



Microalgae- and cyanobacteria-derived phytostimulants for mitigation of salt stress and improved agriculture

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ARTICLE INFO

Keywords:

Phytostimulants
Bio-stimulatory mechanism
Polysaccharide
Phytohormone
Crop productivity
Salt tolerance

ABSTRACT

Soil salinization poses severe abiotic stress that adversely affects plant growth and development, ultimately threatening global food security by inducing physiological abnormalities. In response to escalating nutrient demands, with global requirements quantified at 76 % for nitrogen and 87 % for phosphorus, modern agriculture is increasingly adopting sustainable practices to enhance nutrient recycling and reduce reliance on external inputs. Emerging sources of plant phytostimulants, such as microalgal and cyanobacterial biomass, show promise in augmenting crop yields and bolstering plant resistance to various abiotic factors, including salt stress. The efficacy of these microorganisms stems from their simplistic cellular structure, superior photosynthetic efficiency, capacity for heterotrophic growth, adaptability to varying environmental conditions, potential for metabolic engineering, and the abundance of valuable biomolecules (such as soluble amino acids, micro-nutrients, polysaccharides, and phytohormones) within their biomass. This review provides an analysis of the current research landscape concerning microalgae- and cyanobacteria-derived phytostimulants, highlighting their promise as an innovative and sustainable alternative to synthetic fertilizers in the agricultural sector. Moreover, it identifies various adaptive responses of plants to salinity stress and assesses the potential and challenges associated with the use of microalgae and cyanobacteria-based metabolites for developing new sustainable strategies to enhance crop tolerance to salinity stress.

1. Introduction

By 2050, the projected population will demand a 70 % increment in food production compared to current levels [1]. However, soil health,

essential for global food production, is compromised by degradation from both anthropogenic and natural causes. The rapid spread of soil degradation threatens land fertility, productivity, and the global food supply, thereby endangering food security, ecosystem health, and

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<https://doi.org/10.1016/j.algal.2024.103686>

Received 7 May 2024; Received in revised form 23 June 2024; Accepted 26 August 2024

Available online 30 August 2024

2211-9264/© 2024 Published by Elsevier B.V.

sustainable development. The agricultural sector faces multiple direct impacts, including aridity, diminished vegetation cover, erosion, salinization, water pollution, and depletion of organic carbon [2]. Among abiotic stresses, soil salinity inflicts the greatest damage on crop growth, development, productivity, and food security, especially in economically important crops, as most crops are sensitive to salt stress [3,4].

Soil salinity affects approximately 800 million hectares of agricultural land globally, with an increase of approximately 20 % per year [5]. The presence of salt in the soil results in the formation of reactive oxygen species (ROS) in plants, including hydrogen peroxide (H_2O_2) and superoxide radicals. This disrupts ionic equilibrium, causing disturbances in plant physiology. It initiates stress signaling pathways, resulting in the activation of various biochemical and physiological responses aimed at combating salt stress [6]. Increased oxidative stress results in reduced transpiration rates [7], altered nutrient uptake dynamics, diminished water uptake, and reduced chlorophyll synthesis [8,9], ultimately leading to reduced growth and yield [10]. Addressing salinity-related challenges requires the implementation of a multifaceted approach, encompassing the utilization of natural extracts and specialized fertilizers. To achieve effective solutions, it is crucial to make informed decisions based on thorough understanding and analysis.

Many studies have evaluated the effects of synthetic or organic chemical materials as a means of mitigating the adverse effects of salinity on crop yield and stress tolerance [11–15]. Phytostimulants are a class of bioactive molecules with a complex composition, which are being sought after in sustainable and green ways to stimulate plant growth when applied in small amounts [12]. Following the definition by the European Biostimulants Industry Council [13], a phytostimulant comprises microorganisms and substances aimed at stimulating natural processes in plants or rhizosphere. Phytostimulants enhance nutrient assimilation and utilization efficiency, resistance to abiotic stress, and crop quality [14]. Optimal phytostimulants should be durable, effective, and contain bioactive molecules that promote nutrient cycle closure in agriculture [15].

Microalgae and cyanobacteria can be eco-friendly phytostimulants to promote crop quality and yield [16]. These photosynthetic microscopic organisms, found in diverse aquatic environments such as wet soils, wastewaters, oceans, lakes, rivers, and ponds, comprise up to 30,000 species. They adapt to diverse environments and are widely spread across ecosystems [17]. As a renewable and sustainable bioresource, microalgae and cyanobacteria have extensive applications in the synthesis of biofuels, bioactive compounds, and food additives. Their utility in agricultural biotechnology primarily stems from their biochemical composition, which is rich in nutrients like carbohydrates, proteins, and lipids, which enrich and improve soil quality. Additionally, these organisms possess phytohormones, polysaccharides, amino acids, phenolic compounds, and other metabolites that foster plant growth [18].

Microalgae and cyanobacteria biomass are pivotal in agriculture, particularly as phytostimulants and fertilizers. Their biomass production presents a highly beneficial alternative to other bioresources [19,20]. There are three main advantages to cultivating these photosynthetic microorganisms: a) they can be grown in non-arable areas, thereby preventing competition with land dedicated to food production; b) they can thrive in low-quality waters, minimizing the need for fresh water and nutrients, especially N and P; c) rich biomass composition allows for multiple reactions within the same culture. During autotrophic growth, the above organisms absorb atmospheric carbon dioxide, effectively decreasing the agricultural practice's carbon footprint [21]. Utilizing microalgae and cyanobacteria biomass-derived phytostimulants offers a sustainable strategy to enhance crop yields and mitigate environmental pollution. Over the past two decades, this approach has garnered significant attention from the agrochemical industry and the scientific community.

Numerous studies and commercial trials have substantiated the phytostimulatory properties of cyanobacteria- and microalgae-derived

biomass, extracts, and hydrolysates. These extracts have been subjected to a comprehensive range of biological tests in higher plants, including assessments of nutrient uptake, yield, and resistance to abiotic and biotic stresses [22–26]. The phytostimulant benefits they offer are diverse and interrelated, varying with the microalgae species used, the type of plant treated, and the growth conditions. Additionally, the efficacy of phytostimulants can be linked with the plant phenological stage at the time of application.

Significant improvements in the growth and yield of leafy vegetables (arugula, spinach, and lettuce) and herbs (basil and mint) are among the most observed effects when treated with microalgae and cyanobacteria extracts [27]. For instance, treatment with *Arthrospira platensis* extracts significantly improved the growth of various leafy vegetables, including bok choy, bayam red, and arugula [28]. Similarly, Garcia-Gonzalez and Sommerfeld [29] and El Arroussi et al. [30] reported positive effects on fruiting vegetables like tomatoes and peppers after applying microalgae extract.

Furthermore, a study by Chanda Mutale-Joan et al. [31] demonstrated that treatment with combined extracts of microalgae and cyanobacteria derived from *Dunaliella salina*, *Chlorella ellipsoidea*, *Aphanothece* sp., and *Arthrospira maxima* species enhanced the growth of tomato plants under salt stress conditions. This enhancement was characterized by elevated shoot and root weights and a larger leaf area. The authors' analysis indicated that this effect was closely related to increased leaf photosynthetic pigments, resulting in improved osmotic adaptation and ion homeostasis [31].

Another recent study has demonstrated that the application of extracts derived from microalgae strains *D. salina* and *Chlorella vulgaris* effectively reversed declines in biomass distribution and water balance under both normal and salt stress conditions. This application markedly improves key parameters, such as transpiration rate, stomatal conductance, carotene content, and chlorophyll content. In addition, treatment with microalgae extract effectively reduced electrolyte leakage and lipid peroxidation induced by salt stress [32].

Notably, extracts from three Egyptian seaweeds (*Laurencia obtusa*, *Cytoseira compressa*, and *Ulva fasciata*) have been found to function as effective phytostimulants, enhancing salt tolerance in various plants, including *Vigna sinensis* and *Zea mays* [33]. Additionally, researchers have studied the effects of *D. salina* on *Cucurbita pepo* L. cv. Mabrouka under salt stress, demonstrating its potential benefits [34].

The current literature indicates that microalgae and cyanobacteria extracts enhance plant growth and stress tolerance by increasing the activity of antioxidant enzymes and promoting root growth and nutrient uptake. Consequently, the utilization of phytostimulants based on microalgae and cyanobacteria biomass represents a sustainable solution to enhance nutrient uptake, stimulate growth, and improve crop adaptability, particularly under normal and saline conditions.

Despite their significant potential to enhance crop productivity and offer other agricultural benefits, cyanobacteria and microalgae have been relatively overlooked compared to soil fungi and bacteria. Only 2312 papers focusing on microalgae and cyanobacteria were published between 1919 and 2018, with the majority originating from countries such as the USA, Germany, China, and India [35]. Prior studies have not thoroughly explored the application of phytostimulants derived from these organisms, with this research area gaining attraction only recently. However, notable advancements have been made in the past five years, with new scientific discoveries underscoring the potential of these 'beneficial microorganisms' in sustainable agriculture. These studies have summarized various metabolites from microalgae and cyanobacteria, highlighting their roles as phytostimulants and biofertilizers [16,36]. Nevertheless, their action mechanisms and impacts on plant physiology remain partially understood to date.

This review emphasizes the importance of microorganisms in sustaining soil health and fertility. It critically examines the potential of cyanobacteria and microalgae as phytostimulants to promote crop yield, focusing on the ability of these organisms to provide plant tolerance to

abiotic factors, including their effectiveness in mitigating salinity stress. Furthermore, the review addressed the physiological response of plants to salt stress. It elucidated the bio-stimulatory mechanisms of various microalgal and cyanobacterial extracts, detailing their biologically active compounds, as well as their influence on plants' performance, physiological health, and resilience to environmental stressors under different application modes. The foundation for this review is a decade of research findings, delivering a thorough assessment of the most recent developments in the field.

2. Physiological responses of plants to salinity stress

Salt stress is one of the most prevalent abiotic stressors hindering the growth and productivity of agricultural plants in arid and semi-arid regions of the world [37]. Over-accumulation of ions such as chlorides (Cl^-), sulfates (SO_4^{2-}), sodium (Na^+), magnesium (Mg^{2+}), and calcium (Ca^{2+}) in soil, particularly in the presence of sodium (Na^+) can lead to soil salinity issues. The accumulation of ions increases the alkalinity level, contributing to the global soil salinity problem. This produces osmotic, oxidative, and ionic stress that impairs cellular functions [38].

At the same time, soil salinity negatively affects plants at all stages of their development, ranging from delayed seed germination and slower vegetative growth to the deterioration of the reproductive stage [39]. Seed germination is hindered by reduced osmotic potential, which disrupts water absorption and leads to the accumulation of Na^+ and Cl^- ions [40]. The concentration of salt, pH levels, and their interaction have an inhibitory effect on the germination of *Halostachys caspica* seeds, with salt concentration being the most influential factor, followed by pH value [41].

During vegetative growth, salt stress slows the growth of roots and shoots [37]. Studies indicate that the formation of adventitious roots in *Mentha spicata* L. var. *Crispa* is inhibited when freshly cut shoots are treated with 50 mM NaCl solution [42]. This inhibition is associated with several key physiological changes in plants, including decreased cell division and expansion, ultimately leading to reduced plant biomass [43].

In the reproductive stage, plants are also vulnerable to salt stress. At this stage of the life cycle, this is manifested by inhibition of microsporogenesis, resulting in fewer healthy pollen grains and disruption of the pollination process. Consequently, the number of flowers and fruits decreases, resulting in a decline in overall yield [39,44].

In the initial stages of salt stress, the water-absorption capacity of root systems is reduced, and water loss from leaves is promoted due to osmotic stress, so salt stress is also considered as hyperosmotic stress [45]. This osmotic stress induces various physiological changes, such as nutrient imbalance, membrane disruption, reduced photosynthetic activity, alteration of antioxidant enzymes, and closure of stomata, thereby impeding plant growth [46]. Over time, salt stress leads to ion toxicity, characterized by the accumulation of excessive Cl^- and Na^+ in the cytosol. The entry of these ions into cells causes severe ion imbalance, and excessive uptake may result in significant physiological disruptions, including reduced energy production during photosynthesis and respiration, impaired nitrogen assimilation, and protein synthesis. Elevated Na^+ concentration hinders the uptake of K^+ ions, essential for growth, leading to decreased productivity, promoting premature aging, and potentially causing plant death [47].

Furthermore, salt stress indirectly induces the accumulation of ROS, including hydrogen peroxide, singlet oxygen, and superoxide radicals [48]. Elevated oxidative stress impedes vital processes such as water absorption dynamics, transpiration, nutrient uptake, and chlorophyll biosynthesis, resulting in oxidative damage to various cellular components, including lipids, proteins, and DNA. This disruption of essential plant cellular functions further impedes plants growth and yield [7,32,49]. Ma et al. have demonstrated that these factors collectively contribute to decreased plant growth and yield [9].

On a fundamental level, plant response to salt stress can be

delineated into two primary stages: the initial phase, termed as the shoot ion-independent response, occurs swiftly within minutes to days and is associated with Na^+ sensing and signaling [50]. During this initial stage, salinity's impact on water relations can be significant, leading to stomatal closure and inhibiting leaf expansion [51]. The subsequent phase, known as the ion-dependent response to salinity, unfolds gradually over a more extended timeframe, spanning days to weeks, and involves ion accumulation in the shoot to toxic levels. This accumulation is particularly noticeable in older leaves, resulting in premature leaf senescence and ultimately decreased yield or potential plant demise [52].

Plants develop various physiological and biochemical mechanisms to survive in soil with high salt concentrations. Salinity tolerance can be acquired through the effective management of cytoplasmic ion levels. This encompasses ion homeostasis, compartmentalization, osmotic adjustment, and the bolstered antioxidative processes, including the enhanced ROS scavenging capacity [53]. Several endogenous phytohormones, including brassinosteroids (BR), ethylene, gibberellins, cytokinins, jasmonic acid (JA), salicylic acid (SA), auxin, and abscisic acid (ABA), play a pivotal role in regulating plant responses to salinity stress, thereby enhancing salt tolerance [54]. In response to salt stress, plants accumulate compatible organic solutes such as proline, soluble sugars, glycine betaine, and polyols. These substances, which are low molecular weight and soluble, serve as osmoprotectants. They assist in ROS detoxification, intracellular osmotic adjustment, and maintenance of membrane integrity, all without disrupting cellular metabolism [55]. In addition, the accumulation of osmoprotectants serves a key supportive role in counteracting salt-induced changes [56].

Many researchers have shown a direct correlation between the content of proline and soluble sugars in plants and the salt concentration in their environment. Studies on lettuce (*Lactuca sativa* L.) seedlings have shown that the amount of proline significantly increases with increasing NaCl concentration and prolonged salt exposure [57]. Similarly, research on durum wheat seedlings *Triticum turgidum* subsp. *durum* (Desf.) Husn shows that salinity stress induces the expression of genes related to stress response and the metabolism of proline and soluble sugars, leading to the accumulation of these compounds [58].

Various factors can influence plant response to salinity owing to the complex nature of salinity tolerance. Munns and Tester [52] proposed three main mechanisms for salinity tolerance: ion exclusion, where toxic ions are kept out of the shoot; tissue tolerance, where toxic ions are stored in specific tissues or organelles; and shoot ion-independent tolerance, where growth and water uptake are maintained regardless of shoot Na^+ accumulation. Other factors contributing to salinity tolerance include maintenance of plant water status, transpiration efficiency, leaf area, seed germination, antioxidant production, early seedling growth, and harvest index [59]. While various management practices have been proposed to improve salt tolerance mechanisms, the development of agronomic tools such as regulators and growth stimulants represents an innovative strategy crucial for ensuring crop yields under such challenging conditions [60].

3. Bioactive compounds of microalgae and cyanobacteria that affect growth and salt tolerance

Recently, microalgae extracts and derivatives have attracted interest as phytostimulants that enhance abiotic stress response, promote resource use efficiency (RUE), and improve plant resilience to water deficit. Furthermore, microalgae extracts possess untapped potential as plant phytostimulants for combating salinity stress, a persistent challenge in agriculture. This potential stems from their diverse chemical and biochemical composition, varied biological effects on crops, and shared molecular pathways with higher plants [61].

Microalgae and cyanobacteria are known to contain high amounts of macronutrients, especially K, P, and N [62]. For instance, *Arthrospira* spp. have concentrations of approximately 6.7 %, 2.5 %, and 1.1 % of N, P, and K, respectively, on a dry weight basis. Studies indicate that

biodegradability, non-toxicity, low-cost, and widespread availability [73]. In agriculture, they have emerged as a novel bioactive source of phytostimulants, enhancing crop yield and soil quality. They function as nutrient transporters, soil conditioners, and safe release systems for agrochemicals [19,74,75] and provide defense against abiotic and biotic plant stresses [76–78]. These molecules also serve as carbon and energy sources for other soil organisms [79].

Early studies have demonstrated that algal PSs can induce defense responses in higher plants [80–82]. These PSs are a significant component of commercial algal extracts, constituting up to 30–40 % of their DW [72,83,84]. EPSs have been derived from various microalgae genera, including *Scytonema*, *Rhodella*, *Porphyridium*, *Phaeodactylum*, *Nostoc*, *Navicula*, *Dunaliella*, *Cylindrotheca*, *Chlorella*, *Chlamydomonas*, *Arthrospira*, and *Aphanothece*, with yields ranging from 0.01 to 2.9 g/L [85,86].

Microalgae such as *Porphyridium cruentum*, *I. galbana*, *D. tertiolecta*, *D. salina*, *Chlamydomonas reinhardtii*, *B. braunii*, and *Spirulina* sp. have been identified as promising EPS sources [87,88]. The application of microalgae EPS to soil can enhance its structural integrity by increasing porosity and water-holding capacity. This process facilitates soil moisture retention and creates a more conducive environment for root growth, which is particularly important in saline conditions where water availability is a limiting factor [89].

Guzmán-Murillo et al. [90] reported that EPSs isolated from *D. salina* and *P. tricornutum* enhanced pepper germination under saline stress. Similarly, EPSs from *D. salina* have been observed to promote germination, growth, and salinity stress tolerance in tomatoes and wheat [91–94]. In another work, an aqueous extract from *Scenedesmus* sp., rich in PSs and oligosaccharides, was found to promote the growth, development, and nutritional status of *Petunia × hybrida* [68]. Furthermore, liquid extracts from *S. quadricauda* and *C. vulgaris* have been found to stimulate root development in *Beta vulgaris* L. [95].

While algae and microalgae PSs have been extensively employed as plant defense inducers, cyanobacterial PS have been less explored in the context of phytostimulation. Nonetheless, recent evidence highlights the phytostimulatory properties and signaling capabilities of cyanobacterial PSs [96,97]. For instance, cyanobacterial EPSs are known for their role in soil aggregation owing to their adhesive qualities [98] and capacity to bind heavy metals [99] and sodium ions [100], thus potentially enhancing plant growth in saline or contaminated soils.

Seifkhalhor and coworkers [101] showed that *A. platensis* coating on maize seeds could bind Cd ions, significantly reducing Cd uptake and its toxic effects on the plants, with over a 90 % reduction in Cd content in roots observed on 12-day post-sowing. Similarly, Rachidi et al. [67] found that lower concentrations (0.25, 0.5 and 1.0 g/L) of *A. platensis*-derived crude PSs extract effectively promoted the vegetative growth of tomato plants. Furthermore, crude PSs extracts of cyanobacteria can facilitate the binding of essential nutrients and their subsequent slow release, thereby enhancing the availability of nutrients to plants. This controlled release mechanism is especially beneficial under conditions of salt stress, where nutrient uptake may be impaired. For example, *Phormidium tenue* crude PSs with 58 % carbohydrates and 15 % proteins stimulated growth and superoxide dismutase activity in *Caragana korshinskii* seedlings in desert-cruised areas [102]. Foliar application of PS-rich extracts from *A. platensis* was demonstrated to promote the development of pepper and tomato plants [30]. Similarly, bio-stimulatory properties of *C. reinhardtii*, *Chlorella sorokiniana*, *C. vulgaris*, and *D. salina* PSs extracts were observed in tomato seedlings [103], enhancing defense (LOX, PAL, ROS) and antioxidant (CAT, POD, APX) enzyme activities, along with increasing very long-chain FAs in tomato leaves, indicative of activated plant defense mechanisms [104,105]. These studies have attributed the observed benefits to the ability of EPS to enhance water retention, reduce ion toxicity, and stimulate plant stress responses. In summary, the literature provides substantial evidence that microalgae- and cyanobacteria-derived PS offer promising growth-promoting and biostimulatory properties, potentially enhancing

crop productivity and plant resilience against various stresses, including salinity (Table 1).

3.2. Phenolic compounds

Phenolic compounds (PCs), a diverse group of secondary metabolites, are crucial in several physiological processes in plants, particularly in stress response. This enables plants to interact with, adapt to, and thrive in harsh conditions, such as exposure to UV radiation, drought, and salinity. Higher plants (fruits, vegetables, and spices) produce these compounds [106], as well as algae. Indeed, certain algae species have been reported to contain phenolic acids like protocatechuic acid, gallic acid, caffeic acid, chlorogenic acid, vanillic acid, p-hydroxybenzoic acid, and salicylic acid [107].

In agriculture, PCs primarily protect crops from pathogens and various stress factors, both biotic and abiotic, leveraging their antimicrobial, fungicidal, and antioxidant properties [70]. Moreover, PCs contribute to the mobilization of Ca, Zn, and Fe, as well as overall nutrient uptake enhancement through ion chelation, which also leads to increased soil porosity [108]. In addition, flavonoids and phenolic acids serve as solar filters, shielding plants from UV radiation [109]. These compounds also bolster plant resilience against environmental stressors like heavy metals, salinity, and drought by aiding in the neutralization of reactive oxygen species (ROS) produced during oxidative stress. Furthermore, phenolic acids play a crucial role in defense against various threats, including phytopathogens, insects, and herbivores [110].

Compared to terrestrial plants, phenolics from algae exhibit greater variability, ranging from simple molecules such as phenolic acids to highly complex and specialized compounds. For instance, brown algae typically possess phlorotannins, a type of polyphenols absent in terrestrial plants, which play a role in responding to both abiotic and biotic stress [111]. Marine macroalgae like *Ascophyllum nodosum*, *Fucus serratus*, *Fucus vesiculosus*, and *Saccharina latissimi* are rich in dieckol, eckol, phloroglucinol, and phlorotannins. These compounds, characterized by a higher number of phenolic rings compared to other phenolics, are expected to detoxify ROS more efficiently [112].

Goiris et al. [113] established a clear link between the PC content and the antioxidant activity in microalgal extracts. Among the species examined, *Botryococcus braunii*, *C. vulgaris*, *Isochrysis* sp., *Neochloris oleoabundans*, *Phaeodactylum tricornutum*, and *Tetraselmis suecica* displayed the highest levels of antioxidant activity, closely associated with their significant PC content (1.70 to 4.57 mg/g DW). The carotenoid content, along with the PC content, was confirmed to be a major contributor to algal antioxidant activity when examining the content of bioactive metabolites (carotenoids, fucoxanthin, phenolic acids, and FA profile) in five micro- and one macroalgae [114].

Jerez-Martel et al. investigated several microalgal species (*Ankistrodesmus* sp., *Caespitella pascheri*, *Euglena cantabrica*, and *Spirogyra* sp.) and cyanobacterial species (*A. platensis*, *Nodularia spumigena*, *Nostoc* sp., *Leptolyngbya protospira*, *Nostoc commune*, and *Phormidiochaete* sp.) for their 1,1-diphenyl-2-picrylhydrazyl radical scavenging activity [115]. Among the studied species, *Euglena cantabrica* showed the highest PCs content, notably protocatechuic and gallic acids (55.87 and 2.97 mg/g DW, respectively), and exhibited significant antioxidant activity.

The exogenous application of phenolic compounds can significantly enhance plant development and mitigate the impact of abiotic and biotic stress through various mechanisms. These mechanisms include facilitating the lignification of plant cell walls, which promotes shoot length and prevents pathogens penetration, and influencing the activity of certain enzymes, such as antioxidant enzymes, and the synthesis of certain compounds [116]. Additionally, phenolic compounds can protect the photosynthetic apparatus from oxidative damage and enhance the efficiency of photosystem II, thereby improving the overall photosynthetic performance of plants under salt stress [117].

However, phenolic acids and flavonoids have been scarcely

Table 1
Microalgal and cyanobacterial polysaccharides promoting sustainable agriculture.

Microalgal/Cyanobacterial species	Polysaccharides	Crop	Treatment parameters	Effects	References
<i>Anabaena</i> sp. BEA0300B	PS water extract	Zucchini	The extract was applied as a spray to one of the two cotyledon leaves of 12-day-old plants, using a concentration of 2 g per liter.	Decrease symptoms of <i>Podosphaera xanthii</i> by 25 %	[94]
Consortium of <i>Nostoc</i> sp. F280 and <i>Anabaena cylindrica</i> B1611	Extracellular PS	Lettuce crops	The B1611 and F280 strains were co-cultivated.	Increased plant biomass production	[104]
<i>Anabaena</i> sp., <i>Ecklonia</i> sp., and <i>Jania</i> sp.	PS extract (POL)	Strawberry fruits	Pre-harvest treatment: plants were immersed in PS solutions for 2 min. Post-harvest treatment: Immerse in POL suspensions (0.5, 2.0, and 3.5 mg/mL) for 2 min.	Mitigate spore germination, colony growth, and CFU of fungal pathogen <i>Botrytis cinerea</i>	[93]
<i>Arthrospira platensis</i> , <i>Dunaliella salina</i> , and <i>Phosphoridium</i> sp.	Crude PS	Tomato	Applied with PSs solution of 10 mL/plant (0.25–1 mg/mL, pH 6.8) five time (once a week).	Increase carotenoids, chlorophyll, and protein content	[67]
<i>Chlorococcum</i> , <i>Chlorella</i> , <i>Micractinium</i> and <i>Scenedesmus</i>	ExoPS	Spinach	Seeds were primed with soluble and insoluble microalgae fractions.	Improved plant propagation and sprouting	[69]
<i>Chlamydomonas reinhardtii</i> , <i>Chlorella sorokiniana</i> , <i>Chlorella vulgaris</i>	Crude PS	Tomato	Plants were injected with 10 µL of polysaccharides extract (0.2 mg mL ⁻¹).	Positive influence on phenylalanine ammonia-lyase (up to 188.7 % compared to control)	[103]
<i>Chlorella sorokiniana</i>	Crude PS	Wheat	1) Biomass of microalgae; 2) filtered BG11 medium after the microalgae biomass was harvested; 3) harvested microalgae re-suspended in fresh BG11 medium.	Increase germination, length of roots and shoots, FW, and DW	[105]
<i>Dunaliella salina</i>	ExoPS	Tomato	Spray with PS solution (0.1 g/L, pH 6.0) twice within 3 days.	Reduce negative impacts of salt stress	[30]
	Intracellular PSs	Red pepper	Microalgae extracts with total carbohydrates concentration of 3.4 mg/mL were added to petri dishes where germinated plant seeds.	Reduce negative effects of salt stress, root length increase (24 % at 25 mM NaCl), enhanced CAT activity (51.2 units per mg protein CAT).	[90]
<i>Nostoc muscorum</i> and <i>Oscillatoria</i> sp.	Extracellular PS	Onion	Cyanobacterial extracellular products that exhibited the most significant suppression of <i>Alternaria porri</i> in vitro, were applied to control the disease in vivo	Showed fungicidal efficacy against <i>Alternaria porri</i> , which causes onion purple blotch disease	[84]
<i>Phaeodactylum tricornutum</i>	Intracellular PS	Red pepper	Microalgae extracts with total carbohydrate concentration of 3.4 mg/mL were added to petri dishes where germinated plant seeds.	Reduce negative effects of salt stress, significantly reduced superoxide radical synthesis, as well as lower lipid peroxidation.	[90]
	Crude PS	Tomato	The cotyledon leaves were injected with 10 µL of 0.1 % PS solution	Improve the phenylalanine ammonia lyase, chitinase, 1,3-beta-glucanase and peroxidase activities	[24]

PS - polysaccharide.

investigated compared to other metabolites. Therefore, further research is required to close the knowledge gap, particularly in comparison to the well-established understanding of phenolic biosynthesis in higher plants.

3.3. Phytohormones

Phytohormones (PHs), small organic compounds that regulate cellular processes, play a crucial role in alleviating abiotic stress in plants and adjusting their growth in response to external conditions [118]. These molecules, functioning as signals, are categorized into five types: auxins, cytokinins, abscisic acid, ethylene, and gibberellic acids. Nowadays, brassinosteroids, salicylic acids, and jasmonic acids are also recognized as PHs [119]. Initially discovered in higher plants in small quantities, these signaling molecules have been found to be synthesized by a broad range of cyanobacteria and microalgae [120]. Various algal species, including green, red, and brown algae, diatoms, and cyanobacteria, have been identified as containing the most prominent PHs [121].

Although the mechanism of PH action in microalgae remains unclear, evidence suggests they enhance lipid accumulation enhancement without altering cellular metabolism. Moreover, PHs promote microalgal cell growth through increased activity of corresponding enzymes [122]. During cocultivation, PHs produced by microalgae are transferred to plants through their roots along with other nutrients,

facilitating enhanced plant growth and stress resilience. Additionally, the PH profiles of microalgae may resemble those in higher plants, although there are variations in dominant types and biosynthesis intermediates. [120].

Furthermore, phytohormones can modify or detoxify toxic compounds that impede plant and algal growth. For instance, they assist in the mitigation of phytotoxicity caused by heavy metals and avoid algal inhibition. Consequently, the coexistence of microalgae in plant roots not only confers mutual benefits but also facilitates the release of plant growth-promoting substances, thereby enhancing the overall resilience and productivity of both plants and algae [123].

Auxins serve a multifaceted role in microalgae development and metabolism. They can promote biomass and enhance the accumulation of valuable biomolecules at low concentrations, while at high concentrations, they may hinder cell growth [124]. In microalgae, auxins also function as growth regulators. Specifically, auxins of *S. quadricauda*, *Scenedesmus obliquus*, *Nannochloropsis oceanica*, *C. vulgaris*, and *D. salina* have been shown to enhance cell size and division, as well as chlorophyll and protein content, thus enhancing biomass productivity [125–127].

The synthesis of auxins in cyanobacteria depends on the bioavailability of precursors and has been observed in the presence of tryptophan (Trp), an amino acid excreted by plants. However, not all cyanobacteria can synthesize indole-3-acetic acid (IAA), even when tryptophan is available. Unicellular cyanobacteria tend to release auxins into their environment, whereas filamentous cyanobacteria accumulate

these hormones within their cells [63].

Cytokinins (CKs), purine derivatives with zeatin as their primary form, exist predominantly in their cis structure in microalgae [128]. CKs stimulate cell division and enhance photosynthetic efficiency, contributing to biomass accumulation. These compounds are found in lower concentrations during dark periods and higher concentrations in light. Moreover, under adverse environmental conditions, CKs protect microalgae physiological activities, especially photosynthesis [129]. It has also been postulated that phytohormones from cyanobacteria or microalgae could influence the endogenous phytohormones of plant cells [130]. Likewise, cytokinin-binding proteins from cyanobacteria have been transported into plants for the synthesis of endogenous phytohormones [131,132]. Among microalgae, *Nostoc* sp. was found in high abundance, associating it with the root system of rice plants by developing hormogonia [133]. This association was particularly owing to the presence of the *ipdc* gene in the cyanobacterium, which is responsible for IAA synthesis required for plant growth [134]. CKs from species like *Gracilaria caudata*, *C. vulgaris*, and *Acutodesmus obliquus* increased their pigment content, leading to enhanced photosynthetic rates and, consequently, better biomass yield [135–137]. Moreover, a CK produced by *D. salina*, kinetin, was found to induce the accumulation of the photoprotective pigment β -carotene [138].

Absciscic acid (ABA), a 15-carbon sesquiterpene compound, is primarily found in senescent tissues or organs and serves a physiological role in cell development inhibition [139]. In higher plants, ABA enhances tolerance to temperature and salinity stress by regulating water and ion uptake [140]. In microalgae and cyanobacteria, ABA effectively controls cellular responses to various stresses, including salt, osmotic, oxidative, drought, and nutrient deficiency [139,141]. ABA assists microalgae in entering a dormant state when faced with extreme conditions, enables them to withstand environmental pressures, and increases their stress tolerance. For instance, in *Haematococcus pluvialis*, ABA not only inhibits algal cell growth but also induces cell transition from an active to a stationary phase [142]. Moreover, the activation of the ABA pathway is often associated with carotenoid production, which protects against oxidative stress [16]. In *Nannochloropsis oceanica*, the biosynthesis pathways of ABA and CKs are transcriptionally regulated in opposing directions under N_2 starvation, thus exhibiting antagonistic effects (for endogenous ABA and CKs) in response to this condition. Consequently, exogenous CKs have been found to promote the progression of the cell cycle, whereas exogenous ABA serves as a positive regulator of stress tolerance and growth inhibitor. Lu et al. [143] proposed that CKs and ABA serve a complex role in regulating cellular homeostasis to adapt to varying environmental factors. Similarly, the exogenous role of absciscic acid has been demonstrated to support the stress tolerance mechanism in *Ch. reinhardtii* [144].

Ethylene (ET), an unsaturated hydrocarbon with two carbon atoms, exhibits a range of impacts on plants, from growth and senescence regulation to enhancement of tolerance to biotic and abiotic stress [145]. However, research on ET's role in microalgae and cyanobacteria is relatively limited. Some studies indicate that ET is a growth-promoting agent in species like *Spirogyra platensis*, *Chlorella* sp., and *C. reinhardtii* [146,147]. Although traditionally considered a growth inhibitor, increasing evidence suggests that ET, within specific concentration ranges, can promote growth and biosynthesis [148]. For instance, a concentration of 0.05 mL ET/L markedly enhanced astaxanthin synthesis in *H. pluvialis*, while 0.10 mL E/L had an inhibitory effect [149]. Additionally, ET production in *Spirogyra pratensis*, a filamentous charophyte, has been observed to regulate cell growth and development [150].

Gibberellic acids (GAs) are believed to be present in all vascular plants. GAs participate in the reproductive development of lower plants like ferns and lycophytes [151]. Conversely, their functions in higher plants have evolved to encompass the stimulation of organ growth via promoted cell division and elongation. Additionally, in a variety of species of higher plants, they activate developmental processes like

germination, maturation, and seed growth induction [148]. GAs are also synthesized by certain fungi and bacteria associated with plants, either as symbionts or pathogens. In these organisms, GAs do not serve a developmental function but instead act on the host plant, either aiding infection via immunity suppression [116] or regulating nodule formation in the case of N_2 -fixing rhizobacteria [152]. In microalgae and cyanobacteria, GAs have similar functions to those in higher plants, mainly associated with growth promotion and the stimulation of pigment and protein synthesis [117]. GAs from *Microcystis aeruginosa*, *C. vulgaris*, *Chlorella pyrenoidosa*, and *C. ellipsoidea* have been linked to enhanced cell number and size, as well as promoted growth rates [153–155].

Brassinosteroids (BRs), a novel phytohormone, play a significant role in promoting the cellular uptake of nutrients, regulating cell division and elongation, and enhancing cell antioxidant capacity. It also facilitates the synthesis of photosynthetic pigments, carbohydrates, nucleic acids, and proteins required for growth [156]. BRs, being widely distributed across the plant kingdom, function dually, not only as growth-promoting hormones but also as a defense line against environmental stress [157]. In microalgae, BRs are crucial in resisting abiotic stress, including heavy metals, extreme temperatures, and high salinity [157,158]. Under conditions of high salinity (36 g/L NaCl), six microalgal species (*C. vulgaris*, *Protococcus viridis*, *Acutodesmus acuminatus*, *Nautococcus mamillatus*, *Gyoeffya humicola*, and *Chlorococcum ellipsoideum*) have been observed to rapidly accumulate brassinosteroids. The primary brassinosteroid accumulated is castasterone, with lower amounts of typhasterol, homocasterone, and brassinolide [159]. Furthermore, it was found that BRs of *C. vulgaris* have a stimulatory impact on the nucleic acid and protein content of microalga [160].

Salicylic acids (SAs), widely distributed in plants, are endogenous hormones with superior inhibitory effects against cyanobacteria [161]. In microalgae, the regulatory effects of SAs are primarily expressed through their impact on the antioxidant system. A study by Mirshekari et al. [162] explored the effect of SAs on the green microalga *D. salina* adaptation to N_2 depletion by examining the enzymatic antioxidant system and biochemical changes. Study findings suggested that treatment with exogenous SAs may enhance cellular adaptation to N_2 depletion by establishing an enzymatic balance for regulating metabolite levels and directing them towards growth processes [163]. Furthermore, SAs have been shown to promote antioxidant metabolite accumulation by stimulating H_2O_2 production and enhancing the expression of carotenoid-related genes, thereby providing algal cells with a protective effect against abiotic stress [102,164].

Jasmonic acids (JAs), an endogenous growth-regulating substance, were initially identified as a stress-related hormone in higher plants. It serves an essential role in plant tolerance to abiotic stress and is involved in various molecular and physiological responses [142]. In microalgae, the group of JAs primarily comprises jasmonic acid itself and methyl jasmonate (MJ). These compounds are primarily engaged in signal transfer under abiotic stress conditions. Similar to SAs, JAs are known to enhance carotene-related gene expression in microalgae and enhance the synthesis of antioxidant metabolites like β -carotene and astaxanthin. Moreover, compounds such as MJ, GA, JA, and SA have been shown to stimulate astaxanthin synthesis in *H. pluvialis*, linked with increased transcription of carotenoid genes [165]. Zhao and coworkers [166] demonstrated that signal transduction chemicals (ABA, GA, JA, and SA) can promote astaxanthin synthesis in *H. pluvialis* by over 20 %, which is potentially explained by six metabolic modules and seven nodal metabolites identified via metabolomic analysis.

Chlorella, commonly used as a model organism, provides insights into the effects of PHs on growth and biomolecule synthesis [167]. Several studies suggest that PHs may enhance *Chlorella* tolerance and adaptability to heavy metal contamination and other abiotic stress factors, allowing us to assume that PHs serve a significant role in algal response and adaptability to abiotic stress [168]. In summary, microalgal phytohormones possibly have a distinct function in regulating

cellular processes, as well as in growth, development, and metabolism (Table 2).

3.4. Pigments

Microalgae and cyanobacteria accumulate pigments in their biomass, which exhibit unique bioactivities such as antioxidant, anticancer, and antibacterial activities [173]. Prominent microalgal antioxidants include carotenoids like α - and β -carotene found in *C. vulgaris* and *D. salina*, and fucoxanthin found in *Isochrysis galbana* and *Phaeodactylum tricornutum* [174].

Cyanobacterium *Calothrix elenkenii*, isolated from rice paddies, was found to have the highest carotenoid content [175]. The carotenoid profile in microalgae varies among species and depends on cultivation conditions. In particular, the literature indicates the following microalgae as a source of various carotenoids: *C. vulgaris* – for violaxanthin and neoxanthin; *Chlorella protothecoides*, *Scenedesmus almeriensis*, and *Muriellopsis* sp. – for lutein (4.3–5.4 mg/g DW); *D. salina*, *Chlorella regularis*, and *Chlorella marina* – for lycopene; *H. pluvialis*, *Chlorella* sp., and *Chlorococcum* sp. – for astaxanthin and its esters; *A. platensis* - β -carotene, a provitamin A precursor; *Chlorella ellipsoidea* and *P. cruentum* and– for zeaxanthin (up to 97.4 % and 4.26 mg/g, respectively) [174,176–180].

Carotenoids from microalgae and cyanobacteria are widely employed in industries like cosmetics, feed, food, nutraceuticals, and pharmaceuticals owing to their anti-inflammatory, antioxidant, and anti-cancer properties [181]. In agriculture, they are utilized for soil bioremediation, helping detoxify contaminants and restore soil health due to their ability to interact with pollutants and support microbial communities [182]. Additionally, carotenoids’ antioxidant properties are employed in agriculture to combat plant oxidative stress, enhancing plant resistance and productivity by neutralizing ROS [178]. Carotenoids have been explored for use as a component of fertilizers or bio-pesticides to provide essential nutrients and protect plants from pests and diseases sustainably [183]. They are also instrumental in promoting biofortified crops rich in provitamin A [184]. Moreover, carotenoids contribute to coloring flowers, fruits, and seeds and serve as precursors to plant signaling hormones like strigolactone and ABA [185]. While their role in plant growth and development is established, further detailed study is required to understand the mechanisms of carotenoid transformation and uptake from microalgae biomass.

C-phycocyanin (CPC), a hydrophilic phycobiliprotein predominantly

found in cyanobacteria, has a light-harvesting function. Significant amounts of CPC were found in several cyanobacteria species, including *Anabaena fertilissima* PUPCCC 410.5 [186], *Phormidium* sp., *Synechocystis* sp., *Desertifilum tharense*, *Nostoc* sp., and *Galdieria sulphuraria* [187]. *A. platensis*-derived CPC is utilized commercially in the food industry as a natural blue dye and therapeutically as an antioxidant [188]. CPC exhibits antioxidant activity [189], thus having the potential for soil bioremediation and acting as an agricultural raw material [190].

Recent studies have revealed that CPC possesses phytostimulatory properties [191]. Metwally et al. [192] studied the effects of biopriming treatment of tomato seeds with CPC (*S. platensis* extract), observing an increase in the germination index, shoot and bulb length, and a change in chemical composition, particularly in the accumulation of secondary metabolites including flavonoids and phenolics. Varia et al. [191] found that the CPC application to lettuce in vertical hydroponic systems led to early maturation, increased biomass yield, leaf diameter, and total flavonoid (luteolin and quercetin) content.

The attractiveness of CPC utilization as a psychostimulant lies in well-characterized molecular structure and standardized, more importantly, commercialized extraction and purification processes [193]. Along with the beneficial CPC trait of water solubility contributing to its suitability as a phytostimulant, its photosensitivity and reduced half-life under high light intensity present challenges for its use in outdoor conditions [194]. Nonetheless, CPC can be effectively used as a phytostimulant in controlled conditions like hydroponics and other vertical farming systems.

3.5. Amino acids and polyamines

Protein content in microalgae extract typically ranges from 18 to 46 % DW [195]. The existence of certain amino acids, particularly arginine, and tryptophan (Trp), can significantly enhance the yield and growth of cultivated crops due to amino acids being metabolic precursors of crucial PHs like auxins and SA, as well as various aromatic secondary metabolites with diverse bioactivities [195,196]. Trp is essential in plant metabolism, acting as a fundamental constituent of proteins and a precursor for PHs like auxins and SA, as well as various aromatic secondary metabolites with diverse bioactivities [196]. On the other hand, arginine is a precursor of polyamines (PAs), which are crucial in several biological processes, including embryogenesis, organogenesis, and defense against osmotic stress [197]. In addition, L-amino acids can act as

Table 2
Phytohormones of cyanobacteria and microalgae.

Phytohormones	Cyanobacteria	Microalgae	Physiological impact on plants	References
Auxins	<i>Anabaena</i> sp., <i>Chroococcidiopsis</i> sp., <i>Nostoc</i> sp., <i>Oscillatoria</i> sp., <i>Phormidium</i> sp., <i>Synechocystis</i> sp.	<i>Chlorella pyrenoidosa</i> , <i>Chlorella minutissima</i> , <i>Scenedesmus armatus</i>	Regulation of vascular differentiation, cell division and elongation, stress response, and apical dominance.	[142,168]
Cytokinins	<i>Anabaena</i> sp., <i>Calothrix</i> sp., <i>Chlorogloeopsis</i> sp., <i>Chroococcidiopsis</i> sp., <i>Nostoc</i> sp., <i>Oscillatoria</i> sp., <i>Phormidium</i> sp., <i>Rhodospirillum</i> sp., <i>Synechocystis</i> sp.	<i>Chlorella minutissima</i> , <i>Ecklonia</i> sp., <i>Nannochloropsis oceanica</i>	Nutrient mobilization, cell division, vascular differentiation, shoot differentiation, photo-morphogenic development, apical dominance, and chloroplast biogenesis	[169]
Absciscic acid	<i>Anabaena variabilis</i> , <i>Nostoc muscorum</i> , <i>Synechococcus leopoliensis</i> , <i>Trichormus variabilis</i>	<i>Chlamydomonas reinhardtii</i> , <i>Chlorella minutissima</i> , <i>Coscinodiscus granii</i> , <i>Dunaliella</i> sp., <i>Draparnaldia mutabilis</i> , <i>Nannochloropsis oceanica</i>	Modulation of stress tolerance by stomatal closure, proteins and compatible solutes/osmolytes accumulation, and maintenance of plant water status.	[169]
Ethylene	<i>Anabaena</i> sp., <i>Calothrix</i> sp., <i>Cylindrospermum</i> sp., <i>Nostoc</i> sp., <i>Scytonema</i> sp., <i>Synechococcus</i> sp.	<i>Chlamydomonas reinhardtii</i> , <i>Chlorella pyrenoidosa</i> , <i>Chlorella</i> sp.	Enhancement of plant tolerance to both abiotic and biotic stress factors.	[170]
Gibberellic acids	<i>Anabaenopsis</i> sp., <i>Cylindrospermum</i> sp., <i>Phormidium foveolarum</i>	<i>Chlamydomonas reinhardtii</i> , <i>Chlorella</i> sp., <i>Nannochloropsis oceanica</i>	Modulation of plant photosynthetic efficiency and promotion of photosynthesis redistribution, balancing source–sink relationship.	[171]
Brassinosteroids	–	<i>Chlorella vulgaris</i> , <i>Klebsormidium flaccidum</i> , <i>Raphidocelis subcapitata</i>	Plant stress response: tolerance to salt stress and enzymatic and non-enzymatic defense.	[157,172]
Salicylic acids	–	<i>Dunaliella salina</i> , <i>Haematococcus pluvialis</i> , <i>Scenedesmus</i> sp.	Seed germination, nodulation, senescence, thermo-tolerance, transpiration, stomatal conductance, photosynthetic rate, ion uptake and transport, antioxidant genes upregulation, flowering, and glycolysis.	[66,169]
Jasmonic acids	–	<i>Haematococcus pluvialis</i> , <i>Scenedesmus</i> sp.		

signaling molecules, mitigating abiotic stress-induced damage [23]. Melatonin, derived from L-tryptophan through the shikimate pathway, has recently been demonstrated to promote seed tolerance to adverse environmental conditions during germination [20]. The application of L-amino acids-rich lyophilized *A. platensis* biomass stimulates red beet chlorophyll synthesis, carbon metabolism, and sugar accumulation [198]. This improvement in chlorophyll synthesis may be associated with aminolaevulinic acid accumulation, which can be produced from the C skeleton of externally supplied L-glutamic acid [199].

PAs, low molecular weight aliphatic amines synthesized via the decarboxylation of L-amino acids like L-ornithine and L-arginine [200], are crucial for tolerance to various environmental stresses in bacteria and plants [201]. They play several osmo-protective roles, including protecting nucleic acids, regulating gene expression and protein synthesis, modulating signal transmission, stabilizing cellular membranes, and preventing chlorophyll loss during leaf senescence [202]. Trehalose, a non-reducing disaccharide that functions as a carbon reserve,

osmolyte, and stress protectant, accumulates in algae such as *Scytonema*, *Chlorella*, and *Chlamydomonas* under saline conditions [203]. Polyols, important osmoprotectants such as sorbitol and mannitol, have been identified in species such as *Stichococcus bacillaris*, *Stichococcus chloranthus*, and *Platymonas suecica* under similar conditions [204]. Betaines act as osmolytes or ROS scavengers, thus helping to maintain the structure and function of molecules and membranes [205]. In *Nannochloris* species, betaines constitute 0.023 % of dry weight, while protein hydrolysates, proline, carbohydrates, cytokinin, and cytokinin-like metabolites constitute 88.0 %, 5.7 %, 9.4 %, and 0.012 %, respectively [206]. MacKinnon et al. [207] reported similar levels of betaines in commercial *Ascophyllum nodosum* extracts, and Craigie [208] noted comparable concentrations of cytokinin in commercial algal extracts. Under stress conditions, cyanobacteria such as *Anabaena* sp. and *Synechocystis* sp. have been observed to accumulate PAs [209]. In a study involving PA-containing enzymatic hydrolysates of *A. platensis*, bioactive compounds responsible for enhancing the growth of treated lettuce

Table 3
Application methods of microalgae-based plant biostimulants.

Application method	Microalgae/Cyanobacteria species	Crop	Improvements	References
Seed treatment	<i>Chlamydomonas</i> spp. and <i>Pseudodictyosphaerium</i> spp.	Cucumber and Lettuce	Better yields, promote FW and DW of root and shoot	[211]
	<i>Chlorella ellipsoidea</i> , <i>Chlorella pyrenoidosa</i> , <i>Nanochloropsis gaditana</i> , <i>Spirulina maxima</i>	Tomato	Promote DW and root and shoot length, induce carotenoids accumulation	[212]
	<i>Chlorella vulgaris</i>	Lettuce	Promote DW and root and shoot length, induce carotenoids accumulation	[95]
	<i>Chlorella sorokiniana TH01</i>	Tomato and Rice	Induce early seed germinations	[213]
	<i>Chlorella vulgaris</i> and <i>Scenedesmus quadricauda</i>	Sugar beet	Enhance root tips number, total root length, root surface area, and expression of 55 upregulated genes	[214]
	<i>Dunaliella salina</i> , <i>Nanochloropsis gaditana</i> , <i>Tetraselmis</i> sp.	Tomato	Promote synthesis of metabolites such as linolenic acid, palmitic acid, pyridine-3-carboxamide, phytol, and stearic acid	[212]
	<i>Dunaliella salina</i>	Wheat	Enhance germination and coleoptiles height. Promote the synthesis of Proline and ROS scavenging enzymes (CAT, POD, SOD)	[66]
	<i>Scenedesmus quadricauda</i>	Lettuce	Induce total protein and pigments accumulation, stimulate root and shoot growth, promote total plant, leaves and root weight	[36]
	<i>Tetraselmis marina</i>	Tomato	Promote root uptake of nutrient (N, P, K)	[212]
	<i>Arthrospira platensis</i>	Winter wheat	Enhance plant yield and height. Promote shank length, ear length, and number of grains per ear	[215]
Foliar spraying	<i>Arthrospira platensis</i>	Wheat	Promote spike characteristics and growth parameters	[216]
	<i>Arthrospira platensis</i>	Tomato and Chili	Promote root nodes number, size, and weight	[66]
	<i>Acutodesmus dimorphus</i>	Tomato	Enhance floral production, plant development, and seed germination	[29]
	<i>Chlorella fusca</i>	Spinach and Chinese Chives	Promote plant yield, mineral content, FW, height, leaves number and thickness	[217]
	<i>Chlorella vulgaris</i>	Onion	Promote growth parameters, nutrients and carbohydrate synthesis	[218]
	<i>Chlorella vulgaris</i>	Guar	Induce the synthesis of total phenolic and antioxidant enzyme like GR, APX, CAT, and SOD. Promote shoot length, FW and DW of root and shoot. gth	[219]
	<i>Nannochloris</i> sp.	Tomato	Promote leaves area and number, root length	[220]
	<i>Scenedesmus</i> sp.	Wheat	Enhance DW	[221]
	<i>Anabaena</i> sp. and <i>Calothrix</i> sp.	Wheat seeds	Enhance seed protein content and level of micronutrient concentrations of Cu and Zn	[222]
	<i>Anabaena</i> sp. and <i>Chlorella</i> sp. cell extracts	Cucumber seedling	High concentrations of microalgae cell extracts in hydroponics resulted in a significant enhancement in the length of plant stems	[223]
Soil and root inoculation	<i>Anabaena oryzae</i> , <i>Anabaena doliolum</i> , <i>Aulosira fertilissima</i> , <i>Calothrix geitonos</i> , <i>Hapalosiphon intricatus</i> , <i>Oscillatoria acuta</i> , <i>Phormidium fragile</i> , <i>Plectonema boryanum</i> , <i>Tolypothrix tenuis</i>	Rice seeds	Enhance plant growth and stress tolerance	[224]
	<i>Calothrix ghosei</i> , <i>Hapalosiphon intricatus</i> , <i>Nostoc</i> sp.	Wheat	Promote plant height, DW, grain yields	
	<i>Chlorella vulgaris</i> and <i>Pseudomonas putida</i> consortium	Rice	Increase mobilization of soil P into plants.	[235]
	<i>Chlorella vulgaris</i> or <i>Scenedesmus quadricauda</i>	Sugar beet	Enhance number of root tips, surface, and total root length	[225]
	<i>Chlorella vulgaris</i> , <i>Dunaliella salina</i>	<i>Phaseolus vulgaris</i> L. bean seeds	Significant efficacy in alleviating salinity-induced stress	[32]
	<i>Chlorella infusionum</i> , <i>Chlorella vulgaris</i> , or <i>Scenedesmus quadricauda</i>	Tomato	Promote FW and DW	[226]

DW - dry weight, FW - fresh weight.

were named spermine and spermidine. Indeed, treatment with cyanobacteria increased lettuce DW by about 40 % compared to control, and the spermine leaf content by 64 %, demonstrating the growth-promoting and signaling capabilities of these bioactive molecules [210].

4. Microalgae-based phytostimulants' application methods

The application method of phytostimulants is tailored to the specific needs of crops, which include micronutrient enrichment, nutrient supplementation, or disease suppression [25]. Various methods are employed to deliver microalgal biomass or extracts to agronomic and horticultural crops, depending on the nature of the product and microalgal composition (Table 3). For algal preparations, application methods include a) incorporation into the soil employing suitable carriers; b) soil enrichment with suspended liquid culture or dry algal biomass (e.g., powder, pellets, or granules); c) foliar spraying (culture supernatant, compost tea, and algal leachate) or applying algal culture directly to the substrate/soil [227].

Microalgae extracts are usually available in two forms: liquid/water or liquid-soluble powder. The extracts are typically applied as biomass in powder form for soil applications, while the extract in liquid form can be applied directly to the plant's root system. To prepare the mixture for irrigation, the required dose of extract is thoroughly mixed with water using various irrigation systems, such as a drip system [228].

Similarly, various methods are used to apply cyanobacterial phytostimulants to crops. The most conventional method is foliar spraying (54 %), followed by basal application (26 %)—which involves application into soil or inert hydroponic substrates—and seed coating (18 %). Live cell inoculation is primarily applied to soil or seeds. In contrast, extracellular products are applied to leaves or supplemented to hydroponic media. Cell extracts are often applied via foliar spraying or seed treatment. They may not be suitable for direct soil application due to the soil's physical, microbiological, and chemical characteristics [20]. These methods ensure that phytostimulants are effectively delivered to plants, maximizing their beneficial effects on crop growth and health.

4.1. Seed treatment

Seed treatment with phytostimulants typically consists of three steps: priming, coating, and soaking [229]. Seed priming, a pre-sowing treatment, manages moisture levels to prevent radicle emergence. This technique is known to enhance sprouting and stimulate root formation [230]. When coating seeds with phytostimulants, a uniform layer is applied by spraying or directly coating the seeds. For soaking or dipping, seeds are immersed in phytostimulants for a specified duration (typically 18–24 h) before sowing. These methods effectively promote seedling activation, leading to greater shoot and root length, enhanced seedling vigor, increased germination index, and abatement in harmful microflora on the seeds [231].

Using microalgae live cell suspensions and extracts in seed treatment has shown promising results in enhancing plant growth across an extensive range of crops, including spices, vegetables, and cereals. For example, treating spinach seeds with cell lysates and whole cell extracts from microalgae species, including *Scenedesmus* sp., *Chlorella* sp., *Micractinium* sp., and *Chlorococcum* sp. resulted in improved sprouting, increased seedling weight, and accelerated cotyledon emergence [62]. Additionally, hydrating seeds with extracts from *S. quadricauda* and *C. vulgaris* led to an improvement in sugar beet root length, diameter, surface area, and root tips number, along with promoted sprouting and seedling viability [232]. Similar positive impacts have been observed in cereal crops like wheat and maize when treated with cell-free supernatants and extracts from cyanobacteria *Westiellopsis* spp., *Nostoc* spp., *Hapalosiphon* spp., *Calothrix* spp., and *Anabaena* sp. PCC 7120 [233,234].

4.2. Foliar spraying

Foliar spraying (FS) is a widely adopted method for increasing crop yields due to the rapid plant response to nutrient application compared to other treatments [191]. FS is typically implemented through fertigation (integrating nutrients/stimulants into irrigation systems) or aerial spraying, both proven efficient in enhancing nutrient utilization efficiency [25]. Indeed, applying organic matter via FS was recognized as an efficient agricultural practice, limiting nutrient dispersal into the environment and enabling the use of lower product doses, thereby increasing economic sustainability [235].

The application of phytostimulants like protein hydrolysate, microalgal and plant extracts via FS was shown to improve the marketable (size, firmness, external color, and soluble solids) and nutritional (anthocyanins, carotenoids, titratable acidity, organic acids, and phenolic compounds) qualities of fruits [236,237]. The hydrolysates and extracts from *C. vulgaris*, *A. platensis*, and *Scenedesmus* spp. have been most commonly used in FS [191,238]. Cell extracts of *Anabaena* spp., *C. vulgaris*, *D. salina*, *Nostoc* spp., and *Scenedesmus* spp. have been reported to promote development, pigment content, fruit yield, biomass yield in leaves, and tolerance to abiotic stress like salinity, temperature, and drought in plants like tomatoes, lettuce, capsicum, onion, and beans [239–241].

Plant responses to bioactive metabolites and nutrients in extracts are usually faster when applied via FS than as a soil amendment. Mahmoud and coworkers [242] demonstrated that treating spinach with aqueous extract from *Anabaena sphaerica* via FS was more efficient in promoting nutrient (K and P) uptake, plant DW, and protein content compared with application as soil amendment at the same concentration (10 g/L). Furthermore, grapevine treated with *A. platensis* F&M-C256 extract via FS not only increased berry weight (by 11 %) and sugar content (by 17 %), indicating the extract's ability to stimulate the synthesis of anthocyanins and polyphenols [243]. Another study with winter rape reported that treatment with *Nostoc entophyllum* MACC-612 aqueous extract at a concentration of 0.3 g/L via FS promoted seed productivity without impacting its oil content [244].

4.3. Soil and root inoculation

Roots, the critical interface between soil and plant, serve a crucial role in plant growth by initiating plant defense responses to stressors, conducting external stimuli, and mobilizing nutrients. Maintenance of soil and root health is crucial for sustainable agricultural practices. It can be attained by applying fertilizers and soil conditioners, which restore soil health and offer essential nutrients to the roots.

In general, soil fertilization involves the incorporation of biofertilizers or stimulants at the time of sowing to enhance plant growth. Phytostimulants or biofertilizers aid in agglomerating soil particles with organic molecules, stimulating the biomineralization of complex nutrient substances, and restoring soil microflora [27]. The inoculation of soil with cyanobacteria and/or microalgae can significantly increase the topsoil's organic carbon content and nutrient availability. Maqubela et al. [245] found that soil inoculated by cyanobacteria from an unseeded pot had higher carbon, nitrogen, and mineral content compared to that of seeded pots. However, various factors affecting plant growth can potentially induce the mineralization of soil organic matter [243].

When plants are cultivated using a substrate, introducing phytostimulants into the soil surrounding their roots can enhance their vitality and nutrient availability in the immediate root vicinity. In hydroponic systems, phytostimulant solutions-enriched nutrient solutions can be administered to both the leaves and roots of the plants [246]. This application method enhances nutrient uptake, akin to observations made with soil drench and foliar spray techniques [246,247]. Moreover, phytostimulants have the potential to decrease reliance on synthetic pesticides and stimulants in both outdoor and indoor farming systems, particularly in organic farming. This shift is crucial as synthetic

substances can pose environmental and human health hazards [202].

The utilization of algae as soil fertilizer is commonly achieved through the application of cyanobacteria/microalgae consortia or a combination of cyano- and rhizobacteria [27]. *Anabaena* spp. and *Nostoc* spp., frequently employed cyanobacterial consortia, are applied to various crops, including maize, chickpea, cotton, wheat, and rice. Its application enhanced the N and P availability and increased enzymatic activity (nitrogenase and dehydrogenase) in soil, improving crop yield and productivity [248]. Additionally, the synergy of cyano- and rhizobacteria, like *Pseudomonas putida*, *Azotobacter* spp., *Mesorhizobium ciceri*, and *Brevundimonas diminuta*, has shown benefits in enhancing N₂ fixation, P solubilization, microbial activity, and soil micronutrient content [27,231].

One of the key advantages of cyanobacteria inoculation is the reduction in the chemical NPK demand. Many studies have reported a possibility of partial replacement of chemical NPK fertilizers using live cyanobacteria or consortia, with yields of cereal crops like maize and rice comparable to those achieved with former ones, but with N fertilizer savings of up to 50 % [249]. For green microalgae, the application of *Pseudomonas putida* and *C. vulgaris* consortium has been found to enhance P mobilization and prevent translocation into rice tissues from the soil, demonstrating microalgae's role as both a biofertilizer and a heavy metal sink [250].

The method and timing of phytostimulant application greatly influence the plant's response [251]. For instance, a study on lettuce revealed different responses of root and leaf towards *C. vulgaris* extract applications, specifically root application significantly affected carbon metabolism, leading to increased C content in plant biomass and DW of roots and shoots [36]. Similarly, foliar application of commercial algae-based phytostimulants in spinach and *S. quadricauda* extracts in lettuce enhanced N metabolism, leading to increased N and protein contents in shoots and roots [232]. Foliar application is considered the most efficient method for phytostimulant utilization under conditions of elevated relative humidity and open leaf stomata to increase its penetration inside plant tissues.

5. Advances and critics on utilizing microalgae and cyanobacteria as phytostimulants

Microalgae are increasingly recognized as potential industrial feedstocks due to their capability to grow in brackish waters, outstanding

photosynthetic efficiency, and capacity to regulate their metabolite biosynthesis pathways in response to environmental changes [165,252]. A SWOT analysis of microalgae-based (including cyanobacteria) plant phytostimulants is presented in Fig. 2 to elucidate the strengths, weaknesses, opportunities, and threats associated with the utilization of these phytostimulants to alleviate the negative impacts of abiotic stresses, such as water and salt stress. The positive impact of microalgae biomass on soil health and plant development can be ascribable to the existence of various biomolecules, including polysaccharides, phenolic compounds, biomineral conjugates, soluble amino acids, and N₂-fixing enzymes [253]. Various microalgae species like *C. vulgaris*, *S. platensis*, *S. quadricauda*, *D. salina*, *C. ellipsoida*, *C. infusionum*, *S. maxima*, and *C. elenkinii* have been characterized by phytohormone-like activities, including auxins, cytokinins, gibberellins, abscisic acid, and brassinosteroids, which are crucial for enhancing plant growth, yield, and defense responses, particularly against abiotic stressors [254]. Moreover, cyanobacteria and microalgae can engage in symbiotic relationships with soil microbes, which are remarkably potent as they coexist in the phycosphere and mutually benefit from the synthesis of bioactive compounds or modulate of root system architecture to enhance nutrient uptake and efficiency. [255].

Microalgae- and cyanobacteria-derived phytostimulants have the benefit of requiring limited non-renewable resources for production, leading to a lower environmental footprint. Compared with other photosynthetic organisms, microalgae and cyanobacteria are more amenable to biotechnological enhancements, particularly in metabolic engineering [256]. Phototrophic microorganisms are characterized by high photosynthetic activity, ensuring rapid growth and biomass accumulation. This characteristic makes them particularly valuable for use in regions with saline soils, where traditional crops experience significant stress and yield reduction. Moreover, their high adaptability to environmental changes allows microalgae and cyanobacteria to regulate their metabolic pathways in response to external stressors, including salt stress [257]. These organisms are typically cultivated using either open or closed production systems for mass cultivation. While open systems have lower construction and maintenance costs, they also have lower biomass yields and a higher risk of microbial contamination. Meanwhile, closed systems provide higher biomass yields but need immense inputs of water, electricity, fertilizer, and materials for construction and operation [258]. New production approaches like biorefineries and circular economy are needed to address these challenges without extra

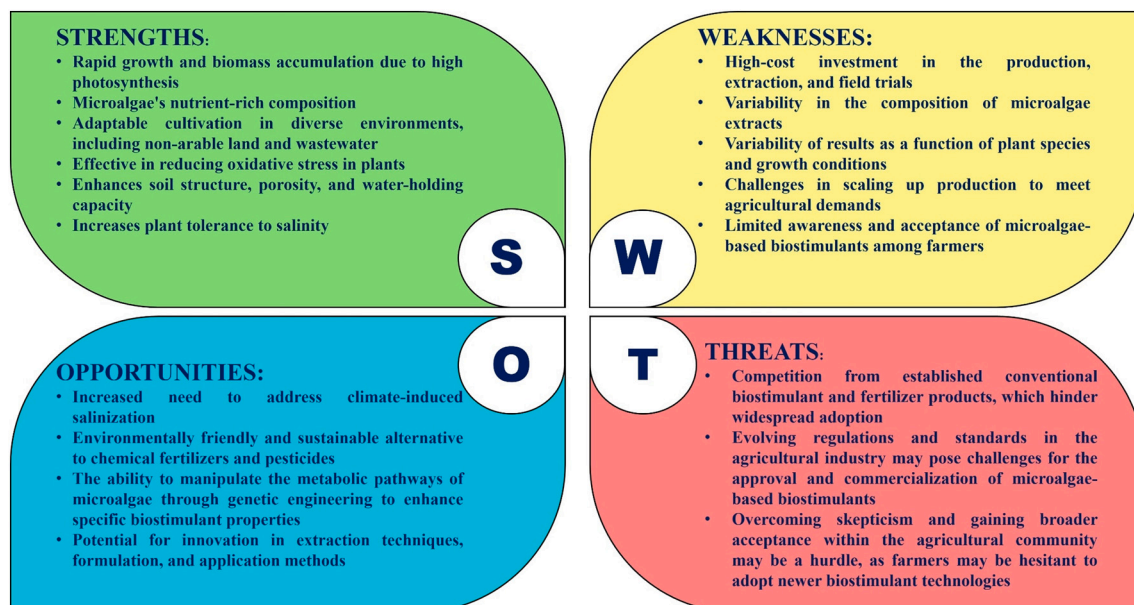


Fig. 2. SWOT analysis of microalgae-based phytostimulants used for mitigating salt stress.

water and greater energy. A microalgae biorefinery refers to a process where the full utilization of algal biomass is achieved post-production, emphasizing sustainability through the integration of production and recovery of industrially valuable molecules [259]. One promising solution is utilizing wastewater as a microalgae cultivation substrate, which offers the crop essential nutrients such as nitrogen and phosphorus, thereby reducing production costs. Microalgae biomass derived from waste streams has become an economically attractive investment for agricultural applications [255,260].

Despite the potential benefits, the application of microalgae-derived phytostimulants in agriculture faces several challenges, specifically a need for more scientific evidence to support the efficacy of microalgae-crop interactions, as the understanding of these interactions is less developed in comparison with other inorganic, organic, and microorganism phytostimulants; the wide variety of microalgae remains unexplored mainly with very limited research on breeding and genetical engineering; biosafety concerns, since many cyanobacterial strains produce toxins like microcystins, nodularins, and anatoxins that can have adverse effects on human neurology and pose significant health risks [261].

Employing cyanobacteria and microalgae (or their extracts) in agricultural practices offers significant benefits. Still, their application is often constrained by high production costs associated with biomass cultivation and compound extraction. When developing market products like food, animal feed, biofuels, or biofertilizers, selecting a cost-effective cultivation method that requires minimal energy input is crucial. Hence, a comprehensive evaluation of the sustainability factors associated with each production stage is essential to identify the most suitable approach for cultivating, harvesting, and processing biomass. However, the optimal approach often varies depending on the species or strain of microalgae or cyanobacteria, necessitating detailed sustainability assessments. State-of-the-art approaches to cultivating photosynthetic microalgae have predominantly centered on growing microalgal cultures in open ponds. Despite the simplicity of these systems, they are prone to limitations in light availability and stresses that inhibit microalgal growth once the biomass concentration exceeds 2–6 g/L in photobioreactors and 0.5 g/L in open ponds [262]. In addition, harvesting and concentration of biomass becomes extremely expensive at these low microalgal cell densities, and the biomass productivity achieved through this method is relatively low [263]. Some systems, like thin-layer cascade photobioreactors, have demonstrated the ability to achieve biomass densities over 30 g/L [264]. Nevertheless, these high-density systems encounter other obstacles, like light limitations. Moreover, the biomass recovery process post-production can be costly and energy-intensive, significantly contributing to the overall cost of biomass production.

In contrast, utilizing extracts from microalgae and cyanobacteria involves isolating specific metabolites, and the methods commonly used for this purpose are often prohibitively costly [69]. A major challenge with using extracts from these sources is the instability of conventional extraction procedures. These methods generally demand large volumes of organic solvents to extract bioactive compounds [265].

Microalgae demonstrate significant potential for bioremediation, capable of growing in non-potable water and efficiently removing contaminants such as nitrate, phosphate, and ammonia from wastewater. They are also effective in reducing biological (BOD) and chemical (COD) oxygen demand [266]. Additionally, their capability to utilize flue gases as a CO₂ source and their carbon concentration mechanism position them as valuable resources for both bioremediation and the production of biomass and metabolites [267].

Despite these advantages, using microalgae biomass for agricultural purposes presents certain challenges. One of the main concerns is biomass production scalability. There are also risks associated with potential biomass contamination by xenobiotics, as well as the possible presence of bacteria, fungi, and viruses, which could impact crop safety and limit the broader application of microalgae in agriculture [268].

Another significant obstacle is ensuring adequate light availability for the crops when using wastewater for biomass production. Industrial wastewater from food processing, livestock, aquaculture, and other sources often has high levels of suspended solids that can impede light penetration into the nutrient medium. This reduction in light availability can affect the photosynthetic rate and, consequently, the productivity of the microalgae biomass [269].

In summary, the application of microalgae and cyanobacteria products in agriculture is indeed constrained by a limited understanding of the complex interactions between these organisms (and their extracts), plants, and the environment. These drawbacks emphasize the necessity for rigorous research and adherence to application guidelines for the successful implementation of the technology in practice. Despite substantial challenges, the exploitation of microalgae and cyanobacteria-based phytostimulants as sustainable means to enhance crop production under sub-optimal and optimal conditions is vital for restoring the environmental sustainability of the agriculture industry [270].

6. Conclusions

The accelerating salinization of arable land worldwide poses one of the most critical threats to modern agriculture. Extracts from red, green, and brown macroalgae, as well as microalgae, offer a valuable option for enhancing defense responses in crops under salinity-stress conditions. Extensive research and reviews have scientifically concluded that introducing phytostimulants derived from cyanobacteria and microalgae into the market could play a pivotal role in achieving sustainable agriculture. The utilization of bioactive substances derived from cyanobacterial and microalgal biomass represents a promising avenue for enhancing crop resilience to salt stress. However, several challenges must be overcome to fully realize the potential of cyanobacterial and microalgal extracts under optimal and suboptimal (salinity) conditions.

Addressing these challenges entails various aspects, including the identification of more productive strains of microalgae and cyanobacteria with pronounced phytostimulatory properties. Field trials are deemed necessary to corroborate laboratory findings concerning the fertilizing, stimulating, or pesticidal activity of extracts derived from microalgae. Although obtaining data through field trialing of microalgae-based products could be expensive, it is essential to instill confidence in consumers and facilitate the entry of these products into the market.

To address these issues effectively, exploring the additive or synergistic effects of cyanobacteria and microalgae to produce crude extracts suitable for a variety of crops, stresses, application methods, and conditions is crucial. Additionally, clarifying the molecular-level effects of specific algal extracts, compounds, or mixtures on plant physiology and phenology is necessary. This approach will enable the exploitation of the biostimulatory functional diversity in algae by extracting specific fractions or chemical classes, moving beyond random sampling of algal diversity.

Advancing cost-effective methods for collecting and dewatering microalgal biomass, essential for phytostimulant mass production, is also important. Furthermore, incorporating zero-waste economy models, utilizing agricultural wastewater and industrial waste, is considered to enhance the commercial feasibility of microalgae- and cyanobacteria-based agricultural practices.

CRedit authorship contribution statement

Fariza K. Sarsekeyeva: Writing – original draft, Investigation, Formal analysis, Conceptualization. **Asemgul K. Sadvakasova:** Writing – review & editing, Visualization, Formal analysis, Conceptualization. **Sandugash K. Sandybayeva:** Writing – review & editing, Visualization, Project administration, Data curation. **Bekzhan D. Kossalbayev:** Writing – review & editing, Visualization, Formal analysis. **Zhiyong Huang:** Methodology, Formal analysis. **Bolatkhon K. Zayadan:** Writing

– review & editing, Investigation, Formal analysis. **Nurziya R. Akmu-khanova:** Writing – original draft, Formal analysis. **Yoong Kit Leong:** Writing – review & editing, Data curation. **Jo-Shu Chang:** Writing – review & editing, Validation, Resources, Conceptualization. **Suleyman I. Allakhverdiev:** Validation, Project administration, Funding acquisition, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

Acknowledgments

This research was funded by the Ministry of Science and Higher Education of the Republic of Kazakhstan and supported by projects AP13068051, AP14870201. BDK was supported from the Tianjin Synthetic Biotechnology Innovation Capacity Improvement Projects (TSBICIP-BRFI-009, TSBICIP-IJCP-001-03). JSC gratefully appreciates the funding provided by the Taiwan National Science and Technology Council (grants NSTC 110-2221-E-029-004-MY3, 112-2622-8-029-003-TE2, 112-2221-E-029-002-MY3, 112-2621-M-029-003, and 111-2622-E-110-020). YKL, JSC, and SIA were supported by the joint grant RSF-MOST (22-44-08001). Fig. 1 was supported under the state contract of the Ministry of Science and Higher Education of the Russian Federation (theme No. 122050400128-1).

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