity [128]. In addition to this physical conditioning, biostimulants act as regulators of the chemical dialogue between the plant and the soil. They influence the production of root exudates that serve as molecular signals for the selective recruitment of beneficial microbial communities, which are capable of specifically metabolizing these compounds to promote plant growth [170].

This molecular communication within the soil–microbe–plant continuum relies on complex signaling where microbial biostimulants, such as rhizobacteria and mycorrhizal fungi, exploit these pathways to optimize nutrient solubilization and osmotic adjustment, consequently strengthening the overall resilience of the host [84,171]. Metagenomic analyses confirm that these products do not simply edit taxonomic diversity, but actively stimulate the metabolic functions of the microbiome essential for crop sustainability [171]. By integrating these chemical and physical feedback mechanisms, biostimulants transform the rhizosphere into a dynamic ecological niche rich in resilient actors and capable of supporting productivity under numerous environmental constraints.

6.2. Hormonal Regulation and Signaling

The control of hormonal status represents a major molecular lever through which biostimulants orchestrate plant development and resilience against environmental aggressions. This mechanism initially operates through a direct intake and modulation of phytohormones: many microbial biostimulants synthesize and release growth regulators, such as auxins, cytokinins, and gibberellins, which dictate cell division and elongation [106]. These exogenous substances remodel the root architecture, significantly increasing the exchange surface and efficiency of water and mineral absorption [128].

Besides this external input, biostimulants act as elicitors capable of inducing the *de novo* synthesis of endogenous hormones in the treated plant [172]. Bioactive compounds such as amino acids, polysaccharides, and certain organic acids function as metabolic precursors or specific activators of hormone signaling pathways [172]. This complex interaction between biostimulating molecules and the plant hormonal machinery leads to profound changes in gene expression [173]. For instance, HSs manipulate root signaling networks and genes dedicated to nitrogen assimilation, therefore optimizing the use of N resources [132]. These transcriptional regulations also allow the mobilization of antioxidant defense systems, mitigating oxidative damage and enhancing cell survival in the face of abiotic stresses [173].

6.3. Improvement of Nutrient and Water Absorption and Transport

Optimizing nutrient and water use efficiency is one of the fundamental roles of biostimulants, allowing productivity to be maintained even under conditions of limited availability [129,130]. This process relies on a synergy between structural modifications and molecular regulations. In the foreground, the remodeling of root architecture induced by HSs and algae extracts plays a decisive role; these compounds either act as analogues of auxin or stimulate its endogenous production [4,128]. This results in a significant increase in the density of lateral roots and root hairs, extending the total exchange surface area and allowing the plant to explore a larger soil volume to capture less mobile nutrients like P [4].

At the molecular level, biostimulants regulate the expression of gene families involved in active transport, notably nitrate (NRT) and phosphate (PHT) transporters [130,132]. A key mechanism identified is the stimulation of plasma membrane H^+ -ATPase activity, generating an electrochemical gradient that promotes ion flux across cell membranes, as already mentioned [132]. At the same time, to optimize water status, these agents promote the accumulation of compatible osmolytes such as proline and soluble sugars [127]. These molecules lower the cellular water potential without disrupting metabolism, allowing the maintenance of turgescence during periods of drought [127].

This support is amplified by microbial symbioses, notably via AMF that physically extend the root system through their network of hyphae, thus accessing resources located beyond the root depletion zone [128,171]. In turn, these microorganisms facilitate the solubilization of complexed minerals in the soil via the secretion of organic acids, making the nutrients directly bioavailable to the host [128]. All of these convergent mechanisms make it possible to reduce input losses through leaching and significantly improve the environmental sustainability of cropping systems [129,130].

6.4. Improvement of Growth and Photosynthesis

The action of biostimulants on plant productivity transcends the simple supply of nutrients; they act as real metabolic regulators that optimize energy use and the synthesis of high value-added compounds [106,172,174]. This stimulation of primary growth is orchestrated by hormonal regulation, where algae extracts and microbial inoculants provide analogs of phytohormones or stimulate their endogenous synthesis. Cytokinins thus promote cell division and delay leaf senescence, while auxins and gibberellins activate tissue elongation and mobilization of reserves, increasing the light interception surface [175,176]. Biostimulants trigger the biosynthesis of chlorophyll and carotenoids, which translates into higher SPAD indexes [4,177]. At the enzymatic level, the application of humic substances can increase the activity of Rubisco by up to 70%, optimizing CO_2 fixation [178]. This is coupled with an improvement in stomatal conductance and electron transport in photosystem II, allowing high net photosynthesis to be maintained under extreme hydric stress [179].

Beyond quantitative yield, biostimulants act as bio-enrichment agents by promoting the accumulation of macro- and microelements (nitrogen, phosphorus, iron, zinc, potassium) in edible tissues [132,180]. They control secondary metabolism via the phenylpropanoid pathway to induce an accumulation of bioactive compounds such as total phenols, flavonoids, and vitamin C [4,119]. This enhancement of antioxidant potential not only improves the nutritional value for the consumer, but also extends the post-harvest shelf life of products [181]. In sum, this synergy between optimized energy capture and rigorous metabolic management allows for more productive and higher quality crops [180].

6.5. Strengthening of Defenses and Stress Tolerance

Strengthening defenses and stress tolerance constitute one of the most critical roles of biostimulants in modern agriculture, offering a concrete response to the resurgence of

climatic hazards and pathogenic pressures [52,82]. Unlike conventional approaches, these agents act as elicitors that activate the plant's intrinsic defense mechanisms, transforming its physiology for increased resilience [99,182].

In the face of abiotic stresses such as drought and/or salinity, biostimulants intervene via several fundamental biochemical levers. They first stabilize oxidative homeostasis by stimulating the activity of key enzymes, which allows neutralizing ROS and limiting membrane damage [183,184]. At the same time, they promote effective osmotic adjustment through the accumulation of compatible osmolytes, thus maintaining cellular turgor without disrupting cellular metabolism [183,185]. This protection extends to the photosynthetic apparatus, whose integrity and stomatal conductance are preserved, ensuring stable net photosynthesis even under drought stress [127,184].

On the biotic level, biostimulants activate innate immunity through systemic induced resistance (ISR), and systemic acquired resistance (SAR) is triggered by many of these beneficial microorganisms or substances (e.g., chitosan). These effects place the products under the scope of plant protection product (PPP) regulations in the EU. Biostimulants, by definition, do not cover these biotic defenses and remain confined to abiotic stress mitigation, even though molecular cross-talk often exists between biotic and abiotic tolerance mechanisms within the plant [106,133]. These mechanisms place the plant in a state of “priming” or physiological alert, allowing immediate mobilization of defenses during a real attack while minimizing the energy cost associated with permanent immune activation [186,187].

Recent omics research reveals that these responses are orchestrated by a fine-grained regulation of gene expression, involving specific TF families like NAC, MYB, and MYC2 [82,187]. Remarkably, this phenomenon of ‘stress memory’ is based on epigenetic modifications, such as histone acetylation or DNA methylation, which modify the accessibility of chromatin at the level of defense genes promoters [187]. By reshaping the molecular architecture of the host, biostimulants are an essential tool for sustainable, productive, and resilient agriculture in the face of environmental fluctuations [52,127].

Table 1 below provides a detailed summary of the diversity of biostimulants, whether microbial or non-microbial in origin, and their main bioactive compounds. This overview makes it possible to correlate the types of products with their specific effects on various plant species, subject to environmental constraints [4,106]. By detailing the molecular modes of action—from activating the proton pump (H^+ -ATPase) by humic acids to triggering ISR by beneficial microorganisms—this table illustrates how the integration of these solutions allows stabilizing yields and improving nutritional quality of crops in the context of climate change [106,128,158]. These complex interactions between bioactive molecules and plant metabolism constitute the foundation for optimized management of plant health and agroecosystem resilience [4,146].

Table 1. Examples of biostimulants, bioactive compounds, and related commercial products—molecular modes of action and impacts on crops.

Biostimulant/ Commercial Product	Type	Bioactive Compounds	Plant Species	Type of Stress	Benefits	Molecular Mode of Action	References
Chitosan	Naturally occurring biopolymer	Glucosamine oligosaccharides and Chito-oligosaccharides	Strawberry, tomato, and rice	Biotic (pathogens) and abiotic (drought, salinity)	Protection against pathogens, reduced sweating, and increased vigor	Activation of the SAR (salicylic acid pathway), induction of defense genes, and modulation of stomatal conductance	[106,133,188]
<i>Ascophyllum nodosum</i>	Algae extracts	Polysaccharides and polyphenols	Soybean	Drought	Increase in biomass and yield	Overexpression of transcription factors related to the response to drought	[126]
Seasol® (<i>Durvillaea</i> spp.)	Algae extracts	Alginates and micronutrients	Strawberry, tomato, and broccoli	Nutritional deficiency	Improved root growth and total yield	Stimulation of nutrient transporters and cell elongation	[189]
Kelpak® (<i>Ecklonia maxima</i>)	Algae extracts	Phytohormones (cytokinins, auxins)	Apple, maize, and barley	Abiotic stresses	Root development and seedling vigor	Modulation of endogenous hormone balance and cell division	[189]
Humic acids	Humic substances	Functional groups (carboxylic and phenolic)	Maize	Oxidative stress/heavy metals	Membrane protection and root growth	Stimulation of membrane H ⁺ -ATPase and activation of xanthine oxidase	[48,158]
Fulvic acid	Humic substances	Low molecular weight molecules	Rice	Salinity/Drought	Improved osmotic adjustment and photosynthesis	Regulation of tonoplastic aquaporin genes (<i>OsTIPs</i>)	[158]
Fulvic acids	Humic substances (fulvic fraction)	Carboxylic-rich low-MW molecules	Arabidopsis and wheat	Low nutrients and mild stress	↑ secondary root growth and membrane hyperpolarization	H ⁺ -ATPase activation; NADPH oxidases; MPK3; Ca ²⁺ channel activation; auxin-signaling cross-talk; ↑ glutamic oxaloacetic transaminase	[158,190]
Fulvic acids	Humic substances (fulvic fraction)	Polyphenolic + fulvic mixture	Osti's Peony	Drought	↑ leaf water content and antioxidant activities and ↓ ROS and proline production and REC	↑ expression of drought-tolerance genes <i>CcCoAOMT</i> , <i>CAB37</i> , <i>AGT1</i> , <i>At4g26520</i> ; lignification for stress resistance	[158,191]

Table 1. Cont.

Biostimulant/ Commercial Product	Type	Bioactive Compounds	Plant Species	Type of Stress	Benefits	Molecular Mode of Action	References
<i>Trichoderma harzianum</i>	Microorganisms	Secondary metabolites and lytic enzymes	Cucumber and tomato	Biotic stresses (pathogens)	Systemic resistance and increased nutrition	Triggering of ISR (jasmonic acid/ethylene pathway) and secretion of siderophores	[4,106,192]
PGPR (<i>Bacillus</i> spp.)	Microorganisms	VOC, IAA, ACC-deaminase	Wheat and maize	Salinity and thermal stress	Maintenance of turgor and growth under stress	Reduction in stress ethylene levels and induction of antioxidant enzymes (SOD, CAT)	[106,128]
Melatonin (phytomelatonin)	Non-microbial biostimulant (indoleamine)	N-acetyl-5-methoxytryptamine	Tomato, peach, pear, strawberry, banana, mango, citrus, kiwi, grapes	Salinity, drought, extreme temperature, heavy metals, post-harvest senescence	Increased germination and photosynthesis, delayed fruit senescence, and improved phenolics/glucosinolates/terpenoids/lipids	Master regulator of plant hormone networks (auxin, CK, GA, ABA, JA, ET) and redox homeostasis; up-regulates carbohydrate/amino acid/lipid/lipidome transcripts	[193–197]
Pepton	PH (animal, enzymatic hydrolysate)	Bioactive peptides and free AAs	Cherry tomato	Moderate environmental stress	Improved flowering, marketable yield, auxin-like activity, and dose-dependent coleoptile elongation	Auxin-like activity via tryptophan → IAA biosynthesis; auxin-responsive gene induction	[146,198]
Trainer®	PH (vegetal, legume-derived)	Legume-derived peptides and α -amylase activators	Dwarf pea and tomato	Nutrient deficiency and drought	Improved shoot length under gibberellin-like activity and coleoptile elongation rate	Gibberellin-like activity; auxin-like activity via tryptophan precursor; α -amylase biosynthesis stimulation	[4,144,198]
Vegetal-derived PHs (legume source)	PH (vegetal, enzymatic hydrolysate)	Free AAs, oligopeptides < 5 kDa, and isoflavone residues	Tomato, lettuce, and grapevine	Salinity, drought, and low nitrogen	$\uparrow$ NUE, $\downarrow$ NO_3^- leaching; shoot DW, root DW, root length, root area	Stimulation of <i>NRT1.1/NRT2.1</i> transcription; citric acid cycle activation	[146,198,199]

ACC: 1-aminocyclopropane-1-carboxylate; IAA: indole-3-acetic acid; CAT: catalase; ISR: induced systemic resistance; PGPR: plant growth promoting rhizobacteria, SAR: systemic acquired resistance; SOD: superoxide dismutase; VOC: volatile organic compounds; CK: cytokinins; GA: gibberellic acid; ABA: abscisic acid; JA: jasmonic acid; ET: ethylene; AAs: amino acids; MW: molecular weight; NUE: nitrogen use efficiency; NO_3^- : nitrate; DW: dry weight; NRT: nitrate transporters; H^+ -ATPase: proton pump ATPase; NADPH: Nicotinamide adenine dinucleotide phosphate; MPK3: Mitogen-Activated Protein Kinase 3; Ca^{2+} : calcium ions; ROS: reactive oxygen species; REC: relative electrolyte conductivity; CCoAOMT: Caffeoyl-CoA O-methyltransferase; CAB37: Chlorophyll a/b-binding protein 37; AGT1: Alanine-Glyoxylate Aminotransferase; At4g26520: Identification code of a specific gene in Arabidopsis; PH: protein hydrolysates; $\uparrow$: increased; $\downarrow$: decreased.

7. Potential Constraints and Limitations

Many synthetic chemical inputs, including fertilizers and pesticides, are employed every year in agricultural settings to promote plant growth and/or counteract (a)biotic stresses. As seen by the examples in this review, the use of biostimulants to promote large-scale agricultural production is still emerging, although they have demonstrated their effectiveness in mitigating climate change-related stresses. Furthermore, biostimulants' use in agriculture has become increasingly accessible in the last decade thanks to their diverse sustainable benefits. The “omics” sciences, along with more recent high-throughput phenotyping technologies, have greatly improved the understanding of the physiological, biochemical, and molecular mechanisms of biostimulants [4]. However, further investigation is needed to address several unanswered questions, including: (i) Can biostimulants be considered a beneficial crop management practice, even if they only slightly modify the ecosystem? (ii) Is using this innovation an effective way to counteract yield losses brought on by (a)biotic stress? (iii) What molecular pathways underpin the reported effects of biostimulants? (iv) To what degree may the plant species/cultivar, environment, and management practices used influence these benefits, and what is the best procedure, time, dose of application, and developmental stage for enhancing plant health and stress tolerance? (v) When used as a substrate drench, foliar spray, or seed treatment, how well can the biostimulants alter the plant-associated microbiome, both qualitatively and quantitatively? (vi) How long does the action of biostimulants last after they are applied topically? (vii) How can the physiological, biochemical, and molecular processes behind the collaborative action of biostimulants be taken into consideration when creating new and targeted biostimulant products? (viii) What are the potential long-term consequences of repeated application of microbial biostimulants on the taxonomic diversity and functional balance of native soil communities? As this review illustrates with multiple examples, their use is only profitable when the plant is experiencing various abiotic stresses. In addition, the application of biostimulants may boost crop output by 2–10%, but it will not (or will only very rarely) raise crop yield by more than 10% [10]. Therefore, economic research that proves the long-term economic viability of their use is required before biostimulants can be considered for use in large-scale agricultural settings. When it comes to minimizing the cost of the biostimulant composition and avoiding excessive production costs during product development, this is typically the case [98,200,201]. However, it must be considered when implementing novel biostimulants in the field. Furthermore, it must be considered that biostimulants should be used in conjunction with other sustainable crop production maximizing techniques, such as appropriate crop management or the application of manures and amendments. Moreover, the application method should also be considered. Varied approaches may result in varied levels of efficiency, required quantity, and environmental impact. Lastly, as biostimulants may be effective for a certain application and species/cultivar but not certainly for others, it is equally critical to fully comprehend their mode of action. As a result, it cannot be presumed that they constantly function following the same scheme, as this could lead to a placebo-like effect when used. The complexity of the mechanisms governing the action of biostimulants calls for greater synergy between academic research and the industrial sector. This collaboration is essential for developing a new generation of solutions with targeted and optimized synergistic effects. While the potential of biostimulants to improve crop productivity and resilience is undeniable, their systemic integration remains contingent on overcoming scientific, regulatory, and economic barriers. A multidimensional approach is, therefore, necessary to transform these innovations into drivers of sustainable and widespread agricultural performance (Figure 2).

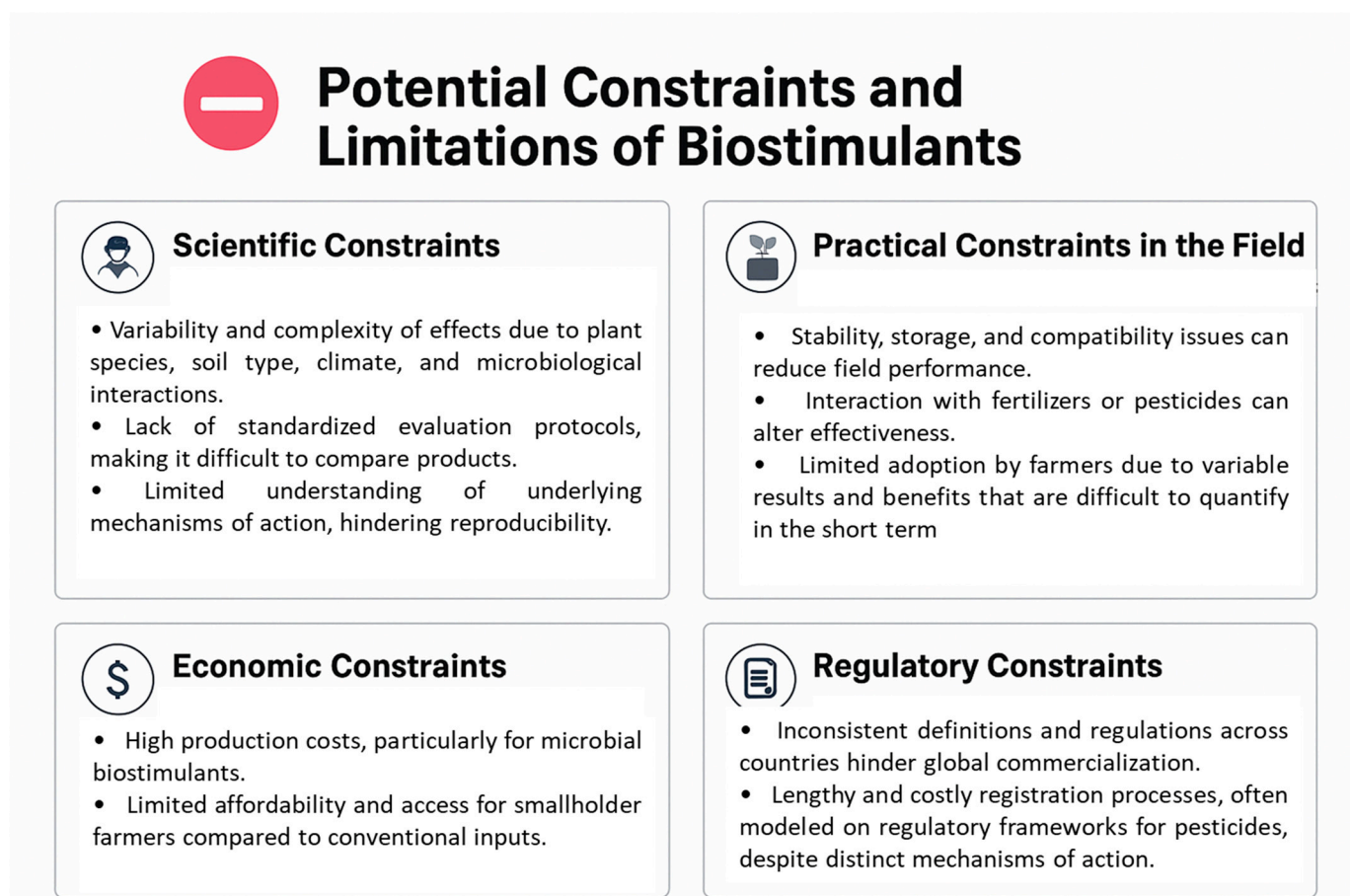


Figure 2. Constraints and limitations of biostimulants in agriculture.

8. Conclusions and Future Prospects

It has been determined that the use and application of biostimulants is on the rise and that the creation of new biostimulants is encouraging and will surely contribute to the sustainable expansion of crop outputs. Although biostimulants can reduce fertilizer inputs and enhance crop productivity, their profitability remains context dependent. It varies according to crop type, market value, local soil climate conditions, and the scale of farming. We can anticipate that in the upcoming years, biostimulants will significantly contribute to economically and ecologically sustainable agro-ecosystems, as well as provide the groundwork for an extensive resilient agriculture program in the future. However, given that these efforts must be directed toward better understanding their effects on plant functioning as well as the fact that their use in crop production programs should constantly be attained by means of eco-friendly methods, further investigation of the mechanisms underlying their action is required. In addition, a full life cycle assessment (LCA) considering production, formulation, and transportation steps is needed to ensure that their overall environmental footprint remains low. Researchers and fertilizer industries urgently need to clarify the different layers of mechanisms that will undoubtedly enable the dissemination of these bio-based products in agriculture. The integration of genomic (next generation sequencing) and phenomic (high-throughput plant phenotyping) techniques creates new avenues for the development of efficient biostimulant formulations to address the changing demands of crops and sustain food security. Additionally, these investigations may provide markers for enhancing current biostimulants, which might be used to generate new biostimulant products. Future biostimulant research and development will also greatly benefit from the mix of different biostimulants classes presented in this analysis. Particularly if we want to create extremely potent and tailored biostimulants, a combination of microbial

and non-microbial components needs to be studied further, with testing under optimal and sub-optimal conditions.

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