Review

Plant Biostimulants to Enhance Abiotic Stress Resilience in Crops

Luciana Di Sario [1] , Patricia Boeri [1], José Tomás Matus [2] and Gastón A. Pizzio [1,2,*]

1 CIT Río Negro, Universidad Nacional de Río Negro, Viedma CP8500, Río Negro, Argentina;
   ldisario@unrn.edu.ar (L.D.S.); pboeri@unrn.edu.ar (P.B.)
2 Institute for Integrative Systems Biology (I2SysBio), Universitat de València-CSIC,
   46908 Paterna, Valencia, Spain; tomas.matus@uv.es
* Correspondence: gapizzio@gmail.com

Abstract: The escalating impact of abiotic stress on crop productivity requires innovative strategies to ensure sustainable agriculture. This review examines the promising role of biostimulants in mitigating the adverse effects of abiotic stress on crops. Biostimulants, ranging from simple organic compounds to complex living microorganisms, have demonstrated significant potential in enhancing plant resilience, stress tolerance, and overall performance. The mechanisms underlying biostimulant action—such as enhancing antioxidant defenses, regulating hormonal pathways, and inducing metabolic adjustments—are reviewed. Furthermore, we incorporate the latest research findings, methodologies, and advancements in biostimulant applications for addressing abiotic stressors, including drought, salinity, high temperatures, and nutrient deficiencies. This review also highlights current challenges and future opportunities for optimizing biostimulant use in sustainable crop production. This revision aims to guide researchers and agronomists in applying biostimulants to improve crop resilience in the context of climate change.

Keywords: crop resilience; sustainable agriculture; plant physiology; stress tolerance; hormonal regulation; antioxidant defense; metabolic adjustments; drought; salinity; temperature extremes; nutrient deficiencies; crop productivity; environmental challenges

1. Introduction

Agriculture and food production face unprecedented challenges in the 21st century, driven by climate change and the concomitant increase in abiotic stress on crop productivity [1]. Abiotic stressors such as drought, salinity, high temperatures, and nutrient deficiencies, among others, pose a significant threat to global food security (Figure 1). As climate change intensifies, the frequency and severity of these stressors continue to rise, requiring the development of innovative and sustainable agricultural practices [2]. In this context, the exploration of plant biostimulants as a strategic tool to enhance crop resilience against abiotic stress has garnered significant attention [3]. Biostimulants, comprising a diverse array of organic compounds derived from different sources (Figure 1), hold immense potential to elicit positive physiological responses in plants. These responses can enhance a plant's capacity to withstand and recover from environmental challenges [4,5]. This comprehensive review provides an examination of the current state of knowledge regarding the use of plant biostimulants to mitigate abiotic stress in crops. Furthermore, this review emphasizes the potential of biostimulants to induce crop resilience under suboptimal environmental conditions and explores their impact on plant physiology, highlighting their promise as a critical tool for sustainable agriculture in the face of climate change.
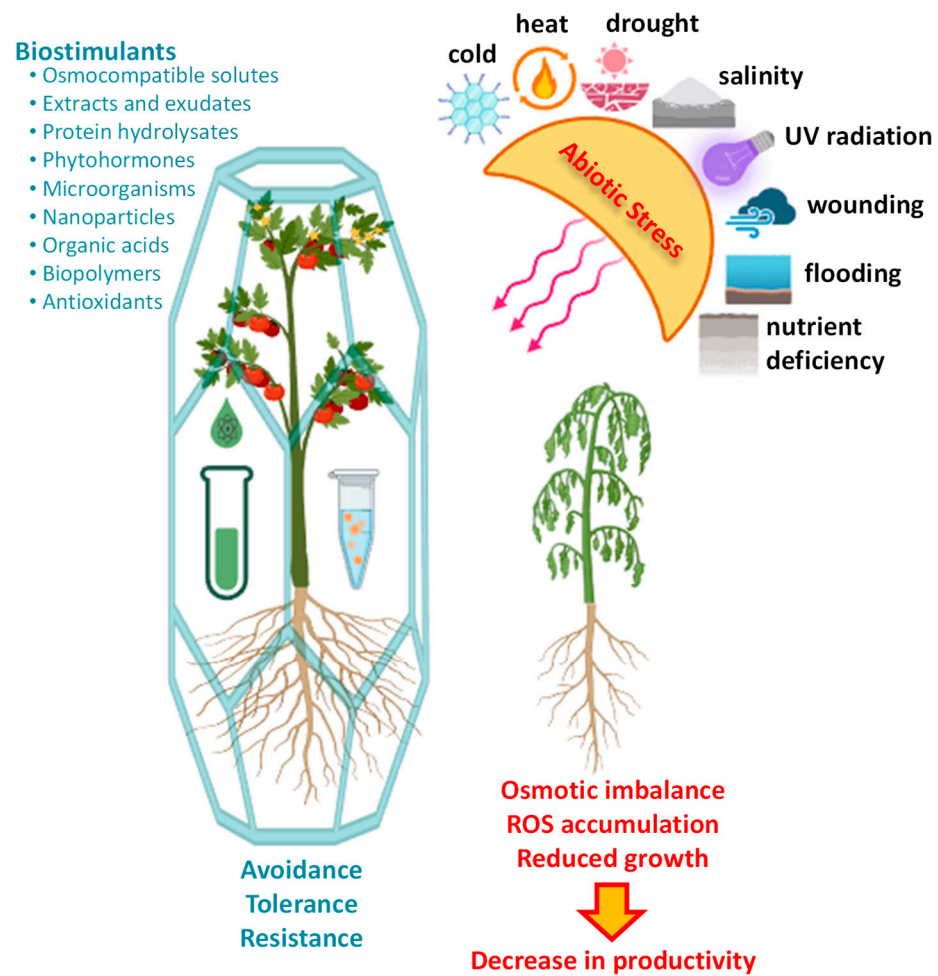
Figure 1. The role of biostimulants in mitigating the negative effects of abiotic stress on crop productivity. Abiotic stress conditions, such as drought, salinity, extreme temperatures, and nutrient deficiencies, induce detrimental changes at morphological, physiological, biochemical, and molecular levels, severely limiting plant growth and productivity. Biostimulants help crops counteract these stress-induced damages, restoring plant performance and enhancing resilience against environmental stressors. Illustration created using BioRender.

2. Abiotic Stress in Crops: Challenges and Implications

Agricultural productivity is intricately linked to the complex interplay between crop physiology and environmental conditions. However, the intensification of abiotic stressors represents a significant threat to global food security [1]. Drought, salinity, extreme temperatures, and nutrient deficiencies— exacerbated by climate change—impose unprecedented challenges to crop yields and agricultural sustainability (Figure 1). Understanding the mechanisms of abiotic stress tolerance is crucial for developing effective strategies to mitigate the adverse effects of these stressors on plant growth and productivity.

Abiotic stress induces a wide range of damage at the tissue, cellular, and molecular levels, leading to altered growth patterns, reduced photosynthetic efficiency, and compromised reproductive success, among other abnormalities [6,7]. For instance, water scarcity triggers stomatal closure, which limits CO_2 uptake and disrupts leaf temperature regulation. Similarly, salinity stress disturbs ion homeostasis, resulting in toxic ion accumulation and osmotic imbalances. These physiological disruptions have direct repercussions on crop yield and quality. Moreover, the economic implications of yield losses due to abiotic stress are profound, affecting farmers' livelihoods and exacerbating global food insecurity [8]. Efforts to counteract the effects of abiotic stress often involve increased resource use, such

as excessive irrigation or fertilizers, contributing to environmental degradation. This highlights the urgent need for sustainable and resilient agricultural practices [9]. Climate change is acting as a catalyst, intensifying the frequency and severity of extreme weather events, including droughts, floods, and heat waves [10]. Predictive models project a grim future for agriculture if adaptive strategies are not implemented to enhance crop resilience and ensure food security.

To address these challenges, it is critical to develop agricultural management strategies that increase crop resilience to abiotic stressors, optimize resource use efficiency, and minimize environmental impact. Biostimulants represent a promising solution, offering innovative pathways to enhance crop resilience and mitigate the detrimental consequences of abiotic stress on global food production [11].

3. Biostimulants to Tackle Abiotic Stress in Crops

Biostimulants represent a diverse group of substances that, when applied to plants, induce physiological and molecular changes, enhancing growth, development, and stress tolerance. These changes include mechanisms from osmotic adjustment to antioxidant defense activation that improve plant resilience under adverse conditions (Figure 1). It is important to distinguish biostimulants from biofertilizers: while biofertilizers primarily focus on nutrient supply, biostimulants exert a broader influence on plant physiology. The EU regulation defines a biostimulant as "a product that stimulates 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: (a) nutrient use efficiency; (b) tolerance to abiotic stress; (c) quality traits; or (d) availability of confined nutrients in the soil or rhizosphere" [12].

Biostimulants can be applied using three main approaches: (1) during seed priming to improve seed performance, (2) as foliar sprays directly onto plant shoots, or (3) as solid or liquid amendments applied to plant substrates, such as soil or hydroponic solutions. The classification of biostimulants encompasses a wide variety of compounds, including phytohormones, organic acids, plant extracts, and microbial-based formulations, among others. Understanding the diversity of these compounds is crucial for tailoring their application to specific crops and environmental conditions, thereby maximizing their effectiveness in enhancing plant performance under abiotic stress.

3.1. Osmocompatible Solutes (OCSs)

These small organic molecules accumulate within plant cells without causing cellular damage. They play a critical role in osmoregulation, maintaining cell volume and counteracting the effects of water stress by increasing water potential [13,14]. OCSs can also protect membranes and modulate signaling pathways, making them potential biostimulants for improving plant abiotic stress tolerance. OCSs accumulate in the cytosols and vacuoles of plant cells in response to osmotic stress, helping maintain cell volume and turgor pressure. This prevents plasmolysis and the shrinkage of cells due to water loss, which can damage cellular structures and disrupt physiological processes [15,16]. In addition, OCSs can modulate signaling pathways involved in stress response, such as abscisic acid (ABA) signaling, which can further enhance stress tolerance. There are a variety of OCSs found in plants, including sugars (i.e., sucrose, raffinose, and trehalose), polyols or sugar alcohols (such as sorbitol, mannitol, and glycerol), amino acids, and derivatives (from proline to betaines).

OCSs have been shown to improve plant tolerance to a variety of abiotic stresses [17–19]. For instance, OCSs can enhance water uptake and reduce water loss through stomata, thereby improving drought tolerance. Moreover, OCSs can alleviate the negative effects of salt stress by reducing the osmotic potential of the soil solution and protecting cells from

salt damage. In addition, OCSs can protect plants from heat and cold stress by maintaining membrane integrity and reducing the accumulation of reactive oxygen species (ROS) [20]. However, the effectiveness of OCSs as biostimulants depends on several factors, such as the type of stress, the plant species, and the formulation and application method, among others. On the other hand, OCSs offer several economic and environmental benefits as biostimulants. For instance, OCSs can enhance plant stress tolerance, reducing the need for chemical fertilizers and pesticides to protect against environmental stresses. In addition, OCSs can improve water and nutrient use efficiently, leading to increased crop yields, even under normal conditions. Moreover, they can reduce the environmental impact given that OCSs are typically derived from renewable resources and have a low environmental footprint [14,16,20]. OCSs are promising biostimulants with the potential to improve plant abiotic stress tolerance and enhance crop productivity (Figure 2). Their effectiveness and sustainability make them an attractive alternative to chemical inputs in modern agriculture. Further research is needed to optimize the use of OCSs as biostimulants and to develop novel formulations with enhanced properties. As our understanding of OCSs grows, their role in sustainable agriculture is likely to expand.
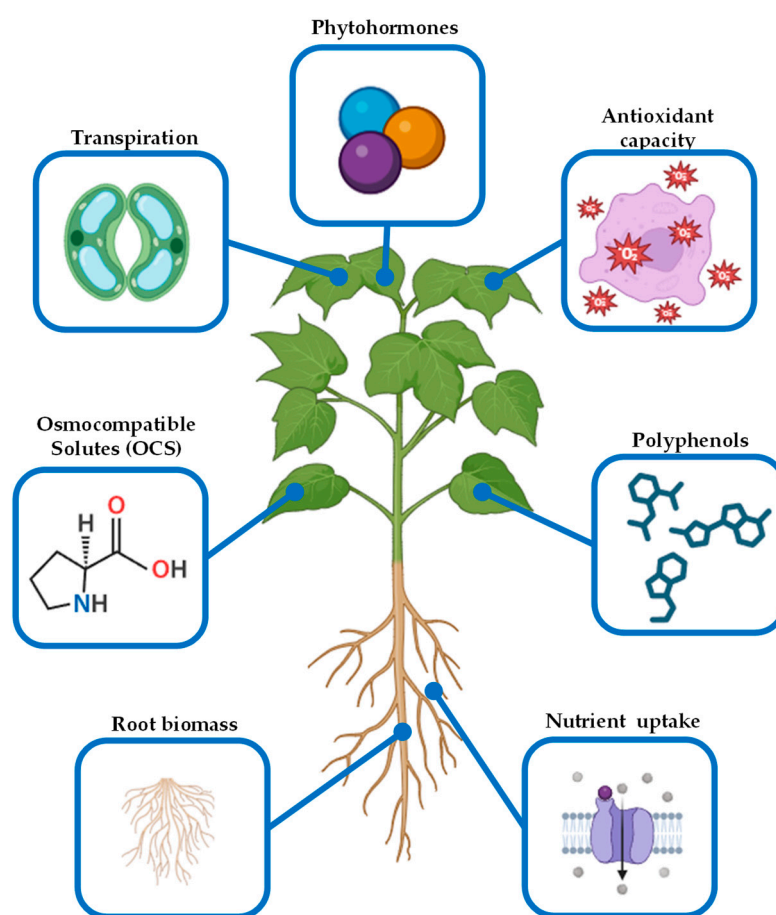

Figure 2. Molecular and physiological biostimulant-induced mechanisms to regulate abiotic stress tolerance in plants. Illustration created using BioRender.

3.2. Antioxidants

Abiotic stress poses a significant challenge to modern agriculture, encompassing a spectrum of environmental factors such as drought, salinity, extreme temperatures, and heavy metal contamination that adversely affect plant growth and development. These stressors induce oxidative stress in plants through the excessive generation of reactive oxygen species (ROS), including singlet oxygen ($^1O_2$), superoxide radicals ($O_2-\bullet$), hydroxyl

radicals (HO•), hydrogen peroxide (H_2O_2), alkoxyl radicals (RO•), and peroxyl radicals (ROO•). While ROS are essential for normal cellular signaling at basal levels, their overproduction under stress leads to oxidative damage, disrupting physiological processes and harming cellular components such as DNA, proteins, lipids, carbohydrates, and enzymes, ultimately triggering programmed cell death [21,22]. Oxidative damage also compromises membrane integrity and induces physiological and biochemical alterations that disrupt metabolism and reduce plant productivity [23,24]. Despite these challenges, plants have evolved endogenous mechanisms to combat oxidative stress. These mechanisms involve precise control of ROS levels through enzymatic and non-enzymatic antioxidant systems.

The enzymatic antioxidant defense system includes peroxidase (POD), superoxide dismutase (SOD), glutathione reductase (GR), catalase (CAT), dehydroascorbate reductase (DHAR), ascorbate peroxidase (APX), and monodehydroascorbate reductase (MDHAR). Non-enzymatic antioxidants include ascorbate (AsA), flavonoids, carotenoids, stilbenes, tocopherols, and other vitamins. These systems work collectively to detoxify excessive ROS and restore antioxidant homeostasis, thereby enhancing plant resilience to abiotic stress [25–27].

Antioxidants have emerged as promising biostimulants for mitigating the effects of abiotic stress. When applied exogenously, antioxidants perform multiple roles to alleviate the adverse effects of abiotic stress [28,29], including ROS scavenging and minimizing oxidative damage to cellular structures and biomolecules such as proteins, lipids, and nucleic acids. Moreover, antioxidants also regulate stress-signaling pathways, modulating the expression of genes involved in stress adaptation and defense mechanisms. They enhance photosynthetic efficiency, ensuring plants have sufficient energy to cope with adverse conditions. Several antioxidants have shown promise as biostimulants, including polyphenols, a diverse group of compounds found in plants, which include flavonoids, tannins, and stilbenes; vitamins, particularly vitamins C and E, which protect membranes by scavenging ROS and maintain cellular redox balance; phytosterols, compounds with structural roles in cell membranes and antioxidant activity; and Coenzyme Q10, an essential cofactor in the electron transport chain that also acts as a potential antioxidant [28–31].

The application of antioxidants as biostimulants presents a proven strategy for enhancing plant abiotic stress tolerance (Figure 2). However, further research is needed to fully elucidate their mechanisms of action under stress conditions, optimize formulations and application methods, and explore synergistic interactions with other compounds. Additionally, identifying novel antioxidant molecules through the screening of plant extracts or synthetic compounds with enhanced stress-protective properties offers a promising avenue for future research. The ability of antioxidants to mitigate ROS-induced damage, regulate stress signaling, and enhance stress adaptation highlights their value as tools for optimizing crop resilience and productivity.

3.3. Phytohormones

Plant hormones are critical signaling molecules that regulate plant metabolism, growth, development, and stress responses. Naturally produced by plants, they act in a coordinated manner to enable adaptation to environmental challenges. Phytohormones have gained attention as promising biostimulants for improving plant tolerance to abiotic stress [32–34]. Among them, abscisic acid (ABA) plays a pivotal role in regulating drought, salt, and cold stress responses by mediating stomatal closure and improving water use efficiency [35]. Similarly, salicylic acid (SA) contributes to plant defense mechanisms against biotic and abiotic stresses [36]. Gibberellins (GAs) are involved in promoting stress-induced growth responses and enhancing antioxidant defense [37]. Cytokinins can promote root growth

and nutrient uptake under stress conditions [38] or auxins can regulate stomatal opening, nutrient uptake, and stress signaling pathways [39].

Phytohormones can alleviate the negative effects of abiotic stresses through different mechanisms, for instance, regulating stomatal opening and water use efficiency or protecting membranes and cellular structures through the enhancement of the antioxidant defense (Figure 2). In addition, phytohormones are able to promote nutrient uptake and metabolism to stimulate growth, enabling plants to better access essential resources under nutrient deficiency and environmental stress [32–34]. Considered one of the first studied biostimulants, their effectiveness can be influenced by factors such as their formulation and application method. Organic carriers and advanced technologies like nano-encapsulation have been developed to improve the delivery and efficiency of phytohormones. Application methods, including foliar sprays and soil treatments, provide flexible strategies to target specific crop requirements and environmental challenges. Ongoing research in this field is focused on developing innovative formulations and application techniques such as precision agriculture and controlled-release systems. Scientists are also investigating the synergistic effects of phytohormones with other biostimulants and nutrient management practices. Furthermore, long-term studies are being conducted to understand the impact of phytohormones on crop health and soil microbiomes, ensuring their sustainable use.

3.4. Extracts, Exudates and Protein Hydrolysates

Protein hydrolysates consist of a diverse combination of amino acids, oligopeptides, and soluble polypeptides, contingent upon the protein source and the applied processing methodologies [40]. These compounds serve as signaling molecules [41,42] and enter the plant cell through both diffusion processes as well as active transport that involve an energy cost [43]. In addition, applied to plants, protein hydrolysates alleviate osmotic stress by modulating primary and secondary metabolism [44]. The exogenous application of these products stimulates different physiological and molecular processes, enhancing nutrient absorption and utilization efficiency. Additionally, whether directly or indirectly, these applications mitigate the adverse effects of both abiotic and biotic stresses, ultimately enhancing crop yield and quality [43,45–48]. Concerning the mechanism of action of protein hydrolysates, studies conducted in lettuce and corn plants suggest that these biocompounds can positively regulate the expression levels of phenylalanine ammonium lyase (PAL). Consequently, they induce the production of secondary metabolites, including flavonoids, terpenes, carbohydrates, sterols, and amino acids, enhancing tolerance to abiotic stress [4]. Nevertheless, despite recent advances in understanding the mechanisms of action of biostimulants, studies aimed at elucidating their bioprotective effects against abiotic stresses remain limited. In relation to this, Paul et al. [49] pointed out that different protein hydrolysates applied to tomato plants could regulate ROS-mediated signaling, inducing changes in the levels of compounds with antioxidant activity, such as phenols and carotenoids. In addition, biostimulants based on seaweed extracts include a wide variety of bioactive compounds, from nutrients to phytohormones [50,51]. Although the mechanism by which these extracts enhance stress tolerance is not fully understood, regulatory molecules, osmoprotectants, transporters, and detoxifying enzymes have been reported to play a role [52]. For instance, betaines and cytokinins are components accountable for stress regulation [53,54]. Moreover, other compounds present in these extracts can act as signaling molecules that regulate key pathways at the transcriptional and/or post-translational level [55]. These molecules, in conjunction with polysaccharides, may undergo an endogenous increase in the presence of algal extracts [56]. The diversity of substances found in protein hydrolysates and seaweed extracts adds complexity to the comprehension of their mechanisms of action as biostimulants. In this context, numerous

studies have highlighted the efficacy of these biocompounds in enhancing plant tolerance to both biotic and abiotic stressors across various agronomically significant species, including soybean (*Glycine max*) [57], rice (*Oryza sativa*) [58], wheat (*Triticum aestivum*) [59], tomato (*Solanum lycopersicon*) [60], arugula (*Eruca vesicaria*) [61], spinach (*Spinacia oleracea*) [62], squash (*Cucurbita pepo*) [63], peas (*Cajanus cajan*) [64], cucumber (*Cucumis sativus*) [65], okra (*Abelmoschus esculentus*), and cassava (*Manihot esculentus*) [66].

These findings not only expand our understanding of the impact of such biostimulants on plant physiology but also offer promising perspectives for enhancing crop productivity and quality in suboptimal environments. Thus, biostimulants derived from protein hydrolysates have the potential to positively transform modern agriculture, providing sustainable and effective solutions to address future challenges.

4. Plant-Derived Biostimulants

Plant-derived biostimulants comprise a heterogeneous set of products able to enhance crop production, impacting flowering, fruit development, root biomass, and responses to abiotic stress. Plant-derived biostimulants include different preparations such as phytohormones, specialized metabolites, extracts, and hydrolysates from whole plants, specific organs, cell cultures, and even plant by-products [67]. Furthermore, the different origins of the plant material used and the methods of preparation and application on crops add complexity to the biostimulant mechanisms of action and their effect on plant physiology. In this regard, the biostimulant action on plants may include mechanisms from hormonal effects [68] to their antioxidant activity [69] (Figure 2).

The phytohormone abscisic acid (ABA) is a key player in plant abiotic stress tolerance induction. For instance, ABA modulates plant transpiration via stomatal regulation under drought and heat stress in wheat (*Triticum aestivum*) [70]. In addition, it was shown that ABA signaling regulates the balance between transpiration and photosynthesis in *Nicotiana benthamiana*, regulating growth and drought stress tolerance [71] (Table 1). Moreover, ABA is capable of triggering osmotic adjustments, inducing proline and galactinol synthesis; galactinol is a precursor of the osmoprotective oligosaccharide raffinose family. Additionally, ABA regulates ripening, sugar accumulation, and color development in *Vitis vinifera* fruits [72]. Furthermore, ABA induces the production of anthocyanins and phenolic content, enhancing the plant's antioxidant capacity [73,74]. Thereby, biostimulants formulated from plant tissues rich in ABA content, such as avocados, citrus, soybean, and figs [75], represent a sustainable strategy for agriculture to cope with abiotic stress; such formulations also have the potential to have a direct positive impact in human health [76]. Nevertheless, synthetic small chemicals with ABA receptor agonist activity, such as iSB09 and AMF4, are emerging as an improved alternative to ABA [77].

Melatonin (MEL) is another multifunctional growth regulator with the advantage of having direct antioxidant capacity (Figure 2). MEL is involved in different physiological processes from growth (i.e., promoting cell division and elongation, biomass accumulation, and meristematic growth), development (i.e., accelerating seed germination and retarding senescence), and stress response (i.e., enhancing drought, salinity, and heat stress tolerance) [78]. For instance, exogenous MEL application improves the germination rate of cotton (*Gossypium hirsutum*) seed by increasing antioxidant capacity and reducing ABA levels [79] (Table 1). Moreover, MEL-treated stevia (*Stevia rebaudiana*) seeds showed increased levels of phenolic compounds, an improvement in germination rate, higher plantlet fresh weight, and more leaves [80]. MEL treatments also enhance root growth and nutrient uptake in crops such as tomato (*Solanum lycopersicum*) [81], cucumber (*Cucumis sativus*) [82], and soybean (*Glycine max*) [83] (Table 1). On the other hand, MEL is able to enhance plant resilience to abiotic stress. For instance, MEL treatment on wheat (*Triticum aestivum*)

improved the drought resistance of Chinese Spring, Shi4185, and Hanxuan10 varieties [84]. The molecular mechanism of this phenotype involves a decrease in drought-induced cell membrane damage through a reduction in hydrogen peroxide levels and an increase in jasmonic acid (JA) content by the transcriptomic regulation of LOX1.5 and LOX2.1 genes (involved in JA synthesis) and transcription factors such as HY5 and MYB86. Moreover, the resveratrol-rich medicinal plant *Polygonum cuspidatum* is a drought-sensitive crop. Exogenous MEL application is not only able to induce stress tolerances in *P. cuspidatum* but also increase resveratrol levels through the induction of stilbene-synthetic gene expression, boosting the antioxidant capacity [85]. Additionally, MEL-induced drought stress tolerance in maize (*Zea mays*) [86] and rice (*Oryza sativa*) [87] through the antioxidant defense system enhancement was also reported. On the other hand, MEL treatment on kiwifruit (*Actinidia chinensis*) plants diminishes oxidative damage induced by flooding, showing reduced ROS accumulation in roots [88] (Table 1). A similar phenotype was also described in wheat (*Triticum aestivum*), in which MEL-treated plants, subjected to flooding, showed an increase in antioxidant enzyme levels and a concomitant reduction in oxidative harm, improving wheat flooding tolerance [89].

Different authors have pointed out the key role of these bio-compounds in enhancing nutrient use efficiency [90]. Moreover, formulations based on protein hydrolysates are widely used due to their ability to enhance nutrient uptake, promote plant growth, and improve stress tolerance [91] (Figure 2). For instance, nitrogen (N) is a key nutrient for plant growth; it is a building block for amino acid and nucleotide synthesis. In this regard, the application of Trainer, a commercial legume-derived plant hydrolysate, increases N content in ornamental crops, such as *Begonia tuberhybrida*, *Pelargonium peltatum*, and *Viola cornuta*, enhancing plant growth and ornamental quality [92]. Trainer-induced nitrogen use efficiency increments were also shown in *Spinacia oleracea* and *Valerianella locusta* [93] (Table 1), with concomitant crop yield enhancement. Additionally, nutrient use efficiency and root growth in *Cannabis sativa* can be enhanced by a biostimulant complex composed of Aloe vera extract, fish hydrolysate, and kelp [94].

Plant-derived biostimulants also influence the synthesis of secondary metabolites, which play a crucial role in plant defense mechanisms against stress. These compounds, which include alkaloids, phenylpropanoids, terpenoids, and phenolic compounds, are essential for enhancing plant resistance to adverse conditions, such as biotic and abiotic stresses [95–97]. Furthermore, several studies have indicated that the exogenous application of plant extracts increases the polyphenol content in crops; for instance, the application of oak extracts in *Vitis vinifera* [98], moringa extracts in *Coriandrum sativum* [99], and alfalfa and red grape extracts in *Capsicum chinensis* [100] (Table 1). Additionally, grapevine treatment with vine-shoot extracts leads to higher terpene and norisoprenoid levels in fruits [101,102]. The application of *Callicarpa macrophylla* extracts, which are rich in Calliterpenone, increases the concentration of menthol in wild mint (*Mentha Arvensis*) [103] and the spry of moringa (*Moringa oleifera*) leaf extract on rose-scented geranium (Pelargonium graveolens), enhances geraniol, linalool, citronellol, and β-caryophyllene synthesis [104].

Understanding the modes of action of biostimulants requires integrating omics technologies, chemical bioprospecting, and mathematical tools, which enable the identification and characterization of active compounds and the detailed analysis of data. This comprehensive perspective is crucial for developing precise and optimized formulations tailored to each crop type [105], thus ensuring more effective and sustainable agricultural practices.

Table 1. Biostimulant effects on crops.

Biostimulant Source	Biostimulant	Treated Crop	Improvement in	Reference
	Abscisic acid	Nicotiana benthamiana	Drought stress tolerance	[71]
		Vitis vinifera	Ripening and fruit quality	[72]
			Antioxidant capacity	[73,74]
	Melatonin	Gossypium hirsutum	Germination/antioxidant capacity	[79]
		Stevia rebaudiana		[80]
		Solanum lycopersicum	Root growth/nutrient use efficiency	[81]
		Cucumis sativus		[82]
		Glycine max		[83]
		Triticum aestivum	Drought stress tolerance	[84]
		Polygonum cuspidatum	Drought stress tolerance/resveratrol levels	[85]
		Zea mays	Drought stress tolerance	[86]
		Oryza sativa		[87]
		Actinidia chinensis	Flood stress tolerance	[88]
		Triticum aestivum	Flood stress tolerance/antioxidant capacity	[89]
	Protein hydrolysates	Begonia tuberhybrida	Nutrient use efficiency/plant growth	[92]
		Pelargonium peltatum		
		Viola cornuta		
		Spinacia oleracea		[93]
		Valerianella locusta		
		Cannabis sativa		[94]
	Extracts	Vitis vinifera	Polyphenol content	[98]
		Coriandrum sativum		[99]
		Capsicum chinensis		[100]
		Vitis vinifera	Terpene and norisoprenoid content	[101,102]
		Mentha Arvensis	Menthol content	[103]
		Pelargonium graveolens	Geraniol, linalool, and citronellol content	[104]
Seaweeds	Fucans	Nicotiana tabacum	Biotic stress tolerance	[106]
	Carrageenans	Zea mays/Cicer arietinum	Plant growth	[107]
		Nicotiana tabacum		[108]
	Alginates	Foeniculum vulgare	Plant growth and development	[109]
	Carrageenans	Pinus radiata	Plant growth	[110]
		Eucalyptus globulus		[111]
	Alginates	Papaver somniferum	Plant growth and development	[112]
		Oryza sativa		[113]
		Arachis hypogaea		
		Triticum aestivum	Drought stress tolerance	[114]
	A. nodosum extract	Solanum lycopersicum	Heat stress tolerance	[115]
	G. rugosa extract		Drought stress tolerance	[116]
Microalgae	*Nannochloris* sp. extract	Solanum lycopersicum	Drought stress tolerance	[117]
	Spirulina platensis	Carica papaya	Plant growth	[118]
		Solanum melongena		[119]
	A. platensis and *Scenedesmus* sp.	Petunia hybrida		[120]
	A. fusiformis	Allium sativum		[121]
	Spirulina platensis	Capsicum annuum	Fruit yield and quality	[122]

Table 1. *Cont.*

Biostimulant Source	Biostimulant	Treated Crop	Improvement in	Reference
Bacteria	PGPR	Phoenix dactylifera	Salt stress tolerance	[123]
		Oryza sativa	Salt stress tolerance	[124]
		Amaranthus viridis	Salt stress tolerance	[125]
		Hordeum vulgare	Drought stress tolerance	[126]
		Zea mays	Salt stress tolerance	[127]
		Solanum lycopersicon	Plant growth/fruit yield	[128]
	PSB	Zea mays	Nutrient use efficiency/salt tolerance	[129]
		Quercus Brantii	Drought stress tolerance	[130]
		Arachis hypogaea	Salt stress tolerance	[131]
		Solanum tuberosum	Plant growth	[132]
		Lycopersicon esculentum	Drought stress tolerance	[133]

5. Biostimulants from Seaweeds (Macroalgae) and Microalgae

Seaweeds, also known as marine macroalgae, are photosynthetic organisms that inhabit marine environments. They are classified as eukaryotic organisms, meaning that their cells contain a true nucleus and other membrane-bound organelles. Seaweeds comprise a group of macroscopic organisms that range in size from 0.5 mm and to 200 feet in length. These macroalgae constitute a significant category for the market of organic plant biostimulants [134]. They exhibit a complex and dynamic taxonomy that allows them to be classified, according to their pigmentation, into red algae (*Rhodophyta*, approximately 7500 species), brown algae (*Phaeophyta*, approximately 2000 species), and green algae (*Chlorophyta*, ~1500 algae) [135,136]. The marine environment they inhabit undergoes a series of constant modifications caused by tidal waves, changes in temperature, evaporation, precipitation, freshwater inflows, and sea level changes [137].

On the other hand, while salinity remains relatively constant in the open ocean, in semi-enclosed conditions, coastal areas, and estuaries, salinity changes are accentuated [138]. Intertidal environments represent transitional areas subjected to abrupt changes and recurrent fluctuations in environmental conditions, including intense radiation, high temperatures, desiccation, and salinity with changing tides, compounded by seasonal meteorological variations [137,139]. In these salt stress situations, algal cells continue to be in contact with water despite having a reduced water potential, while considerable cellular dehydration occurs as a result of desiccation. Both salinity and desiccation constitute two forms of water deprivation, for which the concept of "physiological drought" has been suggested [140]. The stress induced by these conditions causes a loss of water, ions, and electrolytes in the cell membrane, as well as pH modifications, crystallization of solutes, and denaturation of proteins. These events trigger the accumulation of reactive oxygen species (ROS) that modifies the redox homeostasis of the cell, causing an 'oxidative stress' that induces damage to the photosynthetic apparatus, DNA, proteins, and cell membranes [141,142]. However, ROS also acts as signaling molecules for cellular processes, including environmental stress tolerance. Therefore, cells must closely control ROS levels to avoid oxidative damage but allow signaling and tolerance induction [137].

Intertidal algae employ a diverse array of biochemical and physiological mechanisms to regulate homeostasis and sustain cellular integrity in suboptimal environments [143]. As a consequence, they synthesize a myriad of organic compounds, many of which have been recognized for their positive biostimulant effects on plants, including photosynthetic pigments, such as chlorophylls, carotenoids, and phycobiliproteins [144,145]. In addition, macro- and micronutrients are also found in seaweed products in fresh, dried, or extract

forms [146]. On the other hand, among the secondary metabolites implicated in stress responses are polyphenolic compounds, including florotanins, bromophenols, flavonoids, phenolic terpenoids, mycosporine-like amino acids, and halogenated compounds [147,148].

In recent decades, more than 3000 compounds from macroalgae have been described, with recognized applications in the pharmaceutical, cosmetic, agricultural, bioenergy, and food sectors [149,150]. Many of these compounds have been linked to biostimulant effects on photosynthetic activities, nutrient uptake, and polyphenol accumulation, resulting in benefits for growth, resistance, fruit coloration, nutritional composition, and crop quality [55,151]. Thus, it has been demonstrated that most of the polysaccharides and their derived oligosaccharides activate defense and protection responses against a wide range of pathogens in terrestrial plants. Moreover, these compounds vary according to the type of algae used as raw material, with ulvans found in green algae; agarans and carrageenans in red algae; and alginates, fucans, and laminarin in brown algae [152,153]. It has been reported that these alginates and their oligoderivatives can trigger an initial burst of oxidation and activate signaling pathways that induce local and systemic defense responses in plants [106], leading to increased expression of defensive enzymes, such as phenylalanine synthase, ammonium lyase, and lipoxygenase. In turn, these compounds are involved in the synthesis of phenylpropanoids, terpenes, terpenoids, and alkaloids, which also exhibit antimicrobial activities [55,154], as well as stimulants of plant growth, development, and resistance [56,155]. Several investigations have demonstrated the biostimulant effect of these polysaccharides and derived oligosaccharides on agriculturally relevant crops. For instance, carrageenans and oligo-carrageenans showed plant growth enhancement in *Zea mays* and *Cicer arietinum* [107]. Similarly, these compounds promoted photosynthate, basal metabolism, and growth in tobacco (*Nicotiana tabacum* var. *burley*) [108], fennel (*Foeniculum vulgare*) [109], pine (*Pinus radiata*), and eucalyptus (*Eucalyptus globulus*) plants [110,111]. Additionally, a positive effect of alginates on crop growth was shown in poppy (*Papaver somniferum*) [112], rice (*Oryza sativa* var. *japonica*), and peanut (*Arachis hypogea*) [113], as well as drought stress tolerance induction in wheat (*Triticum aestivum*) [114] (Table 1; Figure 2). In addition, carbohydrate-rich *Ascophyllum nodosum* extracts have been reported to induce heat stress tolerance in tomato (*Solanum lycopersicum*) [115]. Furthermore, *Galaxaura rugosa* extracts applied to tomato roots induce drought tolerance [116]. The mechanism of this induction involves activating the abscisic acid (ABA) signaling pathway, leading to improved CO_2 assimilation and water use efficiency. On the other hand, sulfated fucan oligosaccharides induced tolerance against tobacco mosaic virus in *Nicotiana tabacum* [106].

Currently, algae-derived products are one of the most promising and rapidly expanding categories in the biostimulant industry [115,156]. Their application has notable benefits for the agricultural sector, including the efficacy of these products at low concentrations and their ability to enhance the defensive responses of crops under abiotic stress conditions. Additionally, it has been reported that these biostimulants can improve crop yield and protein accumulation [155]. However, the formulation of new biostimulants presents certain difficulties, for instance the variability of the algae used as raw material [157,158]. Moreover, algae are exposed to a wide range of abiotic and biotic factors, such as species, seasonal changes, life cycle, size, age, reproductive status, location, depth, nutrients, salinity, light intensity, ultraviolet radiation, herbivory, and specific harvest times. Finally, some authors have warned about algae's capacity to absorb heavy metals from their environments and bioaccumulate them [159]. Thus, sustained use of these compounds as crop biostimulants could result in the biomagnification of these heavy metals over time. Although these aspects represent significant disadvantages for the industry, algal biostimulants could also be used for the bioremediation of contaminated soils through biosorption processes [160]. Therefore, further research is necessary to help clarify these aspects and drive the advance-

ment of the biostimulant industry. Moreover, seaweeds as plant biostimulants have a wide range of economic and potential applications, and their importance is likely to grow in the future.

Microalgae are photosynthetic single-cell microscopic organisms that are among the most ancient and diverse life forms on Earth. They inhabit a wide range of environments, including freshwater, saltwater, and extreme habitats such as deserts and hot springs. These microorganisms are characterized by their rapid reproduction rates, which make them an exceptionally productive source of biomass. Microalgae are classified based on different criteria, including pigmentation, life cycle, cell structure, and morphology. The group comprises both prokaryotic cyanobacteria, belonging to the divisions *Cyanophyta* and *Prochlorophyta*, and eukaryotic protists, which include *Glaucophyta*, *Rhodophyta*, *Heterokontophyta*, *Haptophyta*, *Cryptophyta*, *Dinophyta*, *Euglenophyta*, *Chlorarachniophyta*, and *Chlorophyta* [161,162].

The cultivation of microalgae, often referred to as unicellular biofactories, has gained attention for its beneficial effects in agriculture, particularly in promoting plant growth and enhancing plant responses to abiotic stress conditions [163–168]. One of the advantages of microalgae cultivation is its relative ease and cost-effectiveness [134]. Given their promising commercial potential as biostimulants and biofertilizers, numerous systems for microalgae biomass production have been developed, ranging from laboratory to industrial scales. Common methods include open pond or racetrack systems, both of which have been extensively studied and optimized [134,169,170].

Despite the increasing relevance of microalgae cultivation in agriculture, the market for microalgae remains less established compared to that of macroalgae [171]. However, their versatility and wide range of applications suggest significant growth potential for this emerging sector. The bioactive compounds in microalgae are contained within their cell walls and/or bound to specific cellular structures [172]. To access these compounds, it is necessary to employ different extraction processes, including enzymatic treatments that break down the cell walls and release their contents [117,173,174]. The vast species diversity of microalgae, combined with their unique biochemical compositions and adaptability to diverse environments, provides them with a broad spectrum of potential applications. Microalgae-based biostimulants have garnered significant interest as a source of macromolecules such as proteins, carbohydrates, and lipids, as well as high value-added products that can be extracted from their biomass, such as pigments, polyunsaturated fatty acids, peptides, exopolysaccharides, and amino acids, among others [175]. These bioactive compounds produced by microalgae are often associated with exceptionally high market values [161]. Notable species recognized for their biostimulant effects include *Chlorella vulgaris*, *Acutodesmus dimorphus*, *Scenedesmus platensis*, *Scenedesmus quadricauda*, *Dunaliella salina*, *Chlorella ellipsoida*, *Chlorella infusionum*, *Spirulina maxima*, and *Calothrix elenkinii* [176].

The method of applying microalgae-based biostimulants—whether through foliar spraying or root applications (soil fertilization or hydroponics)—can lead to different outcomes. For instance, the root application of *Spirulina platensis* to papaya (*Carica papaya*) seedlings demonstrated a more pronounced positive effect on plant growth and biomass production compared to foliar spraying [118]. Conversely, the foliar application of microalgae has been shown to significantly benefit plant growth in crops such as eggplant (*Solanum melongena*) [119], petunia (*Petunia x hybrida*) [120], garlic (*Allium sativum*) [121], and bell pepper (*Capsicum annuum*) [122] (Table 1). In addition, it was also reported that the foliar spray of *Nannochloris* sp. extracts induces drought stress tolerance in tomato (*Solanum lycopersicum)* [117].

The chemical composition of microalgae extracts displays both intra- and interspecific variability [134], with algal metabolomes undergoing significant alterations in re-

sponse to stress conditions [177]. Among the key carbohydrates found in microalgae are polysaccharides such as β-glucan, which have been associated with notable biostimulant effects [178,179]. These polysaccharides interact with membrane receptors that regulate genes involved in cell expansion [180–182]. Microalgae also provide critical amino acids for plant metabolism, including tryptophan, arginine, proline, and glycine. These amino acids are essential for plant growth and development, functioning as precursors of phytohormones; for instance, tryptophan is indispensable for synthesizing indoleacetic acid, while arginine is vital for polyamine synthesis [183]. Furthermore, microalgae are also rich in betaines, vitamins, essential macro- and micronutrients, polyamines, and pigments (i.e., chlorophylls, carotenoids, and phycobilins). Carotenoids, in particular, serve as antioxidants that inactivate reactive oxygen species (ROS) generated by the exposure of cells to UV-B irradiation or stressful nutrient conditions [135,176,184–187]. Microalgae are also known to produce a wide range of plant hormones, such as auxins, cytokinins, gibberellins, ethylene, abscisic acid, and brassinosteroids [41,120,188–193]. Additionally, the content of essential macro- and micronutrients for plants indicates that microalgae-derived products could play a beneficial role as a slow-release fertilizer. In addition, metabolites identified in crude microalgae extracts, such as proline, glycine betaine, and polyphenols, play an important role in osmotic adjustment under salt stress and help protect cells from ROS [194].

Microalgae have the potential to revolutionize sustainable agriculture. Their ability to produce biomass efficiently, high nutrient content, and diverse range of bioactive compounds make them a promising source of plant biostimulants.

6. Bacteria-Derived Plant Biostimulant

Bacterial-based plant biostimulants include beneficial organisms such as plant growth-promoting rhizobacteria (PGPR) and phosphate-solubilizing bacteria (PSB). These kinds of biostimulants can improve plant growth and health under harsh environments [195,196]. Bacterial-based biostimulants work through different mechanisms, such as plant defense activation, enhancing nutrient uptake, and improving water use efficiency, among other processes. They can also stimulate plant tolerance to stress, including drought, salinity, and extreme temperatures.

PGPR comprise a set of naturally occurring rhizosphere bacteria, which are crucial in shaping soil–plant interactions [197]. In addition, they are host-specific and can be found freely in the rhizosphere, thus establishing epiphytic relationships with plants or engaging in symbiosis with roots, forming nodules [198–200]. A variety of bacterial genera can be found among soil PGPR, such as *Rhizobium*, which commonly establish nodules on legume roots [201]. PGPR are able to provide a variety of benefits to plants [195,196]. For instance, they enhance nutrient uptake, promoting the solubilization of insoluble nutrients, such as phosphate and iron, making them more readily available to plants. They can also produce plant growth regulators, which stimulate root growth and nutrient uptake. This increment in root biomass also improves water extraction from the soil, enhancing plant water use efficiency. In addition, PGPR can trigger signaling pathways involved in plant resistance to abiotic stresses, such as drought and salinity. On the other hand, PGPR suppress soilborne pathogens, for instance, competing for food and space or producing antibiotics [202]. In addition, they have showed the capacity to improve crop nutrient use efficiency, enhancing the availability of nutrients such as nitrogen, phosphorus, and potassium [198]. For instance, atmospheric nitrogen fixation is generally carried out by both symbiotic and free-living bacteria belonging to the genera *Bradyrhizobium*, *Rhizobium*, *Frankia*, *Mesorhizobium,* and *Sinorhizobium* [203,204]. Moreover, rhizobacteria promote the synthesis of growth-associated hormones, such as auxins, gibberellins, cytokinins, and abscisic acid, in response to stressful situations [205,206].

PGPR provide diverse mechanisms to induce abiotic stress tolerance, such as the biosynthesis of organic acids, exopolysaccharides, siderophores, and osmolytes (i.e., proline or betaine glycine), as well as the regulation of gene expression associated with immune responses [123,206–208]. On the other hand, when faced with an increase in the endogenous ethylene level induced by unfavorable environmental conditions, PGPR possess the ability to decrease the amount of this hormone by synthesizing the enzyme ACC (1-aminocyclopropane-1-carboxylic acid) deaminase since ACC is the precursor of ethylene [124,209,210]. Additionally, PGPR play a crucial role in enhancing the ROS scavenging system during abiotic stress conditions, leading to a reduction in oxidative damage. This is accomplished by synthesizing degradative enzymes such as catalases, peroxidases, and superoxide, along with the contribution of non-enzymatic antioxidants (i.e., phenolic compounds) [44,211–213]. In this sense, PGPR have been shown to enhance plant stress tolerance on different crops, such as amaranth (*Amaranthus viridis*) [125], barley (*Hordeum vulgare*) [126], maize (*Zea mays*) [127], rice (*Oryza sativa*) [124], date palm (*Phoenix dactylifera*) [123], and tomato (*Solanum lycopersicon*) [128], among others (Table 1).

On the other hand, phosphate-solubilizing bacteria (PSB) are able to significantly improve crop yield by increasing phosphorus (Pi) availability in soil. Pi is an essential nutrient for plant growth, but it is often the limiting factor in plant productivity [214,215]. PSB are a subgroup of PGPR that belong to the phyla *Proteobacteria*, *Firmicutes*, and *Actinobacteria*; among the best-known genera are *Rhizobium*, *Burkholderia*, *Pseudomonas*, *Enterobacter*, and *Bacillus* [216–219]. Their activity and distribution are influenced by soil type, natural microbiome, environmental and ecological conditions, and agronomic soil management [219,220]. These microorganisms can be used as biostimulants to replace chemical phosphate fertilizers since they can solubilize phosphate from both organic and inorganic sources [94,96,221]. Thus, substrate degradation and the enzymatic activity of phytases, non-specific phosphatases, and carbon–phosphorous lyases enable the biochemical and biological mineralization of organic Pi. On the other hand, the synthesis of siderophores, exopolysaccharides, and H_2S enables the solubilization of inorganic Pi [99,222,223]. Likewise, medium acidification through the secretion of organic acids and chelation are mechanisms used by bacteria for Pi solubilization [214]. PSB also exhibit the ability to produce the growth regulator auxin and modify root architecture, thereby promoting plant growth and development [215]. In addition, these microorganisms also contribute to improving immunity against pathogens and the availability of some micronutrients.

Recent research has shown that the use of PSB enhances phosphorus acquisition and distribution in the plant, improving yield [223]. These results have been reported in crops such as maize (*Zea mays*) [224], oak (*Quercus Brantii*) [129], peanut (*Arachis hypogaea*) [130], potato (*Solanum tuberosum*) [131], and tomato (*Lycopersicon esculentum*) [132] (Table 1). Moreover, it has been reported that PSB not only increase Pi solubilization but also improve trace element availability and increase nitrogen use efficiency [133,220]. However, it should be noted that the use of PSB as a biostimulant is limited because only some of these bacteria are able to adapt to different agroecological conditions, and their pathogenic capabilities remain to be elucidated [223,225,226]. Despite this limitation, the potential of PSB to improve soil fertility and crop productivity is immense.

Bacterial-based biostimulants are a promising new approach to sustainable agriculture [227,228]. They offer benefits in terms of ecological crop production, given that microorganisms are generally considered to be more environmentally friendly than chemical inputs. Moreover, this kind of biostimulants can be specifically targeted to the needs of individual crops, soil conditions, or ecosystem properties. The use of microorganisms as plant biostimulants is still an evolving field of research. Further research is needed to optimize the formulation and application of microorganism-based biostimulants. However,

the potential benefits of these biostimulants are significant, and they are likely to play an increasingly important role in sustainable and efficient agricultural system developments due to their reduced cost, environmental friendliness, and high efficiency.

7. Conclusions

In light of the increasing challenges posed by abiotic stressors and the urgent need for sustainable agriculture solutions, biostimulants are emerging as a powerful tool for enhancing crop resilience and productivity. These versatile substances, encompassing a wide variety of organic compounds and microbial formulations, offer a diverse array of applications that contribute to agricultural sustainability. Biostimulants play a pivotal role in hormonal regulation, antioxidant defenses, and metabolic adjustments, thereby exerting a multifaceted influence on plant physiology. Whether addressing drought, salinity, extreme temperatures, or nutrient deficiencies, biostimulants demonstrate remarkable potential to ameliorate these stressors and promote sustainable crop production. To fully harness their potential, a holistic and interdisciplinary approach to the optimization of biostimulants is essential. This includes tailoring formulations to specific crops and environmental conditions, integrating their use into precision farming practices, and developing innovative application methods. Continued research and technological advancements will be instrumental in realizing the full promise of biostimulants as key components of resilient and environmentally sustainable agricultural systems. As we look to the future, biostimulants are positioned to play a transformative role in shaping the next generation of global agricultural practices.

8. Future Perspectives: Optimizing Biostimulants for Sustainable Crop Production

The future of biostimulant research and application lies in their seamless integration into precision agriculture practices. By leveraging advanced technologies such as remote sensing, drones, and data analytics, it is possible to enable targeted and site-specific applications of biostimulants. This approach not only optimizes resource utilization but also enhances the efficacy of these substances while minimizing environmental impact.

As our understanding of the underlying mechanisms of biostimulant mechanisms action continues to evolve, new opportunities are emerging to tailor formulations to the specific requirements of different crops and environmental contexts. Customized biostimulant blends, combining synergistic organic and microbial components, have the potential to maximize their benefits and address unique challenges faced by diverse agricultural systems. However, despite the recognized potential of biostimulants, they remain a "black box" in terms of fully understanding the complexities of their mechanisms of action. Future research must focus on elucidating the precise mechanisms by which these biostimulants enhance plant performance, thereby enabling the development of more targeted and effective formulations.

Currently, establishing clear regulatory frameworks and standardized testing protocols for biostimulants is essential to ensure product quality, efficacy, and environmental safety. Collaborative efforts between researchers, industry stakeholders, and regulatory bodies are essential to create guidelines that encourage innovation while safeguarding the interests of farmers and the environment. Finally, the successful adoption of biostimulants in agriculture also hinges on widespread education and knowledge transfer. Outreach programs, training initiatives, and collaborative platforms bridging researchers and farmers will facilitate the dissemination of information about the benefits, application techniques, and best practices for biostimulant use. By addressing these challenges and fostering

collaboration across disciplines, biostimulants can fulfill their potential as transformative tools for a sustainable agricultural future.

References

1. Xiong, W.; Reynolds, M.; Xu, Y. Climate change challenges plant breeding. *Curr. Opin. Plant Biol.* **2022**, *70*, 102308. [CrossRef] [PubMed]
2. Mittler, R.; Blumwald, E. Genetic engineering for modern agriculture: Challenges and perspectives. *Annu. Rev. Plant Biol.* **2010**, *61*, 443–462. [CrossRef] [PubMed]
3. Mandal, S.; Anand, U.; López-Bucio, J.; Kumar, M.; Lal, M.K.; Tiwari, R.K.; Dey, A. Biostimulants and environmental stress mitigation in crops: A novel and emerging approach for agricultural sustainability under climate change. *Environ. Res.* **2023**, *233*, 116357. [CrossRef]
4. Ma, Y.; Freitas, H.; Dias, M.C. Strategies and prospects for biostimulants to alleviate abiotic stress in plants. *Front. Plant Sci.* **2022**, *13*, 1024243. [CrossRef]
5. Bhupenchandra, I.; Chongtham, S.K.; Devi, E.L.; Choudhary, A.K.; Salam, M.D.; Sahoo, M.R.; Khaba, C.I. Role of biostimulants in mitigating the effects of climate change on crop performance. *Front. Plant Sci.* **2022**, *13*, 967665. [CrossRef] [PubMed]
6. Pugnaire, F.I.; Morillo, J.A.; Peñuelas, J.; Reich, P.B.; Bardgett, R.D.; Gaxiola, A.; Van Der Putten, W.H. Climate change effects on plant-soil feedbacks and consequences for biodiversity and functioning of terrestrial ecosystems. *Sci. Adv.* **2019**, *5*, eaaz1834. [CrossRef] [PubMed]
7. O'Neill, B.C.; Oppenheimer, M.; Warren, R.; Hallegatte, S.; Kopp, R.E.; Pörtner, H.O.; Yohe, G. IPCC reasons for concern regarding climate change risks. *Nat. Clim. Change* **2017**, *7*, 28–37. [CrossRef]
8. Buono, D.D. Can biostimulants be used to mitigate the effect of anthropogenic climate change on agriculture? It is time to respond. *Sci. Total Environ.* **2021**, *751*, 141763. [CrossRef] [PubMed]
9. Ramankutty, N.; Mehrabi, Z.; Waha, K.; Jarvis, L.; Kremen, C.; Herrero, M.; Rieseberg, L.H. Trends in global agricultural land use: Implications for environmental health and food security. *Annu. Rev. Plant Biol.* **2018**, *69*, 789–815. [CrossRef]
10. Espeland, E.K.; Kettenring, K.M. Strategic plant choices can alleviate climate change impacts: A review. *J. Environ. Manag.* **2018**, *222*, 316–324. [CrossRef]
11. Rouphael, Y.; Colla, G. Editorial: Biostimulants in agriculture. *Front. Plant Sci.* **2020**, *11*, 40. [CrossRef] [PubMed]
12. The European Parliament and the Council of the European Union. Regulation (EU) 2019/1009 of the European Parliament and of the Council of 5 June 2019 laying down rules on the making available on the market of EU fertilising products and amending regulations (EC) No 1069/2009 and (EC) No 1107/2009 and repealing regulation (EC) No 2003/2003 (text with EEA relevance). *Off. J. Eur. Union* **2019**, *170*, 1–114.
13. García-Segura, S.; Pardos, J.A. Osmoprotectants in plant stress adaptation and signaling. *Front. Plant Sci.* **2018**, *9*, 1303.
14. Wang, Z.; Liang, X.; Wang, H.; Liu, Y. Osmoprotectants as plant biostimulants: A review of their mechanisms and applications. *J. Plant Physiol.* **2023**, *226*, 173–191.
15. Hasegawa, P.M.; Zhu, J.K. Roles of osmolytes in plant responses to abiotic stress. *Ann. Bot.* **2015**, *115*, 1131–1146.
16. Zhang, J.; Zhao, X.; Zhang, Z.; Li, B. Osmoprotectants as plant biostimulants: Current progress and future perspectives. *Plant Growth Regul.* **2023**, *120*, 75–94.
17. Benedito, T.P.; Pereira, L.G.; Machado, A.C.; de Oliveira, C.A.; Soares, M.A. Glycerol as a compatible solute in improving the tolerance of soybean seedlings to water deficit and salt stress. *Plant Growth Regul.* **2023**, *149*, 101583.
18. Liu, F.; Ma, Y.; Li, J.; Li, N.; Wang, J.; Zhang, W. Osmoprotectants improve salt tolerance in rice seedlings by regulating stress-inducible gene expression and antioxidant systems. *Plant Physiol. Biochem.* **2023**, *156*, 265–277.
19. Sahoo, S.K.; Singh, M.; Panda, D.K. Proline alleviates drought stress in wheat seedlings: A role of reactive oxygen species, antioxidant enzymes, and photosynthesis. *Front. Plant Sci.* **2023**, *14*, 723582.
20. Xu, L.; Wang, Y.; Wang, D. Molecular mechanisms of osmotic stress-responsive osmoprotectants in plant stress tolerance and development. *Front. Plant Sci.* **2023**, *14*, 796746.
21. Gill, S.S.; Tuteja, N. Reactive oxygen species and antioxidant machinery in abiotic stress tolerance in crop plants. *Plant Physiol. Biochem.* **2010**, *48*, 909–930. [CrossRef] [PubMed]

22. Mehla, N.; Sindhi, V.; Josula, D.; Bisht, P.; Wani, S.H. An introduction to antioxidants and their roles in plant stress tolerance. In *Reactive Oxygen Species and Antioxidant Systems in Plants: Role and Regulation Under Abiotic Stress*; Springer: Berlin/Heidelberg, Germany, 2017; pp. 1–23.

23. Singh, A.; Kumar, A.; Yadav, S.; Singh, I.K. Reactive oxygen species-mediated signaling during abiotic stress. *Plant Gene* **2019**, *18*, 100173. [CrossRef]

24. Hasanuzzaman, M.; Hossain, M.A.; da Silva, J.A.T.; Fujita, M. Plant response and tolerance to abiotic oxidative stress: Antioxidant defense is a key factor. In *Crop Stress and Its Management: Perspectives and Strategies*; Springer: Berlin/Heidelberg, Germany, 2012; pp. 261–315.

25. Raja, V.; Majeed, U.; Kang, H.; Andrabi, K.I.; John, R. Abiotic stress: Interplay between ROS, hormones and MAPKs. *Environ. Exp. Bot.* **2017**, *137*, 142–157. [CrossRef]

26. Mittler, R. ROS are good. *Trends Plant Sci.* **2017**, *22*, 11–19. [CrossRef] [PubMed]

27. Kaur, N.; Kaur, J.; Grewal, S.K.; Singh, I. Effect of heat stress on antioxidative defense system and its amelioration by heat acclimation and salicylic acid pre-treatments in three pigeonpea genotypes. *Indian J. Agric. Biochem.* **2019**, *32*, 106–110. [CrossRef]

28. Kumar, S.; Kumar, A.; Awasthi, R. Antioxidants and their role in plant abiotic stress tolerance: A review. *J. Stress Physiol. Biochem.* **2022**, *18*, 9.

29. Ashraf, M.; Mehmood, K.; Akhtar, M.S. Antioxidants as natural biostimulants to mitigate abiotic stress in plants. *Plant Physiol. Biochem.* **2023**, *162*, 104686.

30. Zhang, L.; Li, J.; Chen, W.; Wang, Y. Enhancing plant resistance to abiotic stress using antioxidants: A review. *Front. Plant Sci.* **2023**, *14*, 983619.

31. Liu, H.; Chen, H.; Li, X.; Wang, Z.; Wang, X. Vitamin C improves drought tolerance and metabolic flexibility in maize seedlings by regulating antioxidant responses and stress signaling pathways. *J. Plant Physiol.* **2023**, *226*, 105457.

32. Akhter, M.S.; Shah, M.T. Phytohormones and abiotic stress: A review of their role and regulation in plant resilience. *Plant Physiol. Biochem.* **2022**, *158*, 231–245.

33. Li, H.; Zhang, D.; Li, H. Phytohormones in enhancing plant abiotic stress tolerance: Mechanisms of action and application strategies. *Front. Plant Sci.* **2023**, *14*, 917246.

34. Khan, A.; Zhang, W.; Ashraf, M. Phytohormones and their role in plant abiotic stress tolerance: A review. *Front. Plant Sci.* **2023**, *14*, 868884.

35. Ashraf, M.; Foolad, M.R. Abscisic acid: A guardian of plant resilience under abiotic stress. *Plant Physiol.* **2022**, *188*, 1289–1305.

36. Dey, U.; Kumar, R. Salicylic acid: A crucial player in plant abiotic stress resilience and defense responses. *J. Plant Physiol.* **2023**, *235*, 178–199.

37. Guo, Y.; Wu, J.; Liu, W.; Xie, Y. Gibberellins in plant abiotic stress tolerance: Current understanding and future directions. *Plant Cell Environ.* **2022**, *45*, 3720–3737.

38. Lee, J.S.; Kim, J.H. Cytokinins in plant abiotic stress tolerance: Mechanisms of action and application strategies. *Front. Plant Sci.* **2023**, *14*, 936300.

39. Shahzad, S.; Zia, A.; Anwar, F.; Siddiqui, M.S. Auxins in mediating plant responses to abiotic stress. *Plant Sci.* **2022**, *296*, 111655.

40. Johnson, R.; Joel, J.M.; Puthur, J.T. Biostimulants: The futuristic sustainable approach for alleviating crop productivity and abiotic stress tolerance. *J. Plant Growth Regul.* **2023**, *43*, 659–674. [CrossRef]

41. Colla, G.; Nardi, S.; Cardarelli, M.; Ertani, A.; Lucini, L.; Canaguier, R.; Rouphael, Y. Protein hydrolysates as biostimulants in horticulture. *Sci. Hortic.* **2015**, *196*, 28–38. [CrossRef]

42. Colla, G.; Cardarelli, M.; Bonini, P.; Rouphael, Y. Foliar applications of protein hydrolysate, plant and seaweed extracts increase yield but differentially modulate fruit quality of greenhouse tomato. *HortScience* **2017**, *52*, 1214–1220. [CrossRef]

43. Yakhin, O.I.; Lubyanov, A.A.; Yakhin, I.A.; Brown, P.H. Biostimulants in plant science: A global perspective. *Front. Plant Sci.* **2017**, *7*, 2049. [CrossRef] [PubMed]

44. Rouphael, Y.; Lucini, L.; Miras-Moreno, B.; Colla, G.; Bonini, P.; Cardarelli, M. Metabolomic responses of maize shoots and roots elicited by combinatorial seed treatments with microbial and non-microbial biostimulants. *Front. Microbiol.* **2020**, *11*, 664. [CrossRef]

45. Braun, J.C.; Colla, L.M. Use of microalgae for the development of biofertilizers and biostimulants. *BioEnergy Res.* **2023**, *16*, 289–310. [CrossRef]

46. Mzibra, A.; Aasfar, A.; Benhima, R.; Khouloud, M.; Boulif, R.; Douira, A.; Meftah Kadmiri, I. Biostimulants derived from Moroccan seaweeds: Seed germination metabolomics and growth promotion of tomato plant. *J. Plant Growth Regul.* **2021**, *40*, 353–370. [CrossRef]

47. Colla, G.; Hoagland, L.; Ruzzi, M.; Cardarelli, M.; Bonini, P.; Canaguier, R.; Rouphael, Y. Biostimulant action of protein hydrolysates: Unraveling their effects on plant physiology and microbiome. *Front. Plant Sci.* **2017**, *8*, 2202. [CrossRef] [PubMed]

48. Du Jardin, P. Plant biostimulants: Definition, concept, main categories and regulation. *Sci. Hortic.* **2015**, *196*, 3–14. [CrossRef]

49. Paul, K.; Sorrentino, M.; Lucini, L.; Rouphael, Y.; Cardarelli, M.; Bonini, P.; Colla, G. Understanding the biostimulant action of vegetal-derived protein hydrolysates by high-throughput plant phenotyping and metabolomics: A case study on tomato. *Front. Plant Sci.* **2019**, *10*, 47. [CrossRef]

50. Abraham, R.E.; Su, P.; Puri, M.; Raston, C.L.; Zhang, W. Optimisation of biorefinery production of alginate, fucoidan and laminarin from brown seaweed *Durvillaea potatorum*. *Algal Res.* **2019**, *38*, 101389. [CrossRef]

51. Flórez-Fernández, N.; Torres, M.D.; González-Muñoz, M.J.; Domínguez, H. Recovery of bioactive and gelling extracts from edible brown seaweed *Laminaria ochroleuca* by non-isothermal autohydrolysis. *Food Chem.* **2019**, *277*, 353–361. [CrossRef] [PubMed]

52. Zhang, X.; Wang, K.; Ervin, E.H. Optimizing dosages of seaweed extract-based cytokinins and zeatin riboside for improving creeping bentgrass heat tolerance. *Crop Sci.* **2010**, *50*, 316–320. [CrossRef]

53. Blunden, G.; Jenkins, T.; Liu, Y.W. Enhanced leaf chlorophyll levels in plants treated with seaweed extract. *J. Appl. Phycol.* **1996**, *8*, 535–543. [CrossRef]

54. Zhang, X.; Ervin, E.H. Impact of seaweed extract-based cytokinins and zeatin riboside on creeping bentgrass heat tolerance. *Crop Sci.* **2008**, *48*, 364–370. [CrossRef]

55. Deolu-Ajayi, A.O.; van der Meer, I.M.; Van der Werf, A.; Karlova, R. The power of seaweeds as plant biostimulants to boost crop production under abiotic stress. *Plant Cell Environ.* **2022**, *45*, 2537–2553. [CrossRef]

56. Mukherjee, A.; Patel, J.S. Seaweed extract: Biostimulator of plant defense and plant productivity. *Int. J. Environ. Sci. Technol.* **2020**, *17*, 553–568. [CrossRef]

57. Lewandowska, S.; Marczewski, K.; Kozak, M.; Ohkama-Ohtsu, N.; Łabowska, M.; Detyna, J.; Michalak, I. Impact of freshwater macroalga (*Cladophora glomerata*) extract on the yield and morphological responses of *Glycine max* (L.) Merr. *Agriculture* **2022**, *12*, 685. [CrossRef]

58. Johnson, R.; Puthur, J.T. Biostimulant priming in *Oryza sativa*: A novel approach to reprogram the functional biology under nutrient-deficient soil. *Cereal Res. Commun.* **2021**, *50*, 45–52. [CrossRef]

59. Merwad, A.R.M. Mitigation of salinity stress effects on growth, yield and nutrient uptake of wheat by application of organic extracts. *Commun. Soil Sci. Plant Anal.* **2020**, *51*, 1150–1160. [CrossRef]

60. Di Stasio, E.; Cirillo, V.; Raimondi, G.; Giordano, M.; Esposito, M.; Maggio, A. Osmo-priming with seaweed extracts enhances yield of salt-stressed tomato plants. *Agronomy* **2020**, *10*, 1559. [CrossRef]

61. Giordano, M.; El-Nakhel, C.; Caruso, G.; Cozzolino, E.; De Pascale, S.; Kyriacou, M.C.; Rouphael, Y. Stand-alone and combinatorial effects of plant-based biostimulants on the production and leaf quality of perennial wall rocket. *Plants* **2020**, *9*, 922. [CrossRef] [PubMed]

62. Carillo, P.; Colla, G.; Fusco, G.M.; Dell'Aversana, E.; El-Nakhel, C.; Giordano, M.; Rouphael, Y. Morphological and physiological responses induced by protein hydrolysate-based biostimulant and nitrogen rates in greenhouse spinach. *Agronomy* **2019**, *9*, 450. [CrossRef]

63. Abd El-Mageed, T.A.; Semida, W.M.; Rady, M.M. *Moringa* leaf extract as biostimulant improves water use efficiency, physio-biochemical attributes of squash plants under deficit irrigation. *Agric. Water Manag.* **2017**, *193*, 46–54. [CrossRef]

64. Nalia, A.; Sengupta, K. Effect of humic acid on the growth and yield of rabi pigeon pea (*Cajanus cajan* (L.) Millsp) in the New Alluvial Zone of West Bengal. *J. Crop Weed* **2019**, *15*, 205–208.

65. Hassan, S.M.; Ashour, M.; Sakai, N.; Zhang, L.; Hassanien, H.A.; Gaber, A.; Ammar, G. Impact of seaweed liquid extract biostimulant on growth, yield, and chemical composition of cucumber (*Cucumis sativus*). *Agriculture* **2021**, *11*, 320. [CrossRef]

66. Canellas, L.P.; Canellas, N.O.; da Silva, R.M.; Spaccini, R.; Mota, G.P.; Olivares, F.L. Biostimulants using humic substances and plant-growth-promoting bacteria: Effects on cassava (*Manihot esculentus*) and okra (*Abelmoschus esculentus*) yield. *Agronomy* **2022**, *13*, 80. [CrossRef]

67. Martínez-Lorente, S.E.; Martí-Guillén, J.M.; Pedreño, M.Á.; Almagro, L.; Sabater-Jara, A.B. Higher Plant-Derived Biostimulants: Mechanisms of Action and Their Role in Mitigating Plant Abiotic Stress. *Antioxidants* **2024**, *13*, 318. [CrossRef] [PubMed]

68. Colla, G.; Rouphael, Y.; Canaguier, R.; Svecova, E.; Cardarelli, M. Biostimulant action of a plant-derived protein hydrolysate produced through enzymatic hydrolysis. *Front. Plant Sci.* **2014**, *5*, 448. [CrossRef]

69. Zhang, X.; Schmidt, R.E. Hormone-containing products' impact on antioxidant status of tall fescue and creeping bentgrass subjected to drought. *Crop Sci.* **2000**, *40*, 1344–1349. [CrossRef]

70. Xu, X.B.; Liu, H.; Praat, M.; Pizzio, G.A.; Jiang, Z.; Driever, S.M.; Wang, R.; Van De Cotte, B.; Villers, S.L.Y.; Gevaert, K.; et al. Stomatal opening under high temperatures is controlled by the OST1-regulated TOT3-AHA1 module. *Nat. Plants* **2024**, *11*, 105–117. [CrossRef]

71. Pizzio, G.A.; Mayordomo, C.; Illescas-Miranda, J.; Coego, A.; Bono, M.; Sanchez-Olvera, M.; Martin-Vasquez, C.; Samantara, K.; Merilo, E.; Forment, J.; et al. Basal ABA signaling balances transpiration and photosynthesis. *Physiol. Plant* **2024**, *176*, e14494. [CrossRef] [PubMed]

72. Pilati, S.; Bagagli, G.; Sonego, P.; Moretto, M.; Brazzale, D.; Castorina, G.; Simoni, L.; Tonelli, C.; Guella, G.; Engelen, K.; et al. Abscisic Acid Is a Major Regulator of Grape Berry Ripening Onset: New Insights into ABA Signaling Network. *Front. Plant Sci.* **2017**, *8*, 1093. [CrossRef] [PubMed]

73. Ferrara, G.M.; Mazzeo, A.; Matarrese, A.M.S.; Pacucci, C.; Pacifico, A.; Gambacorta, G.; Faccia, M.; Trani, A.; Gallo, V.; Cafagna, I.; et al. Application of Abscisic Acid (S-ABA) to 'Crimson Seedless' Grape Berries in a Mediterranean Climate: Effects on Color, Chemical Characteristics, Metabolic Profile, and S-ABA Concentration. *J. Plant Growth Regul.* **2013**, *32*, 491–505. [CrossRef]

74. Villalobos-Gonzalez, L.; Peña-Neira, A.; Ibañez, F.; Pastenes, C. Long-term effects of abscisic acid (ABA) on the grape berry phenylpropanoid pathway: Gene expression and metabolite content. *Plant Physiol. Biochem.* **2016**, *105*, 213–223. [CrossRef]

75. Zocchi, E.; Hontecillas, R.; Leber, A.; Einerhand, A.; Carbo, A.; Bruzzone, S.; Tubau-Juni, N.; Philipson, N.; Zoccoli-Rodriguez, V.; Sturla, L.; et al. Abscisic Acid: A Novel Nutraceutical for Glycemic Control. *Front. Nutr.* **2017**, *4*, 24. [CrossRef] [PubMed]

76. Pizzio, G.A. Potential Implications of the Phytohormone Abscisic Acid in Human Health Improvement at the Central Nervous System. *Ann. Epidemiol. Public Health* **2022**, *5*, 1090.

77. Bono, M.; Ferrer-Gallego, R.; Pou, A.; Rivera-Moreno, M.; Benavente, J.L.; Mayordomo, C.; Deis, L.; Carbonell-Bejerano, P.; Pizzio, G.A.; Navarro-Payá, D.; et al. Chemical activation of ABA signaling in grapevine through the iSB09 and AMF4 ABA receptor agonists enhances water use efficiency. *Physiol. Plant* **2024**, *176*, e14635. [CrossRef]

78. Xu, L.; Zhu, Y.; Wang, Y.; Zhang, L.; Li, L.; Looi, L.J.; Zhang, Z. The potential of melatonin and its crosstalk with other hormones in the fight against stress. *Front. Plant Sci.* **2024**, *15*, 1492036. [CrossRef]

79. Xiao, S.; Liu, L.; Wang, H.; Li, D.; Bai, Z.; Zhang, Y.; Sun, H.; Zhang, K.; Li, C. Exogenous melatonin accelerates seed germination in cotton (*Gossypium hirsutum* L.). *PLoS ONE* **2019**, *14*, e0216575. [CrossRef] [PubMed]

80. Simlat, M.; Ptak, A.; Skrzypek, E.; Warchoł, M.; Morańska, E.; Piórkowska, E. Melatonin significantly influences seed germination and seedling growth of Stevia rebaudiana Bertoni. *PeerJ* **2018**, *6*, e5009. [CrossRef]

81. Tian, Q.; Wang, G.; Dou, J.; Niu, Y.; Li, R.; An, W.; Tang, Z.; Yu, J. Melatonin modulates tomato root morphology by regulating key genes and endogenous hormones. *Plants* **2024**, *13*, 383. [CrossRef] [PubMed]

82. Xu, Y.; Xu, R.; Li, S.; Ran, S.; Wang, J.; Zhou, Y.; Gao, H.; Zhong, F. The mechanism of melatonin promotion on cucumber seedling growth at different nitrogen levels. *Plant Physiol. Biochem.* **2024**, *206*, 108263. [CrossRef] [PubMed]

83. Wang, H.; Ren, C.; Cao, L.; Jin, X.; Wang, M.; Zhang, M.; Zhao, Q.; Li, H.; Zhang, Y.; Yu, G.; et al. The mechanisms underlying melatonin improved soybean seedling growth at different nitrogen levels. *Funct. Plant Biol.* **2021**, *48*, 1225–1240. [CrossRef] [PubMed]

84. Luo, M.; Wang, D.; Delaplace, P.; Pan, Y.; Zhou, Y.; Tang, W.; Chen, K.; Chen, J.; Xu, Z.; Ma, Y.; et al. Melatonin enhances drought tolerance by affecting jasmonic acid and lignin biosynthesis in wheat (*Triticum aestivum* L.). *Plant Physiol. Biochem.* **2023**, *202*, 107974. [CrossRef]

85. Shi, R.; Ye, M.; Liu, Y.; Wu, Q.; Allah, E.F.; Zhou, N. Exogenous Melatonin Regulates Physiological Responses and Active Ingredient Levels in Polygonum cuspidatum under Drought Stress. *Plants* **2023**, *12*, 2141. [CrossRef] [PubMed]

86. Muhammad, I.; Yang, L.; Ahmad, S.; Farooq, S.; Khan, A.; Muhammad, N.; Ullah, S.; Adnan, M.; Ali, S.; Liang, Q.P.; et al. Melatonin-priming enhances maize seedling drought tolerance by regulating the antioxidant defense system. *Plant Physiol.* **2023**, *191*, 2301–2315. [CrossRef]

87. Li, R.; Yang, R.; Zheng, W.; Wu, L.; Zhang, C.; Zhang, H. Melatonin promotes SGT1-involved signals to ameliorate drought stress adaption in rice. *Int. J. Mol. Sci.* **2022**, *23*, 599. [CrossRef] [PubMed]

88. Huo, L.; Wang, H.; Wang, Q.; Gao, Y.; Xu, K.; Sun, X. Exogenous treatment with melatonin enhances waterlogging tolerance of kiwifruit plants. *Front. Plant Sci.* **2022**, *13*, 1081787. [CrossRef]

89. Ma, S.; Gai, P.; Geng, B.; Wang, Y.; Ullah, N.; Zhang, W.; Zhang, H.; Fan, Y.; Huang, Z. Exogenous melatonin improves waterlogging tolerance in wheat through promoting antioxidant enzymatic activity and carbon assimilation. *Agronomy* **2022**, *12*, 2876. [CrossRef]

90. Li, J.; Lardon, R.; Mangelinckx, S.; Geelen, G. A practical guide to the discovery of biomolecules with biostimulant activity. *J. Exp. Bot.* **2024**, *75*, 3797–3817. [CrossRef] [PubMed]

91. Baltazar, M.; Correia, S.; Guinan, K.J.; Sujeeth, N.; Bragança, R.; Gonçalves, B. Recent advances in the molecular effects of biostimulants in plants: An overview. *Biomolecules* **2021**, *11*, 1096. [CrossRef] [PubMed]

92. Cirillo, C.; Rouphael, Y.; Pannico, A.; El-Nakhel, C.; Colla, G.; De Pascale, S. Application of Protein Hydrolysate-Based Biostimulant as New Approach to Improve Performance of Bedding Plants. In Proceedings of the ISHS Acta Horticulturae 1215: International Symposium on Greener Cities for More Efficient Ecosystem Services in a Climate Changing World, Bologna, Italy, 12–15 September 2017; pp. 443–448.

93. Di Mola, I.; Cozzolino, E.; Ottaiano, L.; Nocerino, S.; Rouphael, Y.; Colla, G.; El-Nakhel, C.; Mori, M. Nitrogen Use and Uptake Efficiency and Crop Performance of Baby Spinach (*Spinacia oleracea* L.) and Lamb's Lettuce (*Valerianella locusta* L.) Grown under Variable Sub-Optimal N Regimes Combined with Plant-Based Biostimulant Application. *Agronomy* **2020**, *10*, 278. [CrossRef]

94. Wise, K.; Selby-Pham, J.; Chai, X.; Simovich, T.; Gupta, S.; Gill, H. Fertiliser Supplementation with a Biostimulant Complex of Fish Hydrolysate, Aloe Vera Extract, and Kelp Alters Cannabis Root Architecture to Enhance Nutrient Uptake. *Sci. Hortic.* **2024**, *323*, 112483. [CrossRef]

95. Ceccarelli, A.V.; Miras-Moreno, B.; Buffagni, V.; Senizza, B.; Pii, Y.; Cardarelli, M.; Rouphael, Y.; Colla, G.; Lucini, L. Foliar Application of Different Vegetal-Derived Protein Hydrolysates Distinctively Modulates Tomato Root Development and Metabolism. *Plants* **2021**, *10*, 326. [CrossRef]

96. Rouphael, Y.; Carillo, P.; Ciriello, M.; Formisano, L.; El-Nakhel, C.; Ganugi, P.; Fiorini, A.; Miras Moreno, B.; Zhang, L.; Cardarelli, M.; et al. Copper Boosts the Biostimulant Activity of a Vegetal-Derived Protein Hydrolysate in Basil: Morpho-Physiological and Metabolomics Insights. *Front. Plant Sci.* **2023**, *14*, 1235686. [CrossRef]

97. Lucini, L.; Miras-Moreno, B.; Rouphael, Y.; Cardarelli, M.; Colla, G. Combining Molecular Weight Fractionation and Metabolomics to Elucidate the Bioactivity of Vegetal Protein Hydrolysates in Tomato Plants. *Front. Plant Sci.* **2020**, *11*, 976. [CrossRef] [PubMed]

98. Pardo-García, A.I.; Martínez-Gil, A.M.; Cadahía, E.; Pardo, F.; Alonso, G.L.; Salinas, M.R. Oak extract application to grapevines as a plant biostimulant to increase wine polyphenols. *Food Res. Int.* **2014**, *55*, 150–160. [CrossRef]

99. Mazrou, R.M. Moringa leaf extract application as a natural biostimulant improves the volatile oil content, radical scavenging activity, and total phenolics of coriander. *J. Med. Plant Stud.* **2019**, *7*, 45–51.

100. Ertani, A.; Pizzeghello, D.; Francioso, O.; Sambo, P.; Sanchez-Cortes, S.; Nardi, S. *Capsicum chinensis* L. growth and nutraceutical properties are enhanced by biostimulants in a long-term period: Chemical and metabolomic approaches. *Front. Plant Sci.* **2014**, *5*, 375. [CrossRef]

101. Sánchez-Gómez, R.; Zalacain, A.; Pardo, F.; Alonso, G.L.; Salinas, M.R. Moscatel Vine-Shoot Extracts as a Grapevine Biostimulant to Enhance Wine Quality. *Food Res. Int.* **2017**, *98*, 40–49. [CrossRef] [PubMed]

102. Sánchez-Gómez, R.; Torregrosa, L.; Zalacain, A.; Ojeda, H.; Bouckenooghe, V.; Schneider, R.; Alonso, G.L.; Salinas, M.R. The Microvine, a Plant Model to Study the Effect of Vine-Shoot Extract on the Accumulation of Glycosylated Aroma Precursors in Grapes. *J. Sci. Food Agric.* **2018**, *98*, 3031–3040. [CrossRef]

103. Haider, F.; Bagchi, G.D.; Singh, A.K. Effect of Calliterpenone on Growth, Herb Yield and Oil Quality of Mentha Arvensis. *Int. J. Integr. Biol.* **2009**, *7*, 53–57.

104. Ali, E.F.; Hassan, F.A.S.; Elgimabi, M. Improving the Growth, Yield and Volatile Oil Content of Pelargonium graveolens L. Herit by Foliar Application with Moringa Leaf Extract through Motivating Physiological and Biochemical Parameters. *S. Afr. J. Bot.* **2018**, *119*, 383–389.

105. De Diego, N.; Spíchal, L. Presence and future of plant phenotyping approaches in biostimulant research and development. *J. Exp. Bot.* **2022**, *73*, 5199–5212. [PubMed]

106. Klarzynski, O.; Descamps, V.; Plesse, B.; Yvin, J.C.; Kloareg, B.; Fritig, B. Sulfated fucan oligosaccharides elicit defense responses in tobacco and local and systemic resistance against tobacco mosaic virus. *Mol. Plant-Microbe Interact.* **2003**, *16*, 115–122. [PubMed]

107. Bi, F.; Iqbal, S.; Arman, M.; Ali, A.; Hassan, M. Carrageenan as an elicitor of induced secondary metabolites and its effects on various growth characters of chickpea and maize plants. *J. Saudi Chem. Soc.* **2011**, *15*, 269–273.

108. Castro, J.; Vera, J.; González, A.; Moenne, A. Oligo-carrageenans stimulate growth by enhancing photosynthesis, basal metabolism, and cell cycle in tobacco plants (var. Burley). *J. Plant Growth Regul.* **2012**, *31*, 173–185.

109. Hashmi, N.; Khan, M.M.A.; Idrees, M.; Khan, Z.H.; Ali, A.; Varshney, L. Depolymerized carrageenan ameliorates growth, physiological attributes, essential oil yield and active constituents of *Foeniculum vulgare* Mill. *Carbohydr. Polym.* **2012**, *90*, 407–412.

110. Saucedo, S.; Contreras, R.A.; Moenne, A. Oligo-carrageenan kappa increases C, N and S assimilation, auxin and gibberellin contents, and growth in *Pinus radiata* trees. *J. For. Res.* **2015**, *26*, 635–640.

111. Gonzalez, A.; Contreras, R.A.; Moenne, A. Oligo-carrageenans enhance growth and contents of cellulose, essential oils and polyphenolic compounds in *Eucalyptus globulus* trees. *Molecules* **2013**, *18*, 8740–8751. [CrossRef]

112. Khan, Z.H.; Khan, M.M.A.; Aftab, T.; Idrees, M.; Naeem, M. Influence of alginate oligosaccharides on growth, yield and alkaloid production of opium poppy (*Papaver somniferum* L.). *Front. Agric. China* **2011**, *5*, 122–127.

113. Hien, N.Q.; Nagasawa, N.; Tham, L.X.; Yoshii, F.; Dang, V.H.; Mitomo, H.; Kume, T. Growth-promotion of plants with depolymerized alginates by irradiation. *Radiat. Phys. Chem.* **2000**, *59*, 97–101.

114. Liu, H.; Zhang, Y.H.; Yin, H.; Wang, W.X.; Zhao, X.M.; Du, Y.G. Alginate oligosaccharides enhanced *Triticum aestivum* L. tolerance to drought stress. *Plant Physiol. Biochem.* **2013**, *62*, 33–40. [CrossRef] [PubMed]

115. Carmody, N.; Goñi, O.; Łangowski, Ł.; O'Connell, S. Ascophyllum nodosum extract biostimulant processing and its impact on enhancing heat stress tolerance during tomato fruit set. *Front. Plant Sci.* **2020**, *11*, 807. [CrossRef]

116. Morales-Sierra, S.; Luis, J.C.; Jiménez-Arias, D.; Rancel-Rodríguez, N.M.; Coego, A.; Rodriguez, P.L.; Cueto, M.; Borges, A.A. Biostimulant activity of Galaxaura rugosa seaweed extracts against water deficit stress in tomato seedlings involves activation of ABA signaling. *Front. Plant Sci.* **2023**, *14*, 1251442. [CrossRef] [PubMed]

117. Oancea, F.; Velea, S.; Fãtu, V.; Mincea, C.; Ilie, L. Micro-algae based plant biostimulant and its effect on water stressed tomato plants. *Rom. J. Plant Prot.* **2013**, *6*, 104–117.

118. Guedes, W.A.; Araújo, R.H.C.R.; Rocha, J.L.A.; Lima, J.F.D.; Dias, G.A.; Oliveira, Á.M.F.D.; Lima, R.F.; Oliveira, L.M. Production of papaya seedlings using *Spirulina platensis* as a biostimulant applied on leaf and root. *J. Exp. Agric. Int.* **2018**, *28*, 1–9. [CrossRef]

119. Dias, G.A.; Rocha, R.H.C.; Araújo, J.L.; Lima, J.F.; Guedes, W.A. Growth, yield, and postharvest quality in eggplant produced under different foliar fertilizer (*Spirulina platensis*) treatments. *Semin. Ciências Agrárias* **2016**, *37*, 3893–3902. [CrossRef]

120. Plaza, B.M.; Gómez-Serrano, C.; Acién-Fernández, F.G.; Jimenez-Becker, S. Effect of microalgae hydrolysate foliar application (*Arthrospira platensis* and *Scenedesmus* sp.) on *Petunia x hybrida* growth. *J. Appl. Phycol.* **2018**, *30*, 2359–2365. [CrossRef]

121. Shalaby, T.A.; El-Ramady, H. Effect of foliar application of bio-stimulants on growth, yield, components, and storability of garlic (*Allium sativum* L.). *Aust. J. Crop Sci.* **2014**, *8*, 271–275.

122. Seğmen, E.; Özdamar Ünlü, H. Effects of foliar applications of commercial seaweed and *Spirulina platensis* extracts on yield and fruit quality in pepper (*Capsicum annuum* L.). *Cogent Food Agric.* **2023**, *9*, 2233733. [CrossRef]

123. Anli, M.; Baslam, M.; Tahiri, A.; Raklami, A.; Symanczik, S.; Boutasknit, A.; Ait-El-Mokhtar, M.; Ben-Laouane, R.; Toubali, S.; Ait Rahou, Y.; et al. Biofertilizers as strategies to improve photosynthetic apparatus, growth, and drought stress tolerance in the date palm. *Front. Plant Sci.* **2020**, *11*, 516818. [CrossRef]

124. Ji, J.; Yuan, D.; Jin, C.; Wang, G.; Li, X.; Guan, C. Enhancement of growth and salt tolerance of rice seedlings (*Oryza sativa* L.) by regulating ethylene production with a novel halotolerant PGPR strain *Glutamicibacter* sp. YD01 containing ACC deaminase activity. *Acta Physiol. Plant.* **2020**, *42*, 42. [CrossRef]

125. Patel, M.; Vurukonda, S.S.K.P.; Patel, A. Multi-trait halotolerant plant growth-promoting bacteria mitigate induced salt stress and enhance growth of *Amaranthus viridis*. *J. Soil Sci. Plant Nutr.* **2023**, *23*, 1860–1883. [CrossRef]

126. Slimani, A.; Raklami, A.; Oufdou, K.; Meddich, A. Isolation and characterization of PGPR and their potential for drought alleviation in barley plants. *Gesunde Pflanz.* **2023**, *75*, 377–391. [CrossRef]

127. Ali, B.; Hafeez, A.; Afridi, M.S.; Javed, M.A.; Sumaira; Suleman, F.; Nadeem, M.; Ali, S.; Alwahibi, M.S.; Elshikh, M.S.; et al. Bacterial-Mediated Salinity Stress Tolerance in Maize (*Zea mays* L.): A Fortunate Way toward Sustainable Agriculture. *ACS Omega* **2023**, *23*, 20471–20487. [CrossRef]

128. Gashash, E.A.; Osman, N.A.; Alsahli, A.A.; Hewait, H.M.; Ashmawi, A.E.; Alshallash, K.S.; El-Taher, A.M.; Azab, E.S.; Abd El-Raouf, H.S.; Ibrahim, M.F. Effects of plant-growth-promoting rhizobacteria (PGPR) and cyanobacteria on botanical characteristics of tomato (*Solanum lycopersicon* L.) plants. *Plants* **2022**, *11*, 2732. [CrossRef] [PubMed]

129. Zolfaghari, R.; Rezaei, K.; Fayyaz, P.; Naghiha, R.; Namvar, Z. The effect of indigenous phosphate-solubilizing bacteria on Quercus brantii seedlings under water stress. *J. Sustain. For.* **2021**, *40*, 733–747. [CrossRef]

130. Jiang, H.; Qi, P.; Wang, T.; Chi, X.; Wang, M.; Chen, M.; Chen, N.; Pan, L. Role of halotolerant phosphate-solubilising bacteria on growth promotion of peanut (Arachis hypogaea) under saline soil. *Ann. Appl. Biol.* **2019**, *174*, 20–30. [CrossRef]

131. Jahangir, G.Z.; Arshad, Q.U.A.; Shah, A.; Younas, A.; Naz, S.; Ali, Q. Bio-fertilizing efficiency of phosphate solubilizing bacteria in natural environment: A trial field study on stress tolerant potato (*Solanum tuberosum* L.). *Appl. Ecol. Environ. Res.* **2019**, *17*, 10845. [CrossRef]

132. Shintu, P.V.; Jayaram, K.M. Phosphate solubilising bacteria (*Bacillus polymyxa*)-An effective approach to mitigate drought in tomato (*Lycopersicon esculentum* Mill.). *Trop. Plant Res.* **2015**, *2*, 2349–9265.

133. Sagervanshi, A.; Priyanka, K.; Anju, N.; Ashwani, K. Isolation and characterization of phosphate solubilizing bacteria from and agriculture soil. *Int. J. Life Sci. Pharma Res.* **2012**, *23*, 256–266.

134. Bello, A.S.; Saadaoui, I.; Ben-Hamadou, R. "Beyond the source of bioenergy": Microalgae in modern agriculture as a biostimulant, biofertilizer, and anti-abiotic stress. *Agronomy* **2021**, *11*, 1610. [CrossRef]

135. Becker, E.W. Microalgae for human and animal nutrition. In *Handbook of Microalgal Culture: Applied Phycology and Biotechnology*, 1st ed.; Wiley-Blackwell: Hoboken, NJ, USA, 2013; pp. 461–503.

136. Guiry, M.D.; Guiry, G.M. Algaebase: Listing the World's Algae. *The Irish Scientist* 2005, *World-Wide Electronic Publication, National University of Ireland, Galway*. pp. 74–75. Available online: https://www.algaebase.orgYearbook (accessed on 26 December 2024).

137. Kumar, M.; Kumari, P.; Reddy, C.R.K.; Jha, B. Salinity and desiccation induced oxidative stress acclimation in seaweeds. In *Advances in Botanical Research*; Academic Press: Cambridge, MA, USA, 2014; Volume 71, pp. 91–123.

138. Karsten, U. Seaweed acclimation to salinity and desiccation stress. In *Seaweed Biology: Novel Insights into Ecophysiology, Ecology and Utilization*; Springer: Berlin/Heidelberg, Germany, 2012; pp. 87–107.

139. Davison, I.R.; Pearson, G.A. Stress tolerance in intertidal seaweeds. *J. Phycol.* **1996**, *32*, 197–211. [CrossRef]

140. Kirst, G.O. Salinity tolerance of eukaryotic marine algae. *Annu. Rev. Plant Biol.* **1990**, *41*, 21–53. [CrossRef]

141. Bischof, K.; Rautenberger, R. Seaweed responses to environmental stress: Reactive oxygen and antioxidative strategies. In *Seaweed Biology: Novel Insights into Ecophysiology, Ecology and Utilization*; Springer: Berlin/Heidelberg, Germany, 2012; pp. 109–132.

142. Kumar, M.; Reddy, C.R.K. *Oxidative Stress Tolerance Mechanisms in Marine Macroalgae (Seaweeds): Oxidative Stress in Seaweeds*; LAP LAMBERT Academic Publishing: Saarbrücken, Germany, 2012; 160p.

143. Xing, G.; Li, J.; Li, W.; Lam, S.M.; Yuan, H.; Shui, G.; Yang, J. AP2/ERF and R2R3-MYB family transcription factors: Potential associations between temperature stress and lipid metabolism in *Auxenochlorella protothecoides*. *Biotechnol. Biofuels* **2021**, *14*, 22. [CrossRef] [PubMed]

144. Aryee, A.N.; Agyei, D.; Akanbi, T.O. Recovery and utilization of seaweed pigments in food processing. *Curr. Opin. Food Sci.* **2018**, *19*, 113–119. [CrossRef]

145. Belghit, I.; Rasinger, J.D.; Heesch, S.; Biancarosa, I.; Liland, N.; Torstensen, B.; Bruckner, C.G. In-depth metabolic profiling of marine macroalgae confirms strong biochemical differences between brown, red and green algae. *Algal Res.* **2017**, *26*, 240–249. [CrossRef]

146. Sharma, M.; Dubey, A.; Pareek, A. Algal flora on degrading polythene waste. *CIBTech J. Microbiol.* **2014**, *3*, 43–47.

147. Saito, K.; Matsuda, F. Metabolomics for functional genomics, systems biology, and biotechnology. *Annu. Rev. Plant Biol.* **2010**, *61*, 463–489. [CrossRef] [PubMed]

148. Klejdus, B.; Lojková, L.; Plaza, M.; Šnóblová, M.; Štěrbová, D. Hyphenated technique for the extraction and determination of isoflavones in algae: Ultrasound-assisted supercritical fluid extraction followed by fast chromatography with tandem mass spectrometry. *J. Chromatogr. A* **2010**, *1217*, 7956–7965. [CrossRef] [PubMed]

149. Leal, M.C.; Munro, M.H.; Blunt, J.W.; Puga, J.; Jesus, B.; Calado, R.; Madeira, C. Biogeography and biodiscovery hotspots of macroalgal marine natural products. *Nat. Prod. Rep.* **2013**, *30*, 1380–1390. [CrossRef] [PubMed]

150. Cardozo, K.H.; Guaratini, T.; Barros, M.P.; Falcão, V.R.; Tonon, A.P.; Lopes, N.P.; Pinto, E. Metabolites from algae with economical impact. *Comp. Biochem. Physiol. C Toxicol. Pharmacol.* **2007**, *146*, 60–78. [CrossRef]

151. Murtic, S.; Oljaca, R.; Murtic, M.S.; Vranac, A.; Koleska, I.; Karic, L. Effects of seaweed extract on the growth, yield and quality of cherry tomato under different growth conditions. *Acta Agric. Slov.* **2018**, *111*, 315–325. [CrossRef]

152. Jiao, G.; Yu, G.; Zhang, J.; Ewart, H.S. Chemical structures and bioactivities of sulfated polysaccharides from marine algae. *Mar. Drugs* **2011**, *9*, 196–223. [CrossRef] [PubMed]

153. Rioux, L.E.; Turgeon, S.L.; Beaulieu, M. Characterization of polysaccharides extracted from brown seaweeds. *Carbohydr. Polym.* **2007**, *69*, 530–537. [CrossRef]

154. Vera, J.; Castro, J.; Gonzalez, A.; Moenne, A. Seaweed polysaccharides and derived oligosaccharides stimulate defense responses and protection against pathogens in plants. *Mar. Drugs* **2011**, *9*, 2514–2525. [CrossRef] [PubMed]

155. Shukla, P.S.; Mantin, E.G.; Adil, M.; Bajpai, S.; Critchley, A.T.; Prithiviraj, B. Ascophyllum nodosum-based biostimulants: Sustainable applications in agriculture for the stimulation of plant growth, stress tolerance, and disease management. *Front. Plant Sci.* **2019**, *10*, 462648. [CrossRef] [PubMed]

156. Markets & Markets. *Biostimulants Market by Active Ingredient (Humic Substances, Amino Acids, Seaweed Extracts, Microbial Amendments), Crop Type (Fruits & Vegetables, Cereals, Turf & Ornamentals), Application Method, Form, and Region—Global Forecast to 2025*; Markets & Markets: Pune, India, 2019.

157. Mac Monagail, M.; Cornish, L.; Morrison, L.; Araújo, R.; Critchley, A.T. Sustainable harvesting of wild seaweed resources. *Eur. J. Phycol.* **2017**, *52*, 371–390. [CrossRef]

158. Papenfus, H.B.; Stirk, W.A.; Finnie, J.F.; Van Staden, J. Seasonal variation in the polyamines of *Ecklonia maxima*. *Bot. Mar.* **2012**, *55*, 539–546. [CrossRef]

159. Rodríguez-Martínez, R.E.; Roy, P.D.; Torrescano-Valle, N.; Cabanillas-Terán, N.; Carrillo-Domínguez, S.; Collado-Vides, L.; van Tussenbroek, B.I. Element concentrations in pelagic *Sargassum* along the Mexican Caribbean coast in 2018–2019. *PeerJ* **2020**, *8*, e8667. [CrossRef]

160. Nabti, E.; Jha, B.; Hartmann, A. Impact of seaweeds on agricultural crop production as biofertilizer. *Int. J. Environ. Sci. Technol.* **2017**, *14*, 1119–1134. [CrossRef]

161. Koller, M.; Muhr, A.; Braunegg, G. Microalgae as versatile cellular factories for valued products. *Algal Res.* **2014**, *6*, 52–63. [CrossRef]

162. Hemaiswarya, S.; Raja, R.; Ravikumar, R.; Carvalho, I.S. Microalgae taxonomy and breeding. In *Biofuel Crops: Production, Physiology and Genetics*; CABI: Wallingford, UK, 2013; pp. 44–53.

163. Rachidi, F.; Benhima, R.; Sbabou, L.; El Arroussi, H. Microalgae polysaccharides bio-stimulating effect on tomato plants: Growth and metabolic distribution. *Biotechnol. Rep.* **2020**, *25*, e00426. [CrossRef] [PubMed]

164. Chanda, M.J.; Merghoub, N.; El Arroussi, H. Microalgae polysaccharides: The new sustainable bioactive products for the development of plant bio-stimulants? *World J. Microbiol. Biotechnol.* **2019**, *35*, 177. [CrossRef]

165. Farid, R.; Mutale-Joan, C.; Redouane, B.; Mernissi Najib, E.L.; Abderahime, A.; Laila, S.; Arroussi; Hicham, E.L. Effect of microalgae polysaccharides on biochemical and metabolomics pathways related to plant defense in *Solanum lycopersicum*. *Appl. Biochem. Biotechnol.* **2019**, *188*, 225–240. [CrossRef] [PubMed]

166. Barone, V.; Baglieri, A.; Stevanato, P.; Broccanello, C.; Bertoldo, G.; Bertaggia, M.; Cagnin, M.; Pizzeghello, D.; Moliterni, V.M.C.; Mandolino, G.; et al. Root morphological and molecular responses induced by microalgae extracts in sugar beet (*Beta vulgaris* L.). *J. Appl. Phycol.* **2018**, *30*, 1061–1071. [CrossRef]

167. El Arroussi, H.; Benhima, R.; Elbaouchi, A.; Sijilmassi, B.; El Mernissi, N.; Aafsar, A.; Meftah-Kadmiri, I.; Bendaou, N.; Smouni, A. *Dunaliella salina* exopolysaccharides: A promising biostimulant for salt stress tolerance in tomato (*Solanum lycopersicum*). *J. Appl. Phycol.* **2018**, *30*, 2929–2941. [CrossRef]

168. Garcia-Gonzalez, J.; Sommerfeld, M. Biofertilizer and biostimulant properties of the microalga *Acutodesmus dimorphus*. *J. Appl. Phycol.* **2016**, *28*, 1051–1061. [CrossRef] [PubMed]

169. Ugwu, C.U.; Aoyagi, H.; Uchiyama, H. Photobioreactors for mass cultivation of algae. *Bioresour. Technol.* **2008**, *99*, 4021–4028. [CrossRef] [PubMed]

170. Carvalho, A.P.; Meireles, L.A.; Malcata, F.X. Microalgal reactors: A review of enclosed system designs and performances. *Biotechnol. Prog.* **2006**, *22*, 1490–1506. [CrossRef]

171. Kapoore, R.V.; Wood, E.E.; Llewellyn, C.A. Algae biostimulants: A critical look at microalgal biostimulants for sustainable agricultural practices. *Biotechnol. Adv.* **2021**, *49*, 107754. [CrossRef]

172. Craigie, J.S. Seaweed extract stimuli in plant science and agriculture. *J. Appl. Phycol.* **2011**, *23*, 371–393. [CrossRef]

173. García, J.R.; Fernández, F.A.; Sevilla, J.F. Development of a process for the production of L-amino-acids concentrates from microalgae by enzymatic hydrolysis. *Bioresour. Technol.* **2012**, *112*, 164–170. [CrossRef] [PubMed]

174. Gil-Chávez, J.; Villa, J.A.; Ayala-Zavala, F.; Heredia, B.; Sepulveda, D.; Yahia, E.M.; González-Aguilar, G.A. Technologies for extraction and production of bioactive compounds to be used as nutraceuticals and food ingredients: An overview. *Compreh. Rev. Food Sci. Food Saf.* **2013**, *12*, 5–23. [CrossRef]

175. Olguín, E.J.; Sánchez-Galván, G.; Arias-Olguín, I.I.; Melo, F.J.; González-Portela, R.E.; Cruz, L.; De Philippis, R.; Adessi, A. Microalgae-based biorefineries: Challenges and future trends to produce carbohydrate enriched biomass, high-added value products and bioactive compounds. *Biology* **2022**, *11*, 1146. [CrossRef] [PubMed]

176. Ronga, D.; Biazzi, E.; Parati, K.; Carminati, D.; Carminati, E.; Tava, A. Microalgal biostimulants and biofertilisers in crop productions. *Agronomy* **2019**, *9*, 192. [CrossRef]

177. Park, E.; Yu, H.; Lim, J.H.; Choi, J.H.; Park, K.J.; Lee, J. Seaweed metabolomics: A review on its nutrients, bioactive compounds, and changes in climate change. *Food Res. Int.* **2023**, *163*, 112221. [CrossRef]

178. Elarroussia, H.; Elmernissia, N.; Benhimaa, R.; El Kadmiria, I.M.; Bendaou, N.; Smouni, A.; Wahbya, I. Microalgae polysaccharides: A promising plant growth biostimulant. *J. Algal Biomass Utln.* **2016**, *7*, 55–63.

179. Priyadarshani, I.; Rath, B. Commercial and industrial applications of microalgae–A review. *J. Algal Biomass Util.* **2012**, *3*, 89–100.

180. Belkhadir, Y.; Yang, L.; Hetzel, J.; Dangl, J.L.; Chory, J. The growth–defense pivot: Crisis management in plants mediated by LRR-RK surface receptors. *Trends Biochem. Sci.* **2014**, *39*, 447–456. [CrossRef]

181. González, A.; Castro, J.; Vera, J.; Moenne, A. Seaweed oligosaccharides stimulate plant growth by enhancing carbon and nitrogen assimilation, basal metabolism, and cell division. *J. Plant Growth Regul.* **2013**, *32*, 443–448. [CrossRef]

182. Yin, Y.; Wang, Z.Y.; Mora-Garcia, S.; Li, J.; Yoshida, S.; Asami, T.; Chory, J. BES1 accumulates in the nucleus in response to brassinosteroids to regulate gene expression and promote stem elongation. *Cell* **2002**, *109*, 181–191. [CrossRef] [PubMed]

183. Kowalczyk, K.; Zielony, T.; Gajewski, M. Effect of Aminoplant and Asahi on yield and quality of lettuce grown on rockwool. In Proceedings of the Conference of Biostimulators in Modern Agricultura, Warsaw, Poland, 7–8 February 2008; pp. 7–8.

184. Coppens, J.; Grunert, O.; Van Den Hende, S.; Vanhoutte, I.; Boon, N.; Haesaert, G.; De Gelder, L. The use of microalgae as a high-value organic slow-release fertilizer results in tomatoes with increased carotenoid and sugar levels. *J. Appl. Phycol.* **2016**, *28*, 2367–2377. [CrossRef]

185. Chiaiese, P.; Corrado, G.; Colla, G.; Kyriacou, M.C.; Rouphael, Y. Renewable sources of plant biostimulation: Microalgae as a sustainable means to improve crop performance. *Front. Plant Sci.* **2018**, *9*, 1782. [CrossRef]

186. Lemoine, Y.; Schoefs, B. Secondary ketocarotenoid astaxanthin biosynthesis in algae: A multifunctional response to stress. *Photosynth. Res.* **2010**, *106*, 155–177. [CrossRef] [PubMed]

187. Ioannou, E.; Roussis, V. Natural products from seaweeds. In *Plant-Derived Natural Products: Synthesis, Function, and Application*; Springer: New York, NY, USA, 2009; pp. 51–81.

188. Colla, G.; Rouphael, Y.; Lucini, L.; Canaguier, R.; Stefanoni, W.; Fiorillo, A.; Cardarelli, M. Protein hydrolysate-based biostimulants: Origin, biological activity, and application methods. *Acta Hortic.* **2016**, *1148*, 27–34. [CrossRef]

189. Colla, G.; Svecová, E.; Cardarelli, M.; Rouphael, Y.; Reynaud, H.; Canaguier, R.; Planques, B. Effectiveness of a plant-derived protein hydrolysate to improve crop performances under different growing conditions. *Acta Hortic.* **2013**, *1009*, 175–179. [CrossRef]

190. Stirk, W.A.; Bálint, P.; Tarkowská, D.; Novák, O.; Strnad, M.; Ördög, V.; Van Staden, J. Hormone profiles in microalgae: Gibberellins and brassinosteroids. *Plant Physiol. Biochem.* **2013**, *70*, 348–353. [CrossRef]

191. Stirk, W.A.; Ördög, V.; Novák, O.; Rolčík, J.; Strnad, M.; Bálint, P.; van Staden, J. Auxin and cytokinin relationships in 24 microalgal strains. *J. Phycol.* **2013**, *49*, 459–467. [CrossRef]

192. Tate, J.J.; Gutierrez-Wing, M.T.; Rusch, K.A.; Benton, M.G. The effects of plant growth substances and mixed cultures on growth and metabolite production of green algae *Chlorella* sp.: A review. *J. Plant Growth Regul.* **2013**, *32*, 417–428. [CrossRef]

193. Karthikeyan, S.; Balasubramanian, R.; Iyer, C.S.P. Evaluation of the marine algae *Ulva fasciata* and *Sargassum* sp. for the biosorption of Cu (II) from aqueous solutions. *Bioresour. Technol.* **2007**, *98*, 452–455. [CrossRef] [PubMed]

194. Mutale-joan, C.; Rachidi, F.; Mohamed, H.A.; Mernissi, N.E.; Aasfar, A.; Barakate, M.; Mohammed, D.; Sbabou, L.; Arroussi, H.E. Microalgae-cyanobacteria–based biostimulant effect on salinity tolerance mechanisms, nutrient uptake, and tomato plant growth under salt stress. *J. Appl. Phycol.* **2021**, *33*, 3779–3795. [CrossRef]

195. Lugtenberg, B.; Kamilova, K. Microbes as a source of new plant biostimulants: From the rhizosphere to the endosphere. *Plant Soil* **2015**, *387*, 11–34.

196. Azcón-Aguilar, C.; Navarro-Racinés, P.; Gianinazzi, S. The role of microorganisms as elicitors of plant defense responses: From genes to field application. *Plant Soil* **2017**, *412*, 5–26.

197. Bishnoi, U. PGPR interaction: An ecofriendly approach promoting the sustainable agriculture system. *Adv. Bot. Res.* **2015**, *75*, 81–113.

198. Basu, A.; Prasad, P.; Das, S.N.; Kalam, S.; Sayyed, R.Z.; Reddy, M.S.; El Enshasy, H. Plant growth promoting rhizobacteria (PGPR) as green bioinoculants: Recent developments, constraints, and prospects. *Sustainability* **2021**, *13*, 1140. [CrossRef]

199. Alberton, D.; Valdameri, G.; Moure, V.R.; Monteiro, R.A.; Pedrosa, F.D.O.; Müller-Santos, M.; de Souza, E.M. What did we learn from plant growth-promoting rhizobacteria (PGPR)-grass associations studies through proteomic and metabolomic approaches? *Front. Sustain. Food Syst.* **2020**, *4*, 607343. [CrossRef]

200. Gray, E.J.; Smith, D.L. Intracellular and extracellular PGPR: Commonalities and distinctions in the plant–bacterium signaling processes. *Soil Biol. Biochem.* **2005**, *37*, 395–412. [CrossRef]

201. Shahrajabian, M.H.; Petropoulos, S.A.; Sun, W. Survey of the influences of microbial biostimulants on horticultural crops: Case studies and successful paradigms. *Horticulturae* **2023**, *9*, 193. [CrossRef]

202. Camelo, M.; Vera, S.P.; Bonilla, R.R. Mechanisms of action of plant growth-promoting rhizobacteria. *Cienc. Tecnol. Agropecuaria* **2011**, *12*, 159–166. [CrossRef]

203. Dash, N.P.; Kumar, A.; Kaushik, M.S.; Abraham, G.; Singh, P.K. Agrochemicals influencing nitrogenase, biomass of N2-fixing cyanobacteria and yield of rice in wetland cultivation. *Biocatal. Agric. Biotechnol.* **2017**, *9*, 28–34. [CrossRef]

204. Raymond, J.; Siefert, J.L.; Staples, C.R.; Blankenship, R.E. The natural history of nitrogen fixation. *Mol. Biol. Evol.* **2004**, *21*, 541–554. [CrossRef] [PubMed]

205. Chandra, P.; Wunnava, A.; Verma, P.; Chandra, A.; Sharma, R.K. Strategies to mitigate the adverse effect of drought stress on crop plants—Influences of soil bacteria: A review. *Pedosphere* **2021**, *31*, 496–509. [CrossRef]

206. Ilyas, N.; Mazhar, R.; Yasmin, H.; Khan, W.; Iqbal, S.; Enshasy, H.E.; Dailin, D.J. Rhizobacteria isolated from saline soil induce systemic tolerance in wheat (*Triticum aestivum* L.) against salinity stress. *Agronomy* **2020**, *10*, 989. [CrossRef]

207. Ashry, N.M.; Alaidaroos, B.A.; Mohamed, S.A.; Badr, O.A.; El-Saadony, M.T.; Esmael, A. Utilization of drought-tolerant bacterial strains isolated from harsh soils as plant growth-promoting rhizobacteria (PGPR). *Saudi J. Biol. Sci.* **2022**, *29*, 1760–1769. [CrossRef] [PubMed]

208. Hamid, B.; Zaman, M.; Farooq, S.; Fatima, S.; Sayyed, R.Z.; Baba, Z.A.; Sheikh, T.A.; Reddy, M.S.; El Enshasy, H.; Gafur, A.; et al. Bacterial plant biostimulants: A sustainable way towards improving growth, productivity, and health of crops. *Sustainability* **2021**, *13*, 2856. [CrossRef]

209. Gupta, S.; Pandey, S. ACC deaminase producing bacteria with multifarious plant growth promoting traits alleviates salinity stress in French bean (*Phaseolus vulgaris*) plants. *Front. Microbiol.* **2019**, *10*, 1506. [CrossRef]

210. Glick, B.R. Bacteria with ACC deaminase can promote plant growth and help to feed the world. *Microbiol. Res.* **2014**, *169*, 30–39. [CrossRef]

211. Ayuso-Calles, M.; García-Estévez, I.; Jiménez-Gómez, A.; Flores-Félix, J.D.; Escribano-Bailón, M.T.; Rivas, R. *Rhizobium laguerreae* improves productivity and phenolic compound content of lettuce (*Lactuca sativa* L.) under saline stress conditions. *Foods* **2020**, *9*, 1166. [CrossRef]

212. Vurukonda, S.S.K.P.; Vardharajula, S.; Shrivastava, M.; SkZ, A. Enhancement of drought stress tolerance in crops by plant growth promoting rhizobacteria. *Microbiol. Res.* **2016**, *184*, 13–24. [CrossRef] [PubMed]

213. Hashem, A.; Alqarawi, A.A.; Radhakrishnan, R.; Al-Arjani, A.B.F.; Aldehaish, H.A.; Egamberdieva, D.; Abd Allah, E.F. Arbuscular mycorrhizal fungi regulate the oxidative system, hormones and ionic equilibrium to trigger salt stress tolerance in *Cucumis sativus* L. *Saudi J. Biol. Sci.* **2018**, *25*, 1102–1114. [CrossRef]

214. Janati, W.; Bouabid, R.; Mikou, K.; Ghadraoui, L.E.; Errachidi, F. Phosphate solubilizing bacteria from soils with varying environmental conditions: Occurrence and function. *PLoS ONE* **2023**, *18*, e0289127. [CrossRef]

215. Mosimann, C.; Oberhänsli, T.; Ziegler, D.; Nassal, D.; Kandeler, E.; Boller, T.; Mäder, P.; Thonar, C. Tracing of two Pseudomonas strains in the root and rhizoplane of maize, as related to their plant growth-promoting effect in contrasting soils. *Front. Microbiol.* **2017**, *7*, 2150. [CrossRef]

216. Rizvi, A.; Ahmed, B.; Khan, M.S.; Umar, S.; Lee, J. Psychrophilic bacterial phosphate-biofertilizers: A novel extremophile for sustainable crop production under cold environment. *Microorganisms* **2021**, *9*, 2451. [CrossRef]

217. Liang, J.L.; Liu, J.; Jia, P.; Yang, T.T.; Zeng, Q.W.; Zhang, S.C.; Liao, B.; Shu, W.S.; Li, J.T. Novel phosphate-solubilizing bacteria enhance soil phosphorus cycling following ecological restoration of land degraded by mining. *ISME J.* **2020**, *14*, 1600–1613. [CrossRef] [PubMed]

218. Tagele, S.B.; Kim, S.W.; Lee, H.G.; Kim, H.S.; Lee, Y.S. Effectiveness of multi-trait Burkholderia contaminans KNU17BI1 in growth promotion and management of banded leaf and sheath blight in maize seedling. *Microbiol. Res.* **2018**, *214*, 8–18. [CrossRef] [PubMed]

219. Alori, E.T.; Glick, B.R.; Babalola, O.O. Microbial phosphorus solubilization and its potential for use in sustainable agriculture. *Front. Microbiol.* **2017**, *8*, 971. [CrossRef]

220. Dhuldhaj, U.P.; Malik, N. Global perspective of phosphate solubilizing microbes and phosphatase for improvement of soil, food and human health. *Cell. Mol. Biomed. Rep.* **2022**, *2*, 173–186. [CrossRef]

221. Sharma, S.B.; Sayyed, R.Z.; Trivedi, M.H.; Gobi, T.A. Phosphate solubilizing microbes: Sustainable approach for managing phosphorus deficiency in agricultural soils. *SpringerPlus* **2013**, *2*, 587. [CrossRef] [PubMed]

222. De Zutter, N.; Ameye, M.; Bekaert, B.; Verwaeren, J.; De Gelder, L.; Audenaert, K. Uncovering new insights and misconceptions on the effectiveness of phosphate solubilizing rhizobacteria in plants: A meta-analysis. *Front. Plant Sci.* **2022**, *13*, 858804. [CrossRef] [PubMed]

223. Raymond, N.S.; Gómez-Muñoz, B.; van der Bom, F.J.; Nybroe, O.; Jensen, L.S.; Müller-Stöver, D.S.; Oberson, A.; Richardson, A.E. Phosphate-solubilising microorganisms for improved crop productivity: A critical assessment. *New Phytol.* **2021**, *229*, 1268–1277. [CrossRef]

224. Adnan, M.; Fahad, S.; Zamin, M.; Shah, S.; Mian, I.A.; Danish, S.; Zafar-ul-Hye, M.; Battaglia, M.L.; Naz, R.M.M.; Saeed, B.; et al. Coupling phosphate-solubilizing bacteria with phosphorus supplements improve maize phosphorus acquisition and growth under lime induced salinity stress. *Plants* **2020**, *9*, 900. [CrossRef]

225. Timofeeva, A.; Galyamova, M.; Sedykh, S. Prospects for using phosphate-solubilizing microorganisms as natural fertilizers in agriculture. *Plants* **2022**, *11*, 2119. [CrossRef]

226. Rafi, M.M.; Krishnaveni, M.S.; Charyulu, P.B.B.N. Phosphate-solubilizing microorganisms and their emerging role in sustainable agriculture. In *Recent Developments in Applied Microbiology and Biochemistry*; Elsevier: Amsterdam, The Netherlands, 2019; pp. 223–233.

227. Wu, W.; Li, X.; Liang, X.; Wang, D. Microorganisms as plant biostimulants: A review of their mechanisms and applications. *J. Plant Physiol.* **2023**, *226*, 384–403.

228. Wang, Z.; Liang, X.; Wang, H.; Liu, Y. Microorganism-based biostimulants: A new strategy for enhancing crop productivity and abiotic stress resilience. *Adv. Agron.* **2023**, *158*, 1–31.