SEAWEED-DERIVED BIOSTIMULANTS: A SUSTAINABLE APPROACH FOR ENHANCING SEED GERMINATION AND EARLY ABIOTIC STRESS TOLERANCE

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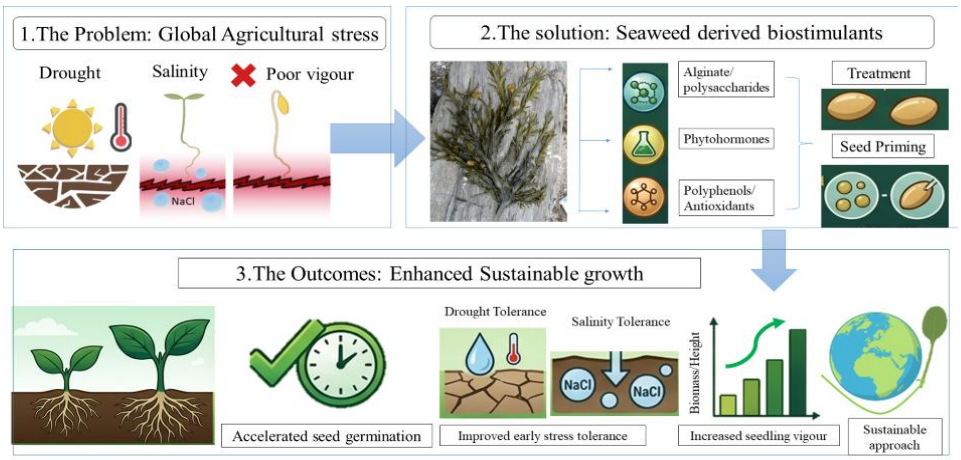
ABSTRACT

Seaweed-derived biostimulants offer a sustainable approach in improving seed germination and the resilience of young plants to abiotic stresses. However, existing reviews have largely focused on foliar and field applications, leaving a fragmented evidence base for seed-stage applications that is rarely synthesised across physiological, biochemical and molecular scales. This review addresses this gap by critically synthesising research on the classification, biochemical composition, extraction methods and mechanisms of action of seaweed biostimulants, with a particular focus on seed-based applications. Brown, red and green seaweeds contain polysaccharides, phytohormones, phenolic compounds and osmoprotectants, though their relative abundance varies substantially with species, harvest season and extraction method. This batch-to-batch variability remains a major challenge limiting the reproducibility and commercialisation of seaweed biostimulants. Extraction techniques range from conventional aqueous, alkaline and enzymatic methods to emerging ultrasound-, microwave and supercritical fluid assisted approaches, with no single method providing the best balance between bioactive recovery, scalability, cost-effectiveness and environmental sustainability. At physiological, biochemical and molecular levels, seaweed extracts accelerate metabolic activation, reserve mobilisation, antioxidant defence and stress-responsive gene expression. This review presents an integrated mechanistic framework linking these responses. Cross-study comparison of seed-priming trials involving cereals, legumes and vegetables indicates consistent improvements in germination speed, uniformity and seedling vigour under salinity, drought and heat stress, though gaps persist in field-scale validation and long-term formulation stability. In conclusion, specific research priorities are identified such as standardised dose response protocols, omics based mechanistic validation and seed pelleting delivery systems as the most direct route from laboratory findings to climate resilient seed technologies.

KEYWORDS: Seaweed biostimulants, seed priming, abiotic stress, germination, sustainable agriculture, marine algae

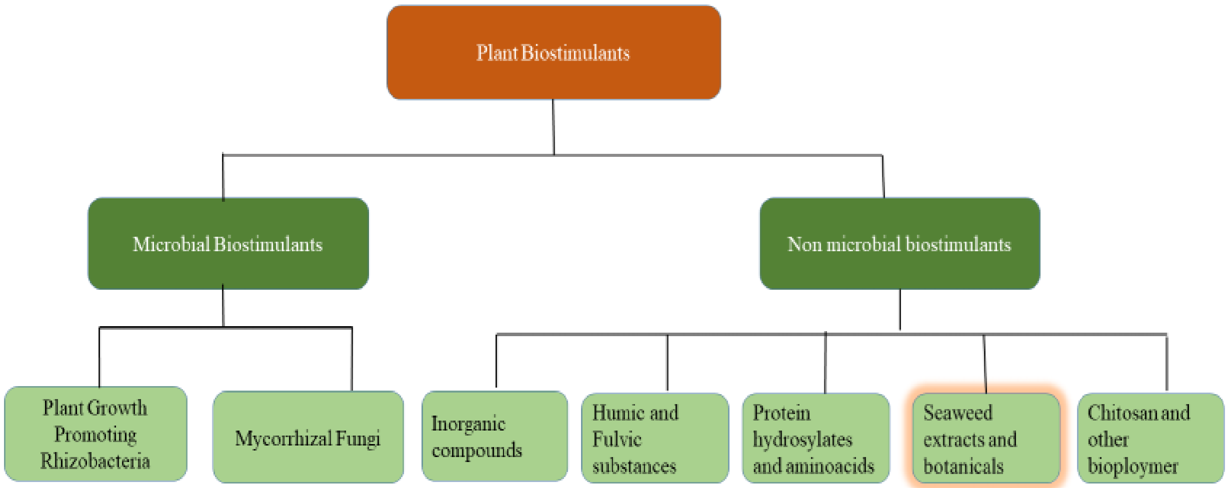
Graphical Abstract



INTRODUCTION

Biostimulants are substances or products that enhance plant nutritional processes, independent of their nutrient content, to improve nutrient use efficiency, increase tolerance to abiotic stress, and enhance crop quality.It encompasses a diverse range of substances and microorganisms, including humic substances, protein hydrolysates, and seaweed extracts, all of which share the common goal of enhancing plant physiological processes and mitigating environmental challenges[1] (Fig 1) These advanced agricultural inputs differ from conventional fertilizers because they stimulate plant's natural physiological processes rather than directly supplying nutrients, leading to enhanced uptake efficiency and improved plant vigor [2]The application of biostimulants leads to enhanced nutrient use efficiency, fostering more robust plant development and increasing yields even in suboptimal growing conditions. This is achieved through various mechanisms, such as enhanced nutrient assimilation, improved root architecture, and modulated hormonal signaling, ultimately leading to superior crop performance and resilience[3][4]

Fig 1. Classification of plant biostimulants based on origin and composition



Global food security faces unprecedented pressure from a rapidly expanding population, climate-change-induced environmental stress, and the degradation of arable land [5]. Seedling establishment, a developmentally critical and stress-sensitive stage for final crop yield, is particularly vulnerable to these pressures [6]. Seaweed-derived biostimulants rich in polysaccharides, phytohormones, and secondary metabolites present a sustainable strategy for addressing these challenges[7][8][9]**.**Unlike terrestrial crops, seaweed cultivation does not require arable land or freshwater[10][11]**.**It typically requires minimal material and energy inputs, actively sequestering atmospheric carbon dioxide helping to mitigate climate change without requiring agricultural land[12][13][14].Brown, red and green seaweeds, yield a variety of polysaccharides such as alginate, fucoidan, carrageenan, agar, and ulvan each possessing distinct structural characteristics and biological activities that contribute to their biostimulant properties[15]The presence of various antioxidants, plant growth promoters, and unique biomolecules within seaweed extracts further enhances plant defense mechanisms, offering a potential protective strategy against various environmental stressors[16]. Consequently, these extracts serve as a sustainable alternative to synthetic chemicals often used in agriculture, mitigating their detrimental effects on human health and the environment [17]The drive to develop novel, nature-based agricultural inputs emphasizes the significant bioactive potential of seaweed polysaccharides[18]

The rapidly growing global population demands a significant increase in food production, placing immense strain on agricultural systems already challenged by climate change and environmental degradation, while various stresses further threaten food security by diminishing crop yield and quality, highlighting the urgent need for sustainable and effective mitigation strategies[19][20]These natural compounds possess a complex array of bioactive molecules that modulate plant physiological processes, thereby contributing to sustainable agriculture by reducing reliance on synthetic fertilizers and pesticides. Traditional agricultural practices often rely on an intensive application of agrochemicals, which, while increasing yields, pose substantial environmental risks to aquatic ecosystems and biodiversity through surface runoff and pesticide residues[21].Conversely, biostimulants derived from seaweeds offer an environmentally benign alternative, aligning with sustainable agricultural paradigms like the "Green Deal" and "Farm to Fork" strategies by reducing ecological footprints while improving crop resilience and productivity[22]The physiological processes instigated by these natural compounds, which are produced by microorganisms or plants, include enhanced nutrient absorption and translocation, alongside improved tolerance to diverse abiotic stressors[23] These biostimulants, whether applied directly to seeds, seedlings, or introduced into the rhizosphere, beneficially impact plant productivity and growth, especially under environmental stresses, including drought, salinity, and temperature extremes[24].They achieve this through multifaceted mechanisms, such as modulating phytohormone signaling pathways, enhancing antioxidant defense systems, and optimizing nutrient uptake efficiency[25]. This complex interplay of benefits underscores their potential to foster resilient agricultural systems, particularly in regions facing severe environmental constraints and food insecurity[26] [27]

Despite the growing body of literature on biostimulants and seaweed extracts, existing reviews largely focus on general plant growth promotion, foliar applications, or field-level productivity, with limited emphasis on seed-stage interventions and mechanistic insights during germination under abiotic stress conditions. Furthermore, there remains a lack of integrated understanding of how specific seaweed-derived bioactive compounds influence physiological and biochemical pathways during early plant development. In this context, the present review aims to provide a comprehensive and focused analysis of seaweed-derived biostimulants in enhancing seed germination and early seedling establishment under abiotic stress. It specifically examines (i) the classification and biochemical composition of seaweeds, (ii) extraction and formulation approaches, (iii) mechanisms of action at physiological and molecular levels and (iv) evidence from seed-based applications such as seed priming across various crop systems. By synthesizing recent advances, this review seeks to bridge existing knowledge gaps and offer mechanistic insights and practical perspectives for utilizing seaweed biostimulants to improve seed vigor and stress resilience in sustainable agriculture.

CLASSIFICATION OF SEAWEED AND THEIR BIOACTIVE COMPOUND PROFILES

Seaweeds, a diverse group of multicellular marine algae, are broadly categorized into three primary divisions based on their distinct photosynthetic pigments [28]. These divisions, namely brown algae, red algae, and green algae, each possess unique biochemical profiles and structural characteristics[29] (Table 1). The classification of seaweeds, their major bioactive compounds, and their functional roles in promoting seed germination and early plant growth are summarized in Fig 2.This classification is based not only on their visible pigmentation but also on inherent differences in their light-harvesting systems and the diversity of bioactive compounds they produce[30] These pigments play crucial roles in their adaptation to various depths and light conditions within marine ecosystems[31]**.**Specifically, brown algae are characterized by the dominance of fucoxanthin, a carotenoid that masks chlorophylls and facilitates light absorption in deeper waters[32] Red algae are distinguished by the presence of phycobiliproteins, including phycoerythrin and phycocyanin, which enable them to efficiently absorb green and blue light that penetrates to greater depths[33].These distinct pigment compositions allow each algal group to thrive in specific marine photic zones, influencing their evolutionary trajectories and the consequent biosynthesis of diverse secondary metabolites[34]. This taxonomic differentiation based on pigmentation also correlates with significant variations in their chemical composition, influencing their potential as sources of diverse bioactive compounds[35][36].Key bioactive compounds include alginates, carrageenans, laminarin and phytohormones, each contributing uniquely to the physiological functions and ecological success of various seaweed species[37].Furthermore, the vast phytochemical diversity of algae, exceeding that of terrestrial plants by a factor of ten, includes phenolic compounds, sterols, and an array of pigments such as astaxanthin, β-carotene, lutein, and zeaxanthin, which contribute significantly to their functional properties[38][39] Alginates, derived primarily from brown algae, are linear anionic polysaccharides comprised of β-D-mannuronic acid and α-L-guluronic acid residues linked by 1,4-glycosidic bonds known for their emulsifying and gelling properties [40].Their biological activity is largely mediated through hormone-like effects, antioxidant protection, and modulation of metabolic pathways during early growth. Conversely, carrageenans are a complex family of sulfated linear polysaccharides extracted from red algae, notable for their gelling, thickening, and stabilizing capacities in aqueous solutions, attributed to their distinct sulfate ester content and sugar backbone configurations [41].Laminarin, a β-glucan storage polysaccharide predominantly found in brown algae, functions as an energy reserve and exhibits prebiotic and immunomodulatory effects within biological systems [42]. Its branched structure and solubility contribute to its efficacy in modulating gut microbiota and stimulating immune responses [43].These compounds are increasingly recognized for their role in enhancing seed germination, root initiation, and seedling vigor. Phytohormones, specifically auxins and cytokinins, are pivotal plant growth regulators present across various seaweed types, driving their rapid proliferation and adaptive responses to environmental stressors. These endogenous compounds facilitate cell division, elongation, and differentiation, enabling seaweeds to exhibit remarkable growth rates and resilience in dynamic marine environments [44]. Beyond these established compounds, a comprehensive chemical analysis of seaweed extracts consistently reveals a significant presence of other important bioactive molecules, such as carotenoids and phenolic compounds, contributing to their broad functional spectrum [45][46]. This intricate interplay of diverse bioactive compounds, ranging from structural polysaccharides to highly specialized secondary metabolites and phytohormones, collectively underpins the remarkable adaptability, resilience, and growth dynamics observed across different seaweed taxa. This multifaceted biochemical toolkit positions seaweeds as exceptional natural resources for biotechnological exploitation, leveraging their inherent capacity for rapid biomass accumulation and the synthesis of high-value compounds. Such broad chemical diversity and synergistic bioactivities enable seaweeds to thrive in challenging marine environments and offer a sustainable source for a range of bio-based products, from agricultural biostimulants to novel therapeutic agents[47] Seaweeds, classified into brown, red, and green algae, exhibit distinct biochemical compositions that underpin their functional diversity. Their rich repertoire of bioactive compounds, including polysaccharides, phytohormones, and antioxidants, plays a critical role in enhancing seed germination and early plant growth by improving hydration, regulating metabolic and hormonal activities, and increasing stress resilience. This functional potential positions seaweeds as valuable and sustainable resources for the development of natural biostimulants aimed at improving crop establishment and agricultural productivity.

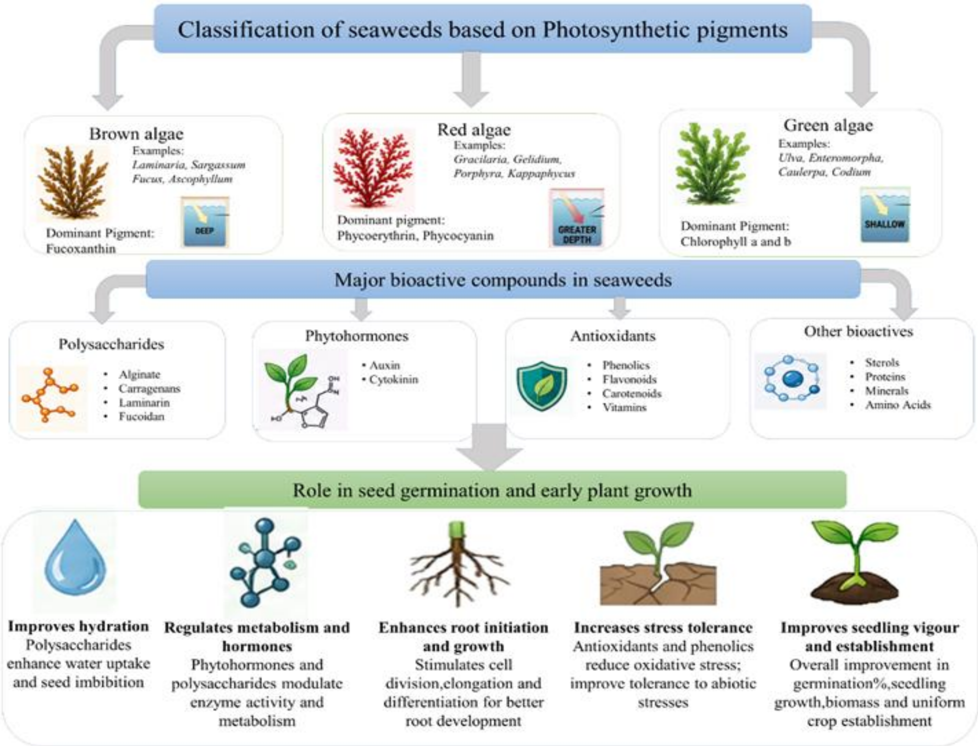


Fig 2. Classification of seaweeds, their bioactive compounds, and their role in seed germination.

EXTRACTION AND FORMULATION OF SEAWEED BIOSTIMULANTS

The efficacy of seaweed biostimulants is inherently linked to the extraction and formulation method employed, since these processes determine the final composition and bioavailability of active constituents[51]. No extraction method is universally superior; each represents a distinct trade-off between yield, selectivity, bioactivity retention, scalability, and environmental footprint, and the appropriate choice depends on the target compound class and the intended seed-based application. This section evaluates the primary methods such as liquid extracts, powdered forms, and commercial formulations on these comparative terms (Table 2) An overview of the extraction, processing, and formulation workflow is presented in Figure 3.

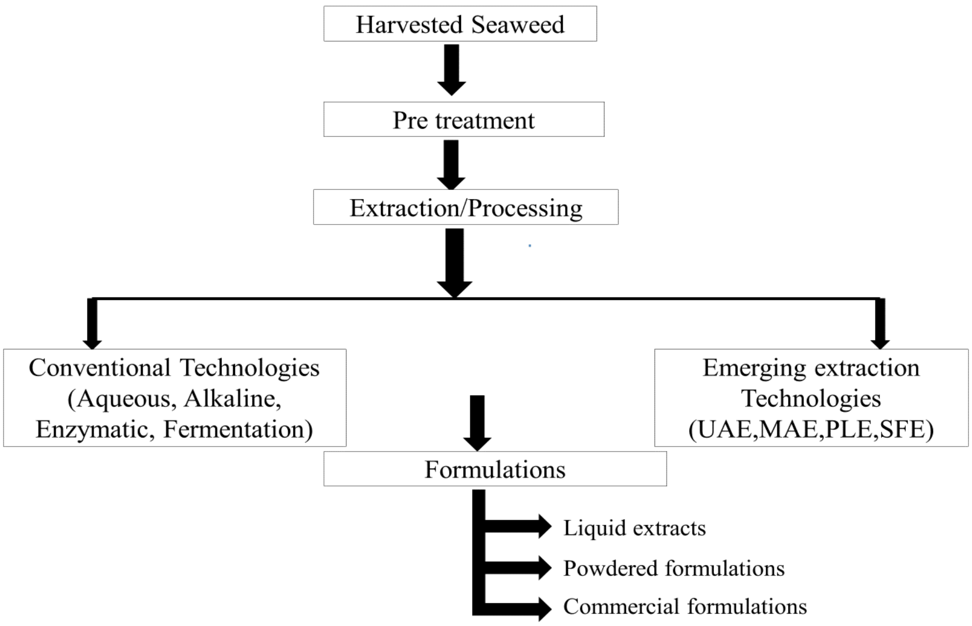


Fig 3. Overview of Extraction Technologies and Formulation Strategies for Seaweed derived Biostimulants

Liquid Extracts

Liquid extracts are the most common type of seaweed biostimulants, typically prepared using aqueous, alkaline, or enzymatic methods to target specific bioactive compounds [23]Aqueous extraction is preferred for being eco-friendly and cost-effective, isolating hydrophilic compounds like polysaccharides and proteins under controlled temperatures. Hot aqueous extraction dissolves more polysaccharides but requires careful temperature control to prevent degradation. Cold aqueous extraction preserves heat-sensitive compounds but yields lower polysaccharide concentrations [52].Alkaline extraction uses potassium hydroxide or sodium carbonate to solubilize structural polysaccharides and phenolics, modifying their structure to boost bioactivity[53].It is widely used to extract fucose-containing sulphated polysaccharides and can break down complex polysaccharides into more bioactive forms[54].Enzymatic extraction uses specific hydrolases to gently release target compounds while preserving heat-sensitive molecules [52]. It is highly selective but requires careful optimization of enzyme concentration, pH, and temperature to maximize yield and bioactivity of compounds like phenolics and polysaccharides [55]. This mild approach recovers fragile molecules that would otherwise be damaged by extreme pH or high temperatures [56].

Across all three methods, seaweed-to-solvent ratio, extraction time, and temperature directly determine the bioactive profile of the final product; optimal ratios typically range from 1:10 to 1:20 (w/v), with extraction times of 2–6 hours and temperatures of 50–80 °C depending on the target compound and species [27][57]. To preserve the bioactivity and shelf stability of these sensitive compounds after extraction, stabilization techniques such as microencapsulation or adding natural antioxidants are vital, especially during storage and field application[58].Fermentation boosts biostimulant efficacy by producing beneficial microbial metabolites and breaking down complex macromolecules into plant-available forms [59][60]. Selecting appropriate stabilizers such as humic acids or chitosan and using sterile filtration are also critical for ensuring long-term stability and microbial integrity of liquid formulations. This biotransformation can increase phytohormone levels while reducing antinutritional factors, thereby enhancing the extract's biostimulant properties [61]. Collectively, the production of liquid seaweed biostimulants represents a delicate balance between extraction efficiency and compound integrity. Aqueous, alkaline, and enzymatic methods each offer distinct advantages for isolating specific bioactive fractions, yet their success is contingent upon rigorous control of operational parameters and downstream stabilization strategies. The emerging role of fermentation and advanced stabilizers further underscores the dynamic nature of this field. Moving forward, standardized protocols that integrate these diverse techniques will be essential for translating laboratory-scale innovations into consistently effective agricultural products.

Powdered Forms

Powdered seaweed biostimulants provide an alternative to liquid formulations, mainly produced through spray drying, freeze drying (lyophilization), and milling—each method conferring unique properties to the final product [62]. Lyophilization, in particular, safeguards the structural and nutritional integrity of seaweed by eliminating moisture without passing through a liquid phase, a critical feature for preserving volatile bioactive compounds [63]. The selection of whole seaweed powder versus extracted powder is determined by the target concentration of bioactive compounds and the intended application. Extracted powders, in particular, offer a more concentrated form of biostimulatory agents[64].Key quality indicators for powdered biostimulants include moisture content, particle size distribution, and solubility, all of which govern handling characteristics and overall efficacy[65]. A major benefit of powdered biostimulants compared to liquid formulations is their improved stability and lower transportation costs, resulting from the elimination of water. Moreover, powdered products generally display extended shelf-life, as they are less prone to microbial spoilage and chemical degradation, rendering them especially well-suited for seed treatments and dry application techniques [66]. As the industry grows, strict quality checks on moisture content, particle size, and solubility will remain key to ensuring easy handling and reliable performance in the field. Ultimately, powdered forms resist microbial and chemical breakdown better than liquids, making them ideal for seed treatments and dry applications, an advantage that highlights their growing role in sustainable farming.

Commercial Formulations

Commercial seaweed biostimulant products vary widely, from single-species extracts to complex multi-algae blends and enriched mixtures containing macro/micronutrients and beneficial microbes. These diverse formulations are designed to deliver broad plant support, meet specific crop requirements, and improve nutrient use efficiency across different agricultural systems. Single-species products, such as those based exclusively on Ascophyllum nodosum or Ecklonia maxima, typically exploit the unique phytochemical makeup of one algal species to achieve specific biostimulatory outcomes [2]. Conversely, multi-algae blends harness the synergistic effects of compounds from different species, potentially providing a wider range of bioactive benefits and greater tolerance to diverse abiotic stresses[67] Combination of essential macronutrients (NPK), vital micronutrients such as iron, copper, zinc, and manganese, along with beneficial microbial inoculants, mark a further advancement in seaweed commercial formulation. These integrated solutions boost both plant growth and soil health [68]. This integrated approach is particularly beneficial for promoting sustainable agricultural practices by reducing reliance on synthetic inputs and improving overall ecosystem resilience [69].The commercial seaweed biostimulant market offers something for every grower from simple single-species extracts to complex blends packed with nutrients and beneficial microbes. Single-species products give targeted results by tapping into the unique chemistry of one alga, while multi-algae mixes bring together different species to create a wider, more balanced range of benefits that help plants cope with various stresses. Then there are the value-added formulations that go a step further by throwing in NPK, micronutrients like iron and zinc, and helpful microbes all working together to feed the plant and improve the soil at the same time. This layered approach to formulation design means farmers can pick products that match their specific needs, whether they want precision or an all-in-one solution, while also cutting back on synthetic inputs and building healthier, more resilient farming systems.

Emerging and Innovative Extraction Technologies

While conventional and established extraction methods remain the backbone of seaweed biostimulant production, a new generation of innovative technologies is rapidly gaining momentum, driven by the dual imperatives of sustainability and efficiency.

Ultrasound-assisted extraction (UAE) uses high-frequency sound waves above 20 kHz to create cavitation bubbles in the solvent, which physically break down algal cell walls and greatly improve mass transfer. This approach typically achieves 1.5 to 2.5 times higher yields than traditional methods while using less solvent and requiring shorter processing times[77][78] .Recent work has shown UAE-optimized recovery of phycoerythrin from Padina cruentum at 33.85 mg/g and polysaccharides from Kappaphycus alvarezii at 61.25% yield, highlighting its effectiveness across different types of seaweed[79].

Microwave-assisted extraction (MAE) is another environmentally friendly technique that uses dielectric heating to break down seaweed cell structures, allowing for fast and selective release of target compounds. MAE has shown strong results in recovering polyphenols, polysaccharides, and phlorotannins, while cutting extraction time and solvent use compared to traditional methods[80].Studies have reported MAE-optimized yields of fucoidans from Fucus vesiculosus (12.25%) and Laminaria saccharina (0.47 mg/mg sugar content) in just one minute, demonstrating the efficiency of this green approach across various brown seaweed species[81].

Hybrid methods such as ultrasound-microwave assisted extraction (UMAE) have demonstrated synergistic benefits; for example, UMAE applied to Alaria esculenta produced the highest phenolic levels (>2 mg GAE/100 mg extract) and better antioxidant activity than either ultrasound or microwave alone [82].Likewise, Garcia-Vaquero[83]found that UMAE of Ascophyllum nodosum yielded 10.4 g glucose equivalent/100 g dry weight of total soluble carbohydrates—far surpassing conventional and single-technique extractions.

Pressurized liquid extraction (PLE) and supercritical CO_2 extraction (SFE) provide additional environmentally friendly options, especially for heat-sensitive and non-polar bioactive compounds. PLE works at high temperatures and pressures beyond the solvent's normal boiling point, which improves solubility and diffusion while keeping solvent use to a minimum[84] SFE uses supercritical CO_2—a safe, non-toxic, and non-flammable solvent—and is particularly well-suited for extracting fucoxanthin and other carotenoids from brown seaweeds with high precision and virtually no residual solvent left in the final product[85]

Furthermore, the integration of these advanced techniques with Natural Deep Eutectic Solvents (NADES) biocompatible solvent systems derived from naturally occurring metabolites represents a frontier in sustainable extraction, offering enhanced compound specificity and reduced environmental impact [86]. Despite the promising outcomes of these innovative methods, no universally effective technique has yet emerged; outcomes remain highly dependent on the algal matrix, target compounds, and operational parameters. Consequently, integrated and hybrid approaches combining physical, enzymatic, and green solvent strategies within biorefinery frameworks are increasingly advocated as the most viable path toward scalable, sustainable seaweed biostimulant production.

MECHANISMS OF ACTION IN SEEDS

Physiological mechanism

Seaweed-derived biostimulants enhance seed physiology through metabolic activation, hormonal modulation, osmotic regulation, reserve mobilization, and stress tolerance—collectively ensuring faster, more uniform germination and vigorous seedling establishment [87][88]. These effects are typically achieved through seed priming, a pre-sowing conditioning technique that improves germination uniformity and seedling vigor [89]. For example, red seaweed extracts applied to kale seeds enhanced germination rates, emergence, and maturity [90]. Seed vigor indicators such as electrical conductivity and accelerated aging responses further confirm improved membrane integrity and stress tolerance in treated seeds [91].

The stimulatory effects stem from the biochemical composition of seaweed extracts, which contain enzymes, phytohormones, minerals, and low-molecular-weight compounds [92] These extracts enhance nutrient absorption and growth regulator uptake when applied as seed treatments[93].Polysaccharides and hydrophilic compounds in the seaweed extract improve osmotic balance, promoting water absorption essential for cellular rehydration and enzyme activation[94]**.** Enhanced water uptake facilitates reserve mobilization like hydrolysis of starch, lipids, and proteins into sugars, fatty acids, and amino acids that fuel embryo growth thereby enabling rapid and robust seedling establishment[95][96].Growth regulators present in this extract such as auxins and cytokinins accelerate root protrusion and improve water-use efficiency[97].

Beyond promoting germination, Seaweed biostimulants significantly enhance tolerance to abiotic stresses including salinity, drought, and temperature extremes[25].They maintain ion homeostasis by reducing Na^+ accumulation and enhancing K^+ uptake[98], induce compatible solutes like proline and glycine betaine for osmotic protection[99], and upregulate stress-responsive genes while modulating abscisic acid-to-gibberellin ratios[100].

Hormonal crosstalk represents a key regulatory mechanism underlying these physiological responses.Seaweed extracts contain auxins, cytokinins, gibberellins, abscisic acid, and brassinosteroids that supplement or modulate endogenous hormone pools, biosynthesis, and signalling[101]. Ascophyllum nodosum extracts, for instance, increase gibberellin and decrease abscisic acid levels, promoting dormancy release[102].

In summary, seaweed biostimulants enhance seed physiology through a coordinated network of metabolic activation, hormonal modulation, osmotic regulation, reserve mobilization, and stress tolerance. These integrated effects collectively ensure faster and more uniform germination and the establishment of vigorous seedlings capable of withstanding early stage environmental challenges.

Biochemical Mechanism

Seaweed biostimulants enhance seed performance through coordinated biochemical modifications encompassing enzymatic activation, antioxidant defense, secondary metabolite accumulation, and gaseous signalling [103].

Enzymatic activation upregulates hydrolytic enzymes such as α-amylase and proteases, hydrolyzing stored starch and proteins into sugars and amino acids to fuel embryo development and radicle emergence[104] [105]. Alongside primary metabolism, seaweed biostimulants boost secondary metabolite production accumulating compounds that protect and signal during germination and early growth [106]**.** A key biochemical adaptation is the strengthening of antioxidant systems, which mitigates cellular damage from oxidative bursts triggered during germination and by environmental stressors [107]. Consequently, enhanced antioxidant capacity bolsters seedling vigor and supports improved establishment and growth under adverse conditions [108]. Antioxidant defense is critical during germination, when reactive oxygen species (ROS) act as signaling molecules promoting dormancy release at optimal concentrations but cause oxidative damage when excessive[109]. Seaweed extracts reduce ROS levels by enhancing antioxidant enzyme activity—such as superoxide dismutase, which converts superoxide radicals into H_2O_2—thereby protecting membranes and nucleic acids and improving metabolic efficiency[110][111][112][113].

Secondary metabolites accumulate in treated seeds, contributing to adaptive defense and ROS scavenging [114][105]. For example, extracts from Ecklonia maxima, Jania adhaerens, and Anabaena minutissima increase endogenous gibberellin levels, promoting germination and emergence [93]. Gaseous signaling molecules nitric oxide and hydrogen sulfide (H_2S) represent emerging pathways that modulate hormonal and enzymatic activities, enhancing germination vigor and stress tolerance[88].Collectively, the beneficial effects of seaweed biostimulants on seeds arise from a web of linked biochemical processes—enzymatic reserve breakdown, antioxidant enhancement, ROS homeostasis, protective metabolite buildup, and gas-mediated signaling. This metabolic synergy drives the physiological gains in germination vigor, seedling establishment, and environmental resilience.

Molecular Mechanism

The physiological and biochemical changes observed in seaweed biostimulant-treated seeds are ultimately regulated at the molecular level through coordinated alterations in gene expression, epigenetic modifications, and the activation of signal transduction pathways. These molecular events govern the synthesis of enzymes, regulatory proteins, and structural components involved in seed dormancy release, germination, and seedling establishment, thereby translating external biostimulant signals into tangible developmental outcomes

Sulfated polysaccharides like carrageenan modulate jasmonate, salicylate and ethylene pathways, while transcription factor upregulation enables developmental reprogramming in seeds[115][116]. Epigenetic changes such as histone methylation further regulate chlorophyll and antioxidant genes by altering chromatin accessibility[117]

Different A. nodosum extracts produce divergent transcriptional responses, showing that composition and extraction method dictate which genetic pathways are engaged [118][119]. RNA sequencing and microarray analyses reveal broad gene expression reprogramming, with extract-specific effects on photosynthesis, nutrient uptake, and cell wall genes that enhance growth[120][121][122]. Biostimulants activate cascades involving receptor-like kinases and G-proteins that relay signals intracellularly, reshaping gene expression and protein activity to strengthen defense and growth pathways[123][8**].** Recent transcriptomic and RNA-sequencing studies further demonstrate that seaweed-derived biostimulants regulate genes involved in antioxidant metabolism, osmotic adjustment, hormone signaling, and cell-cycle regulation, thereby coordinating seed germination and early seedling development.

In summary, seaweed biostimulants operate at the molecular level through a sophisticated network of gene expression reprogramming, epigenetic modifications, hormone signaling crosstalk, and signal transduction. These interconnected molecular mechanisms collectively coordinate the transition from seed dormancy to active germination and establish a developmental framework for robust seedling growth, underscoring the multi-layered regulatory capacity of seaweed-derived biostimulants in seed physiology.

SEED-BASED APPLICATIONS OF SEAWEED BIOSTIMULANTS IN CROP SYSTEMS

Seed-based delivery systems represent one of the most efficient approaches for exploiting the biostimulatory potential of seaweed extracts during early crop establishment. Compared with foliar or soil application, seed priming enables controlled exposure of the embryo to bioactive compounds during imbibition, thereby activating metabolic repair, mitochondrial respiration, ATP generation, and hydrolytic enzyme activity prior to radicle emergence[124].Seaweed extracts contain phytohormones such as cytokinins, auxins, and gibberellins, along with betaines, laminarin, alginates, and sulfated polysaccharides that collectively stimulate germination, antioxidant defense, osmotic adjustment, and stress-responsive signaling pathway[125].These compounds promote α-amylase activity, reserve mobilization, mitochondrial activation, and ATP synthesis, thereby accelerating seed metabolic readiness before radicle emergence[87]. Consequently, seaweed-mediated seed priming frequently induces physiological preconditioning against abiotic stresses such as salinity, drought, and heat stress through enhanced antioxidant enzyme activity, membrane stabilization, osmolyte accumulation, and stress-responsive gene expression[126][127][128]. Representative studies demonstrating the effectiveness of seaweed-derived seed priming under normal and abiotic stress conditions are summarized in Table 3.

CONSTRAINTS IN USING SEAWEED BIOSTIMULANTS AS SEED PRIMING

Despite the potential of seaweed-derived biostimulants for seed priming, their wider application is constrained by several factors, including variability in composition, dose-dependent responses, limited field validation, unclear mechanisms of action, contamination risks, and sustainability concerns. These constraints and their potential mitigation strategies are summarised in Table 4.

Lack of standardization: The composition of seaweed extracts varies with species, harvest season, geographical origin, and extraction methods, resulting in inconsistent efficacy [142]

Dose- and crop-specific responses: The effectiveness of seed priming depends on crop species, genotype, and application concentration, with excessive doses potentially reducing germination or growth [69]

Limited field validation: Most studies have been conducted under controlled laboratory or greenhouse conditions, while long-term multi-location field evaluations remain limited.

Unclear mechanisms of action: Although improvements in stress tolerance are widely reported, the molecular and physiological mechanisms are not yet fully understood.

Heavy metals and iodine contamination: Seaweed biomass may accumulate heavy metals (e.g., As, Cd, Pb, Hg) and excessive iodine from polluted coastal waters, making the composition and safety of seaweed biostimulants highly dependent on harvest-site environmental quality [101] [143].

Overexploitation of wild seaweed resources: The increasing demand for seaweed biostimulants raises concerns regarding the sustainable harvesting of wild seaweed resources, particularly species such as Ascophyllum nodosum, emphasizing the need for sustainable harvesting practices and expanded seaweed cultivation. Dependence on wild-harvested seaweed biomass may place pressure on natural populations if harvesting is not sustainably managed, highlighting the importance of cultivation and certified harvesting practices [41]

Regulatory and quality issues: The absence of globally harmonized standards for formulation, quality control and commercialization limits wider adoption of seaweed biostimulants [144]

CONCLUSION AND FUTURE PROSPECTS

Seaweed-derived biostimulants have emerged as a promising and sustainable strategy for enhancing seed germination, seedling establishment, and early tolerance to abiotic stresses. Their effectiveness is attributed to a diverse array of bioactive compounds, including polysaccharides, phytohormones, phenolic compounds, osmoprotectants, vitamins, and minerals, which collectively regulate physiological, biochemical, and molecular processes involved in seed germination and early plant development. Through improved water uptake, reserve mobilization, antioxidant defense, hormonal modulation, and stress-responsive gene expression, seaweed-based seed treatments consistently improve germination performance, seed vigor, and stress resilience across a wide range of crop species.

Despite these promising advances, several challenges continue to limit their widespread agricultural adoption. Variability in seaweed species, harvesting season, geographical origin and extraction methods leads to inconsistent bioactive composition and product performance. Furthermore, limited field-scale validation, incomplete understanding of molecular mechanisms, concerns regarding heavy-metal contamination, sustainable biomass sourcing, and the absence of globally harmonized quality standards remain important constraints that must be addressed.

Future research should prioritize the following key areas, based on their potential scientific impact and practical feasibility:

- Generate transcriptomic, proteomic, and metabolomic datasets from seeds during germination in at least one major cereal and one legume treated with well-characterized seaweed extracts to determine whether molecular mechanisms identified in vegetative tissues also operate during seed germination.
- Run full dose response trials (not single-concentration comparisons) for the seaweed–crop–stressor combinations already shown to be promising in Table 3, to establish crop specific yet transferable dose response relationship
- Compare different extraction technologies e.g., aqueous (conventional) versus ultrasound-assisted extraction (modern) using the same seaweed species and crop under identical priming conditions to determine whether higher extraction efficiency translates into superior seed performance.
- Conduct multi-location, multi-season field trials of the most promising laboratory-validated seed-priming protocols, explicitly reporting environmental covariates (soil type, background salinity, temperature regime) to begin closing the laboratory-to-field validation gap while also evaluating economic feasibility and cost-benefit.

- Evaluate seed coating, seed pelleting, nano-encapsulation, and controlled-release formulations incorporating seaweed extracts for small-seeded crops under adverse establishment conditions.

From a practical and regulatory perspective, translating these research priorities into deployable seed technologies will require harmonized biostimulant definitions, standardized quality-control protocols, and streamlined registration pathways across jurisdictions (e.g., the EU Fertilising Products Regulation). Without such harmonization, even mechanistically validated products may face inconsistent regulatory approval and limited commercial adoption. Overall, bridging the mechanistic, dose–response, formulation, and field-validation gaps identified throughout this review will be critical for translating seaweed-derived biostimulants from promising laboratory findings into robust, commercially viable, and climate-resilient seed technologies.

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AUTHOR CONTRIBUTIONS

Tharani N: Conceptualization, literature search, writing original draft and editing, Manonmani V: Conceived the idea, writing review and editing, Raja K, Senthil Kumar M, Sathya Moorthy P, Johnson I: Visualization and supervision

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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Table 1. Key structural and bioactive signatures of main seaweed groups

Type of seaweed (Division)	Signature polysaccharides (cell wall)	Key Pigment phenolic compound	Typical bioactivities	Example species / notes	References
Brown seaweeds (Ochrophyta Phaeophyceae)	Alginate, laminarin, fucoidan (sulfated fucans)	Phlorotannins (phloroglucinol polymers) and carotenoid fucoxanthin	Strong antioxidant effects and biostimulant activity, soil amendment, compost additive	Ascophyllum, Sargassum, Laminaria(kelp), Padina; often richest in phenolics and sulfated polysaccharides among seaweeds	[48]
Red seaweeds (Rhodophyta)	Agar, carrageenans (κ-, ι-, λ-carrageenan) as major sulfated galactans	Bromophenols, other phenolics; phycobiliprotein pigments (phycoerythrin, phycocyanin) confer red/purple colour	Widely used hydrocolloids (food/pharma); used for soil conditioners	Kappaphycus, Gracilaria, Chondrus, Porphyra; industrial source of agar and carrageenan; key source of long-chain PUFAs and vitamin B12	[49]
Green seaweeds (Chlorophyta)	Ulvan and related sulfated rhamnose-rich polysaccharides; cellulose and other neutral sugars	Phenolic acids, flavonoids; chlorophyll a and b dominate pigmentation	Exhibits prebiotic effects; Primarily nutritional/feed uses	Ulva(sea lettuce), Caulerpa, Enteromorpha; high carbohydrate and lipid content; emerging functional-food ingredients	[50]

Table 2: Extraction Methods and Formulation Strategies of Seaweed Biostimulants

Category	Seaweed Used	Method / Formulation Type	Key Principle	Target Bioactive Compounds	Advantages	Lin Ch
Liquid Extraction	Polysiphonia, Ulva, Cladophora	Aqueous extraction (hot: boiling; cold: soaking)	Water-based diffusion of solubles	Phenolics, minerals, pigments, polysaccharides	Simple; non-toxic; preserves bioactivity	Lov tim var
	Brown seaweed (Cystoseira barbata)	Alkaline extraction (KOH/Na_2CO_3)	Alkaline hydrolysis of cell wall polysaccharides	Alginate, phenolics, antioxidants	High extraction yield; strong bioactivity	Str mo cor
	Red seaweed (Solieria chordalis)	Enzymatic extraction	Enzyme-mediated cell wall degradation	Oligosaccharides, peptides	High specificity; eco-friendly; enhanced bioactivity	Enz opt req
	Brown, Red, Green seaweeds (e.g., Sargassum, Laminaria, Grateloupia)	Microbial fermentation (submerged & solid-state)	Microorganisms enzymatically break down cell walls and convert complex compounds into bioactive forms	Polysaccharides (fucoidan, galactan), phenolics, organic acids, peptides	Higher yield; enhanced bioactivity; eco-friendly; no toxic solvents	Pro var mic cor lon pro
Powdered Form	Brown seaweed (Sargassum muticum)	Freeze drying	Sublimation removes water at low temperature	Hormones, pigments, polysaccharides	Preserves bioactivity; minimal degradation	Hig ene
	Brown seaweed (Sargassum muticum)	Spray drying	Rapid drying via atomization	Polysaccharides, minerals	Scalable; cost-effective	The deg
	Brown & red seaweeds (Sargassum, Gelidiella)	Milling / whole seaweed powder	Mechanical grinding of dried biomass	Full nutrient + hormone spectrum	Low-cost; minimal processing	Var cor slov
Commercial Formulation	Red seaweed (Kappaphycus alvarezii)	Single-species extracts	Standardized extraction of one species	Carotenoids, phenolics, sugars	Consistent composition; strong plant response	Lin div cor
	Ecklonia maxima + Ascophyllum nodosum (with vegetal extract)	Multi-algae blend / combined biostimulant formulation (VO + SWE)	Synergistic interaction of seaweed- and plant-derived bioactives	Phytohormones, polysaccharides, amino acids, phenolics	Enhanced yield and nutritional quality	Cor var for cor
	Seaweed extract + additives	Value-added mixes (NPK + microbes)	Integration with nutrients and beneficial microbes	Nutrients + bioactives + microbial metabolites	Enhanced plant growth and soil microbiome	Cor and issu

Table 3. Effects of Seaweed-Derived Biostimulants Seed priming on Seed Germination and Stress Resilience across different crop Systems

Crop	Seaweed Source	Stress Type	Resilience Metric	Key Finding
Rice	Sargassum myricocystum, Kappaphycus alvarezii	Non-stress	Increased α-amylase, catalase content and increase in vigor index	Strong increa activity, and vi
Wheat, corn, canola	Sargassum bovianum	Salinity	Decreased mean germination time and increased plumule length	Improved gern salinity stress

Tomato	Ascophyllum nodosum, Sargassum spp.	Salinity (75 mM NaCl)	Increased vigor index I & II and higher root/shoot length	2% Sargassum vigor under sal
Soybean	Ascophyllum nodosum	Stress (seed aging)	Increased heterotrophic growth	Improved gern seeds
Wheat	Cystoseira barbata	Non-stress	Increased biomass +20–25%	Strong early se
Kale	Gracilaria gracilis, Ulva lactuca	Non-stress	Increase in seedling weight (~+28%) and length (~+18%)	Enhanced ger when compare
Lentil	Sargassum, Ulva, Gracilaria	Non-stress	Increased root elongation index	lowest extract biostimulant fo
Watermelon (Citrullus lanatus)	Ulva lactuca	Salinity	Germination percentage, seedling growth, SOD/CAT/POD	8% extract g improved antic
Wheat	Ulva linza, Corallina officinalis	Non-stress	Increased Biomass & mitotic index	Low-dose extr early seedling
Spinach	Ascophyllum nodosum	Heat stress(30^0 C)	Germination %, Germination rate index, Germination speed, Seedling length, H_2O_2, and MDA	Priming with 0 germination, vi heat stress vers
Okra (Abelmoschus esculentus)	Kelpak® made from Ecklonia maxima	No direct stress treatment	Germination percentage (GP), Mean Germination Time (MGT), Germination Index (GI), coefficient of velocity of germination (CVG), Germination Rate Index (GRI)	Kelpak® at 1: response impr control
Grammosciadium platycarpum	Commercial seaweed extract (Armadine brand)	Salinity stress at 0, 2, and 4 dS m^{-1} NaCl	Germination percentage, germination rate, mean germination time, seed vigor, fresh and dry seedling weight, chlorophyll a/b, MDA, SOD, APX, and H_2O_2	Seaweed prin reduced salin germination an chlorophyll, a accumulation
Arabidopsis thaliana	Brown seaweed Ascophyllum nodosum; extract Super Fifty (SF)	Drought stress	Reduced ROS accumulation, higher relative water content, lower ion leakage, improved stomatal behavior, maintained shoot apical meristem function and cell-cycle activity	SF strongly damage and through multip transcriptional
Tomato (Solanum lycopersicum)	Ulva lactuca extract	Salinity stress at 4 and 8 $dS \cdot m^{-1}$ NaCl-adjusted nutrient solution	Fresh weight, H_2O_2, antioxidant activity, soluble sugars, total proteins, chlorophyll	Seed priming salinity dama reduced oxidat physiological t
Wheat (Triticum aestivum L.)	Hormophysa cuneiformis (brown) and Actinotrichia fragilis (red)	Salinity (100 and 150 mM NaCl)	Growth, chlorophyll, carotenoids, osmolytes, ion homeostasis, MDA, antioxidant enzymes (SOD, CAT, POD), protein profiles	Seaweed prim enhancing gr balance, antiox and MDA, w more effective

Constraint	**Source of Variability**	**Mitigation Strategy**
Heavy metals / iodine	Coastal pollution, harvest site	Aquaculture sourcing, batch testing

Over-exploitation	Wild harvest dependence	Cultivation programs, quota systems
Batch variability	Species, season, processing	Standardized extraction protocols, quality certification
Limited field validation	Lab-based studies	Multi-location field trials
Regulatory issues	No global standards	Harmonized regulations

Table 4. Critical constraints and mitigation strategies for seaweed-derived seed priming biostimulants