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REVIEW ARTICLE

Seaweeds as sustainable alternative for enhancing agriculture

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Abstract

The existing dominance of chemical inputs in agriculture has pushed the invaluable soil resource to its brink. The adoption of high yielding varieties by farmers worldwide has demanded the use of chemical fertilizers and plant protection agents. While these practices have played a crucial role in achieving food security, they have also given rise to rather serious complications, including the deterioration of soil health, the presence of chemical residues in agricultural produce and environmental pollution. This has necessitated the formulation of efficient alternative inputs that help agriculturists to achieve ample crop yields while ensuring the sustenance of soil health and productivity. The vast sea of seaweeds is an excellent candidate that suits best for the current scenario, being a wholesome provider for plant health and productivity. The presence of plant growth regulators and several bioactive compounds that can stimulate vigorous plant growth, elicit plant defense mechanisms against biotic and abiotic stressors and enhance yield are some of the promising reasons which make seaweeds a suitable biostimulant for crop production. This review is an attempt to enrich the existing knowledge on seaweeds by exploring the agricultural benefits of seaweeds and elucidating the underlying mechanisms through which these benefits are realized.

Keywords: biostimulants; marine algae; plant health; stress tolerance

Introduction

Plants are photoautotrophs that fix carbon dioxide through photosynthesis. This vital reaction requires sunlight, water and nutrients. Water is supplied through rainfall and irrigation, while nutrients are provided by the soil's inherent fertility and through the application of manures and fertilizers (1). Current crop production technologies demand the use of chemical fertilizers for maximum output per unit arable area. Chemical fertilizers, however beneficial they may be, their indiscriminate use leads to run-off to nearby water bodies leading to eutrophication, contamination of ground water, all causing environmental pollution (2). These chemicals may cause both short- and long-term health risks to humans through direct and indirect exposure. Direct exposure, particularly through the consumption of agricultural produce containing chemical residues, can lead to a range of health issues including nasal and throat irritation, cancer, methemoglobinemia and other serious complications (3). The innate properties of soil are also worsened using fertilizers. A plethora of deleterious effects are imposed upon the soil which includes and not limited to decline in soil organic matter, increase in soil pH ultimately leading to the loss of soil floral and faunal diversity (4). Organic manures, being highly complex in nutrient composition, are suitable alternate that can be used in place of chemical inputs. In addition to supplying plant nutrients, organic manures offer the added benefit of improving the physical, chemical and biological properties of the soil (5). Among the existing organic plant nutrient sources, seaweeds are emerging as effective biostimulants that not only enhance plant health and yield but also function as soil conditioner (6). Seaweeds are exploited in many ways, as source of nutrition or dietary supplement which are rich in vitamins and minerals or feed supplements for farm animals or as an organic manure in agriculture (7). Seaweeds are rich in bioactive compounds such as phytohormones (auxins, cytokinins, gibberellins, abscisic acid and ethylene), polysaccharides and oligosaccharides (alginates, agar, kappa, lambda and iota carrageenans) (8), phenolics such as phlorotannins, amino acids and vitamins-all of which contribute to enhanced plant growth and yield. This diverse biochemical composition gives seaweeds a distinct advantage over other organic inputs in improving soil health and fertility (9, 10). It is noteworthy that the quality and yield of certain bioactives such as the polysaccharides content of seaweeds may vary according to the seaweeds under study and the season of harvest. For instance, the agar content of *Gracilaria gracilis* showed no seasonal fluctuation, in contrast to the carrageenan and alginate contents of *Calliblepharis jubata* and *Sargassum muticum* respectively (11).

Seaweeds are marine algae classified into three different phyla based on their pigmentation: Chlorophyta (green algae), Phaeophyta (brown algae) and Rhodophyta (red algae) (12). Enhanced nutrient uptake, stress resistance, disease management are some of the benefits of seaweeds that are well documented. The seaweed extracts provide beneficial effects in all stages of plant growth from seed germination till yield. *Laminaria* sp. and *Ascophyllum* sp. are rich in essential vitamins and minerals that support metabolic processes during seed germination (13). Essential nutrients are available in easier plant uptake form, thereby promoting plant growth (14). Seaweed extracts offer multiple benefits, acting as potential plant growth promoters through the production of phytohormones and plant growth regulators (15, 16). They also provide protection against various biotic stresses including fungal, bacterial and viral pathogens, insect pests and nematodes (17, 18), as well as abiotic stresses such as drought, salinity and oxidative stress. These protective effects are attributed to the presence of compounds like betaines and cytokinins and to their ability to enhance ion uptake by plants (19, 20). Additionally, seaweeds serve as effective organic agents for improving soil fertility by contributing polysaccharides, proteins and fatty acids that aid in water and nutrient retention in the soil (21). Considering the above, although chemical fertilizers provide essential plant nutrients in a quick manner, they lack the diverse bioactive compounds present in seaweeds -compounds that not only aid in plant growth and yield but also contribute to overall plant and soil health.

Seaweeds in agriculture

Seaweeds as soil conditioners

Soil health and soil quality are defined as the soil's capacity to function as a vital living system within the constraints of land use. This functionality not only sustains the soil's biological productivity but also helps maintain environmental quality and supports human health (22). It plays a critical role in achieving high productivity of agricultural crops and sustainable agriculture. Seaweeds are fast emerging and promising candidates in soil management practices and green agriculture. Their overall benefits are shown in Fig. 1. They affect the physical, chemical and biological properties of soil which in turn affect plant growth by improving water retention, growth of beneficial microorganisms along with adding nutrients to the soil (23).

Phycocolloids are anionic in nature and act as cation exchangers, thereby enhancing the nutrient-holding capacity of the soil. Their gelling properties form a thin hydrating layer on the soil surface which improves soil structure and helps prevent erosion (24). Polysaccharides present in seaweeds, such as alginates and fucoidans, possess chelating properties that enhance the bioavailability of certain nutrients. These compounds also promote the aggregation of soil particles, thereby improving soil structure (12). Alginic acid, in particular, exhibits soil-conditioning properties by forming high molecular weight polymers through chelation with metal ions (25). The application of seaweeds to soil has also been shown to increase soil pH, subsequently enhancing phosphorus availability to plants (26).

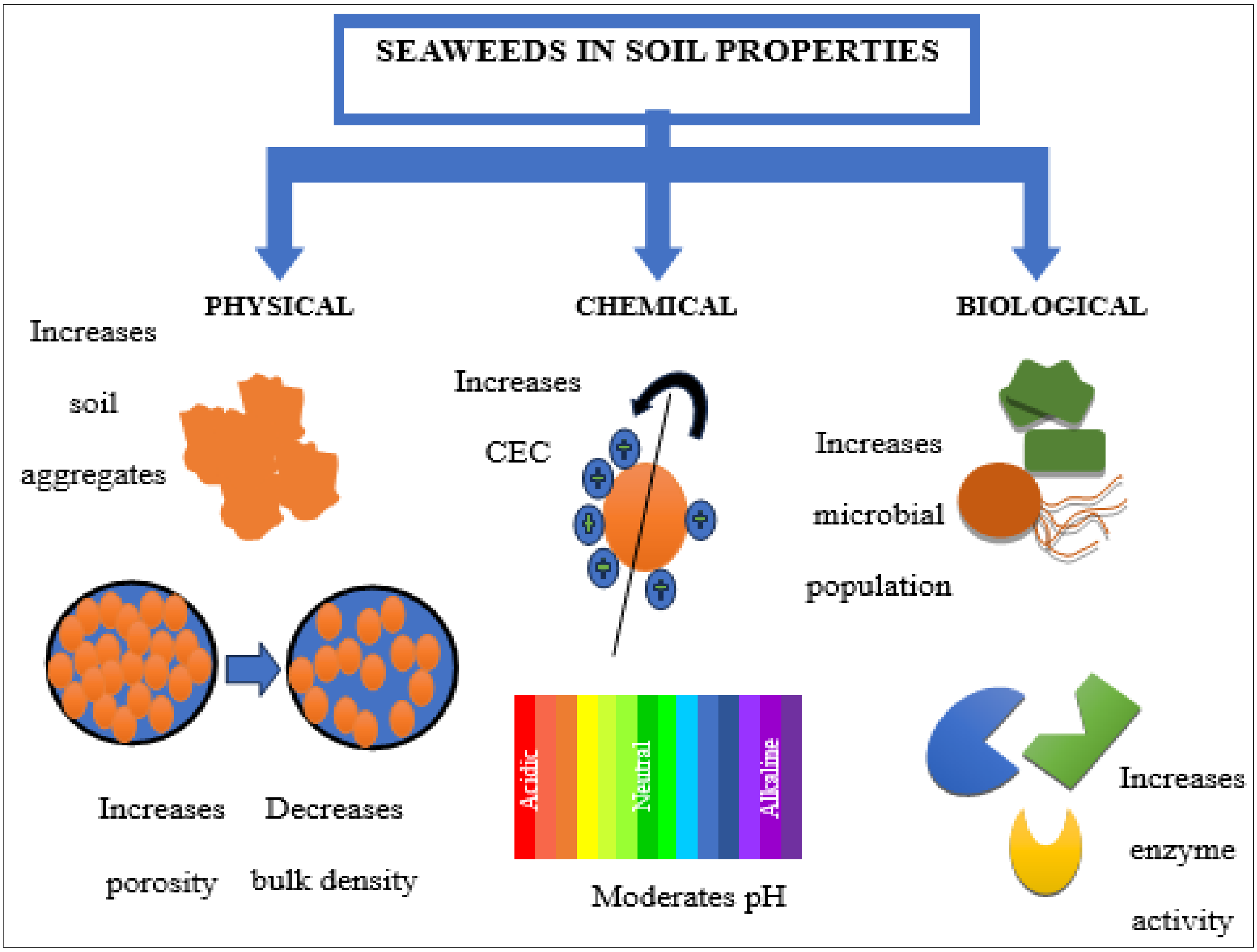

Fig. 1. Benefits of seaweeds to soil properties.

The application of seaweed extract from *Ascophyllum nodosum* (Linnaeus) Le Jolis creates a favourable environment for microbial growth, thereby enhancing the positive effects on the rhizospheric microbiome (27). Adding seaweed extracts from *Lessonia nigrescens* Bory and *Lessonia flavicans* Bory to soil at the rate of 40 g kg^{-1} dramatically increased the microbial populations of bacteria, fungi and actinomycetes by 172 %, 67 % and 57 % respectively and higher bacteria:fungi ratio and enhanced the activity of invertase, urease, proteinase and phosphatase enzymes (28). Red and green algal extracts (*Gracilaria verrucosa* (Linnaeus) J.V.Lamouroux, *Gracilaria amansii* (Lamouroux) J.Agardh, *Eucheuma cottonii* (Doty)) have stimulatory effects on the growth and colonization of arbuscular mycorrhizal (AM) fungi like *Gigaspora margarita* (N.C. Schenck & G.S. Smith) and *G. caledonium* (N.C. Schenck & G.S. Smith) on plant roots (29). Extract of *Ascophyllum nodosum* activated the expression of Nod C gene of *Sinorhizobium meliloti* (Nicholas & Van Gundy), by mimicking the effect of flavonoid, which is a bacteria-plant signalling molecule and thus increasing the number of nitrogen fixing nodule formation in plants (30). The activity of soil enzymes is enhanced by the application of seaweeds resulting in increased nutrient turnover which is due to its influence on soil microbial communities (31). Seaweed extract of *Sargassum horneri* can induce the soil enzyme and microbial activity, thus promoting the improvement of soil quality and is beneficial for plant development (32). It is brought about by the addition of organic matter to the soil by the seaweed biomass, which increases the water and nutrient holding capacity of the soil. Seaweed extracts also improve soil structure, as the humic acids and alginates they contain bind to soil particles and promote the formation of aggregates, leading to the development of crumb structure (33).

Seaweeds for plant nutrient uptake

High crop production can be achieved using synthetic fertilizers; however, excess application does not necessarily result in increased yields. This implies that the plant nutrient use efficiency (NUE) is reducing. The application of seaweed extracts has been shown to enhance NUE in crops, offering a more sustainable approach to nutrient management. For instance, *Kappaphycus alvarezii* and *Gracilaria edulis* (S.G.Gmelin) P.C.Silva extracts when sprayed through foliar application at the rate of 10 % has found to increase the uptake of N, P and K and subsequently increasing the grain and stover yield in maize by 18.54 % and 26.04 % respectively (34). Under rainfed conditions, a 15 % foliar spray of *Kappaphycus alvarezii* extract resulted in a 57 % increase in grain yield and a higher straw yield in soybean compared to the control, attributed to enhanced nutrient uptake of N, P, K and S (35). Similarly, the application of *Ecklonia maxima* (Osbeck) Papenfuss extract as a root treatment to *Brassica rapa* (Linnaeus) significantly increased the concentration of P and K in leaves while reducing Na levels (36). Foliar application of *Kappaphycus* and *Gracilaria* extracts at 15 % concentration on black gram enhanced the uptake of N, P and K, leading to yield increases of 51 % and 44 % respectively (37). Similarly, extract from *Laminaria japonica* has been shown to promote deeper root growth, increased root density and greater root surface area in sugarcane, thereby resulting in a better water and nutrient uptake (38).

Seaweeds for plant growth

The role of seaweeds as biostimulants and plant-growth promoting agents is primarily attributed to the presence of growth hormones such as auxins, cytokinins and giberellins, along with vitamins, trace elements and humic acids. The occurrence of these plant growth hormones in various seaweed species is listed in Table 1. They also contain the major elements such as N, P and K in sufficient quantities that are required for plant growth. Seaweeds are also rich sources of vitamins and their precursors, amino acids, minerals and osmolytes, all of which are readily available for plant uptake (39). The shift toward residue-free food production can be supported using seaweeds as natural biofertilizers in place of chemical fertilizers. Seaweed-derived formulations are non-toxic, non-polluting and biodegradable and therefore do not pose the environmental hazards commonly associated with chemical fertilizers. Various seaweed extracts, including those from *Sargassum wightii* (Greville), *Caulerpa* sp., *Kappaphycus alvarezii, Hypnea* sp., *Gracilaria* sp. have been applied to crops such as rice, black gram, brinjal, tomato and chilli. These applications have resulted in enhanced seed germination and establishment, increased growth and yield parameters and better yield quality (40-42). These effects are depicted in Fig. 2.

In addition to the previously mentioned compounds, seaweeds also contain bioactive molecules such as polysaccharides, polyphenols and polyamines, all of which contribute to plant growth promotion and can serve as alternatives to chemical inputs (43, 44). The effectiveness of seaweed extracts in enhancing plant growth has been shown to depend on the concentration of these polysaccharides (45). These include carrageenans, fucoidans, ulvans, alginates and others. Carrageenans, in particular, are major structural polysaccharides found in red seaweeds; they are sulphated linear polysaccharides known to promote plant growth by regulating photosynthesis, cell division and the synthesis of nitrogenous bases such as purines and pyrimidines (46).

Carrageenans stimulate photosynthesis by enhancing the activity of ribulose-1,5-bisphosphate carboxylase/ oxygenase (Rubisco), thereby increasing carbon fixation, which leads to greater leaf biomass and plant height in tobacco (47). Kappa-carrageenans induce the synthesis of plant growth hormones like IAA, GA_3 and zeatin, thus acting as a stimulant for plant growth (48). Kappa, lambda and iota-carrageenans in *Calliblepharis jubata* (Goodenough & Woodward) Kützing and *Chondracanthus teedei* (Mertens ex Roth) Kützing have shown to stimulate seed germination and plant growth in *Brassica oleracea* (Linnaeus) (49). Alginates are the major constituents in the cell walls of brown seaweeds (47), whereas ulvans are the major constituent in green seaweeds (50). Alginate derived oligosaccharides (ADO) stimulated germination, growth and shoot elongation by enhancing nitrogen assimilation and basal metabolism (51). A mixture of oligo-alginates derived from gamma radiation-induced degradation of alginates has been shown to increase root length by 37.5 %, shoot length by 63.5 %, total chlorophyll content by 43 % and carotenoid content by 31.4 % in *Papaver somniferum* (Linnaeus). It also enhanced nitrogen assimilation via a 31.7 % increase in nitrate reductase activity and elevated alkaloid content by 40.7 % (52).

Table 1. Occurrence of plant growth hormones in various seaweeds

Plant hormones	Seaweeds	Extraction methods	Analytical method	Benefits	References
Auxins	*Caulerpa racemosa* (Forsskål) J.Agardh (Green)	Solvent extraction (ethyl acetate)	UV Spectroscopy	Improved nutrient uptake and accelerated plant growth due to enhanced root attributes.	(24, 56–62)
	Solieria chordalis (C.Agardh) J.Agardh (Red)	Enzyme assisted (glycosidases & proteases)	-		
	Cladophora glomerata (Linnaeus) Kützing and *Ulva flexuosa* (Kützing) (Green), *Polysiphonia fucoides* (Hudson) Greville (Red)	Supercritical fluid extraction using CO_2	HPLC with DAD (diode array detector)		
	Laminaria and *Ascophyllum nodosum* (Brown)	Acid extraction (pH: 3–3.5)	FT-IR and FT-Raman Spectroscopy		
	U. fasciata (Delile) (Green) and *Dictyota humifusa* Hörnig, Schnetter & Coppejans (Brown)	Solvent extraction (ethanol), purified using DEAE-Sephadex-octadecyl silica column	HPLC-MS		
	Padina durvillaei Bory *(Brown)* and *Ulva lactuca (Green)*	Water extraction	UHPLC-MS		
	Kappaphycus alvarezii and *Gracilaria edulis* (Red), *Sargassum tenerrimum* (J.Agardh) (Brown)	Solvent extraction (diethyl ether)	ESI-MS		
	Porphyra acanthophora (E.C.Oliveira & Coll, *Gelidium floridanum* W.R.Taylor, *Gracilaria birdiae* E.M.Plastino & E.C.Oliveira and *Chondracanthus teedei* (Red)	Solvent extraction (ice cold ethanol) and purified by combined cation anion exchanger	High performance liquid hromatography with tandem mass spectroscopy (HPLC-MS/MS)		
Cytokinins	*Cladophora glomerata* (Green)	Supercritical fluid CO_2 extraction	Reverse phase-HPLC with photo diode array detector	Promotes cell division, increases cell expansion, chlorophyll synthesis and prolongs leaf photosynthetic period, enhances defense system in plants	(24, 61–64)
	U. fasciata (Green) and *Dictyota humifusa* (Brown)	Solvent extraction (ethanol), purified using DEAE-Sephadex-octadecyl silica column	HPLC-MS		
	Padina durvillaei (Brown) and Ulva lactuca (Green)	Water extraction	UHPLC-MS		
	Kappaphycus alvarezii and *Gracilaria edulis* (Red), *Sargassum tenerrimum* (Brown)	Solvent extraction (n-butanol)	ESI-MS		
	Porphyra acanthophora, Gelidium floridanum, Gracilaria birdiae and Chondracanthus teedei (Red)	Solvent extraction (ice cold ethanol) and purified by combined cation anion exchanger	Ultra performance liquid chromatography (UPLC)		
	U. fasciata, *U. lactuca*, *U. taeniata* (Setchell) Setchell & N.L.Gardner and *U. reticulata* (Forsskål) (Green)	Solvent extraction (methanol, water and formic acid in the ratio 15:4:1)	HPLC		
Gibberellins	*Caulerpa racemosa* (Green)	Solvent extraction (chloroform)	UV Spectroscopy	Stem elongation, leaf area expansion, breaks seed dormancy, improves seed germination, fruit and grain development	(58, 62–65)
	U. fasciata (Green) and *Dictyota humifusa* (Brown)	Water extraction	HPLC-MS		
	Kappaphycus alvarezii and *Gracilaria edulis* (Red), *Sargassum tenerrimum* (Brown)	Solvent extraction (ethyl acetate)	ESI-MS		
	Sargassum swartzii (C.Agardh) (Brown)	Acid and alkaline digestion (CH_3COOH and KOH)	HPLC		
	U. fasciata, *U. lactuca*, *U. taeniata* and *U. reticulata* (Green)	Solvent extraction (methanol, water and formic acid in the ratio 15:4:1)	HPLC		

Abscisic Acid	*U. fasciata* (Green) and *Dictyota humifusa* (Brown)	Solvent extraction (ethanol)	HPLC-MS	Enhances stress tolerance, aids in stomatal closure, aids in fruit ripening	(24, 61, 65)
	Porphyra acanthophora, *Gelidium floridanum*, *Gracilaria birdiae* and *Chondracanthus teedei* (Red)	Ice cold water/methanol/ acetic acid extraction and purified by solid phase extraction	UPLC-ESI-MS/MS		
	Sargassum swartzii (Brown)	Acid and alkaline digestion (CH_3COOH and KOH)	HPLC		
Brassinosteroids	*Sargassum swartzii* (Brown)	Acid and alkaline digestion (CH_3COOH and KOH)	HPLC	Enhances cell division, elongation, improves plant growth and development and	(65, 66)
	Ecklonia maxima (Brown)	Solvent extraction (Methanol)	UPLC-MS		
Salicylic acid	*Solieria chordalis* (Red)	Enzyme assisted (glycosidases & proteases)	-	Enhances defense responses against abiotic stress, improves physiological processes and regulates stomatal movement	(56, 63–65)
	Padina durvillaei (Brown) and *U. lactuca* (Green)	Water extraction	UHPLC-MS		
	Sargassum swartzii (Brown)	Acid and alkaline digestion (CH_3COOH and KOH)	HPLC		
	U. fasciata, *U. lactuca*, *U. taeniata* and *U. reticulata* (Green)	Solvent extraction (methanol, water and formic acid in the ratio 15:4:1)	HPLC		

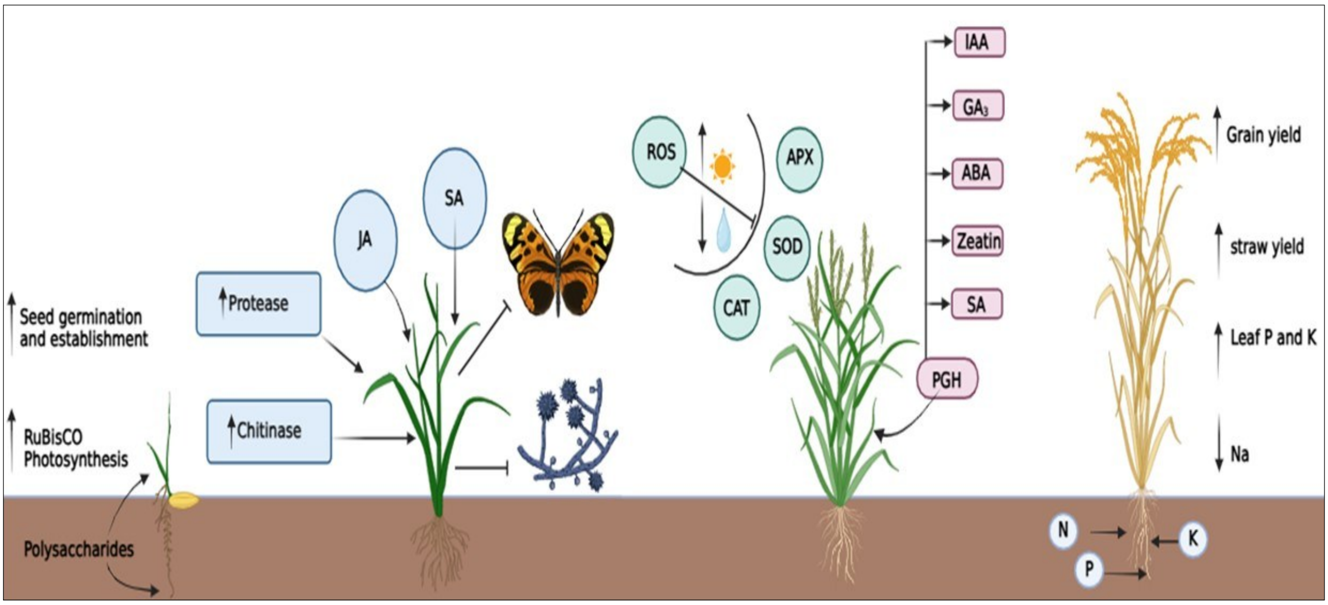

Fig. 2. Seaweeds for plant health and yield.

Ulvans along with alginate obtained from *Ulva lactuca* and *Padina gymnospora* (Kützing) Sonder when treated to seeds, resulted in increased germination percentage (45). Fucoidan from *Sargassum horridum* Setchell & N.L. Gardner at lower concentrations (0.6 mg mL^{-1}) promoted root growth, whereas higher concentrations (20 mg mL^{-1}) of fucoidans promoted shoot growth and yielded high biomass in mung bean. Fucoidan obtained from *Eisenia arborea* Areschoug showed greatest shoot length growth and total plant length by 16.2 % and 11.9 % at 2.5 and 10 mg mL^{-1} respectively (53). The plant growth stimulation activity of fucoidans is due to the presence of sulphate groups, which has shown positive effect on root and shoot length, dry weight and chlorophyll content (54). Phlortannins are polyphenols unique to seaweeds and may constitute up to 15 % of the dry weight of brown seaweeds (55). Eckol is one such polyphenol that shows auxin-like activity and seeds treated with eckol showed increased root length, a higher number of seedlings and also yielded enhanced seedling growth and seedling weight (44).

Seaweeds for biotic stress tolerance

Seaweed polysaccharides function both as biostimulants and as inducers of resistance against biotic and abiotic stressors, as summarized in Table 2. Seaweeds enhance plant protection against various biotic factors including bacterial, fungal and viral pathogens as well as insect pests and abiotic stresses such as drought, extreme temperatures and oxidative damage. With climate change contributing to increased pest and disease outbreaks, seaweed-based formulations offer an effective and environmentally friendly alternative for crop protection. Foliar spray of seaweed extracts from *A. nodosum, Kappaphycus* sp., *Ulva* sp., etc. has been shown to control fungal and bacterial diseases, as well as insect pests in crops. This effect is attributed to the activation of the plants' natural defense system, particularly through jasmonic acid and salicylic acid pathways, indicating that seaweed-derived biomolecules act as elicitors that trigger plant defense responses (66).

Table 2. Seaweeds for biotic and abiotic stress management

Seaweed	Crop	Extraction	Type of stress	Mechanism	References
Sargassum wightii	Okra	Aqueous extract	Salinity	Catalase, ascorbate peroxidase and guaiacol peroxidase activity increased; accumulation of secondary metabolites.	(82)
Sargassum spp.	Tomato	Hydroalcoholic extract	Salinity	Increased concentration of proline, enhanced expression of NCED1, HSP70 PIP2, P5CS1, ERD15, Fe-SOD, CAT1, cAPX2, PAL5-3 genes.	(83)
Ulva lactuca	Tomato	Solvent (methanol, hexane, chloroform, n-butanol) extract	Salinity	Seed priming resulted in high shoot and root biomass due to high glycine betaine content - high photosynthetic activity due to enhanced total chlorophyll content; high total phenols and antioxidants reduce H_2O_2 production.	(84)
Kappaphycus sp. and *Eucheuma* sp.	Rice	Solid and liquid commercial extracts	Fungicidal stress	Decreased stomatal closure due to increased Ca^+ and K^+ levels and presence of GA_3 and cytokinins; decline in transcript levels of stress responsive genes like Heat Shock Factors – regulating temperature	(85)
Kappaphycus alvarezii	Tomato	Commercial extract	Fungal pathogen	Enhanced peroxidase, phenylalanine ammonia lyase and β-1,3-glucanase activity.	(86)
Gracilaria dura	Wheat	Water extract (homogenized and filtered sap)	Water stress	Accumulation of solutes like proline lowered osmotic potential of seaweed-treated plants; improved chlorophyll content and reduced activity of superoxide dismutase, peroxidase and glutathione reductase; upregulation of expression of genes coding for catabolism of ABA, leading to induction of stomatal closure.	(19)
Dictyota dichotoma	Rice	Solvent extraction (1:1 v/v chloroform:methanol)	Fungal pathogen	Enhanced activity of defense enzymes like β-1,3-glucanase, peroxidase, polyphenol oxidase and phenylalanine ammonia lyase; h free proline accumulation.	(87)
Kappaphycus alvarezii	Rice	Solid commercial extract	Fungal pathogen	beta-D-xylosidase upregulation for secondary cell wall reinforcement; pathogenesis related Bet v 1 family, chalcone synthase, chitinase, WRKY and MYB families upregulated.	(88)
Ecklonia maxima	Maize	Solvent (methanol) extract	Drought stress	Increased levels of phenylalanine, tryptophan, coumaroylquinic acid and linolenic acid metabolites result in root growth promotion, improved water and nutrient uptake and alleviation of oxidative stress	(89)

Metabolomic analysis of leaf and root samples after the application of seaweed extracts from *Durvillaea potatorum* (Labillardière) J.E. Areschoug and *Ascophyllum nodosum* to *Arabidopsis thaliana* (Linnaeus) revealed that it induced the accumulation of metabolites related to plant growth such as tricarboxylic acid cycle (TCA) metabolites. Lysophospholipids and glucosinolates are also accumulated in response to seaweed extract application, along with differential modulation of lipids, amino acids, carbohydrates and secondary metabolites such as phenylpropanoids. These changes collectively contribute to enhanced energy generation, carbon and nitrogen metabolism, remodelling of cell membrane and activation of defense systems (67). The defense mechanisms triggered by seaweed extracts against biotic and abiotic stressors include increased enzymatic activity, elevated total phenolic content and upregulation of genes involved in plant defense responses (68). The foliar treatment of *A. nodosum* extract on tomato and sweet pepper showed reduced load of foliar pathogens, *Alternaria solani* (Sorauer) and *Xanthomonas campestris* (E.F. Smith) Dowson through a couple of mechanisms. The increase of total phenolic content in the plants and upregulation of genes like PIN II and ETR-1 involved in the salicylic acid (SA), jasmonic acid (JA) and ethylene (ET) pathways for plant defense resulted in significant reduction in the disease severity (15).

Seaweeds contain bioactive molecules that function as bio-elicitors mediating plant response to stress. These include oligosaccharides, polysaccharides, peptides, proteins and lipids (69). Polysaccharides from the cell walls of seaweeds are alginates, carrageenans, fucans, laminarins and ulvans which can activate defense mechanisms in plants through SA, JA and ethylene signalling pathways (47). Carrageenans found in the cell walls of red seaweeds, increased the transcription of defense genes like chitinase, proteinase and sesquiterpene cyclase which reduced the disease severity of *Phytophthora parasitica* var. *nicotianae* (Dastur) Tucker in tobacco (70). Laminarins in brown seaweeds induced phenylalanine ammonia lyase (PAL), lipoxygenase (LOX) enzyme activity and four families of pathogenesis related (PR1, PR2, PR3 and PR5) proteins with antimicrobial activities. These conferred protection against soft rot bacterium, *Erwinia carotovora* subsp. *carotovora* (Hildebrand) Dowson in tobacco (71).

Plant defense mechanisms against viral pathogens like tobacco mosaic virus (TMV) are activated by sulphated fucans, which trigger cytosolic acidification, induction of PAL and LOX and accumulation of defense signal SA and the phytoalexin scopoletin (71). Alginate extracted from brown seaweeds exhibits inhibitory activity against TMV by the formation of large aggregates of viral particles on leaf surface, thereby blocking the entry of viral RNA into plant cells. Additionally, the anionic polysaccharides may interact with the cationic amino groups of TMV, preventing its interaction with cell membrane (72).

Seaweeds for abiotic stress tolerance

Ascophyllum nodosum extract applied to spinach through root application at early plant growth stage has been found to increase the biomass, chlorophyll content, protein concentration and antioxidative capacity. Glutamine synthetase plays an essential role in nitrogen metabolism by catalysing inorganic nitrogen (ammonia) to organic form (glutamine) (73), which was found in abundance by the application of *Ascophyllum nodosum* extract, resulting in increased plant biomass and total soluble protein content. The chlorophyll content of leaves was significantly increased due to the cytokinin like effects and betaines present in the seaweed extract. In seaweed extract-treated plants, the transcription of betaine aldehyde dehydrogenase (BADH) and choline monooxygenase (CMO)-enzymes involved in glycine betaine synthesis-was upregulated (74), leading to increased chlorophyll content and enhanced resistance to osmotic stress. Additionally, the activity of chalcone isomerase (CHI), a key enzyme in the biosynthesis of flavanone precursors and phenylpropanoid molecules, was elevated, thereby contributing to plant defense (75, 76).

Application of seaweed extracts helps minimize oxidative damage in plants by enhancing the antioxidant activity of enzymes such as superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX) which scavenge the reactive oxygen species (ROS) and prevent oxidative degradation. Seaweed extracts also mitigate drought and salt stress by modulating the plant stress hormone abscisic acid (ABA). Extracts from *A. nodosum* have been shown to increase tolerance against heat stress by increasing the accumulation of soluble sugars and heat shock proteins (77).

Ulva rigida (C. Agardh) is rich in bioactive compounds including amino acids, minerals and plant growth promoting substances. Application of *U. rigida* extract to wheat has shown to alleviate salinity stress by inhibiting chlorophyll degradation and enhancing antioxidant potential through the activation of defense-related enzymes. The rich macronutrient content of algal extracts such as P, K and Mg combined with the presence of auxins, promotes plant growth and increases biomass under salt stress. Additionally, the abundance of glycine betaine and quenching of free radicals by antioxidants in algal extract prevented the degradation of chloroplast membrane, thereby increasing the total chlorophyll content of plants. Isocitrate dehydrogenase (ICDH) provides NADPH to counteract oxidative stress, SOD acts as the first line of defense against ROS (78). The activities of both enzyme activities were increased when plants are treated with seaweed extract providing defense against oxidative stress created due to salt stress. Glutathione reductase (GR) which plays a key role in plant growth and in detoxifying cells from H_2O_2, also showed increased activity under salinity stress following seaweed extract application (79). Similarly, glutathione S-transferase (GST) responsible for mitigating lipid peroxidation caused by salt stress exhibited enhanced activity with seaweed treatment (80). In addition, the activities of phosphoenol pyruvate carboxylase (PEPC) and glutamate dehydrogenase (GDH)-enzymes involved in carbon and nitrogen metabolism essential for the biosynthesis of carbon skeletons and amino acids-were upregulated, thereby promoting plant growth under saline conditions (81).

Seaweeds as animal feed

Animal feeds should aim not only to enhance productivity but also to support overall health. Seaweeds offer a promising feed resource for livestock, as they are rich in a wide variety of complex carbohydrates including ascophyllans, alginates, sulphated galactans, xylans, laminarins, carrageenans and fucoidans (90). These compounds function as prebiotics, positively modulating the composition and/or activity of gut microflora, thereby promoting animal health and well-being. These compounds, when fed to livestock provide resistance against stressors like food borne toxins, unpleasant temperatures and boosted their immune system. This, in turn, leads to increased productivity and improved quality of animal products obtained from livestock (91). Significant reduction in methane gas production of up to 99 % and enhancement in the digestion of ruminants can be brought by the incorporation of about 2 % of fermented seaweeds along with cattle feed. This is advantageous from a climate change mitigation perspective, as it reduces the emission of greenhouse gases from the agricultural sector (92).

Future prospects

From the standpoint of incorporating seaweeds as organic inputs within integrated nutrient management systems and as soil conditioners, they possess desirable qualities that make them well-suited for such agricultural practices. This enables agriculturists and farmers to achieve sustainable use of natural resources and increased productivity per area of arable land, which is the need of the hour. Seaweeds may also be one of the essential components in tackling against the rapid urbanization and growing population that has continuously been leading to reduced availability of cultivable lands and increasing demands of agricultural produces. It is therefore clear to the scientific community and benefactors about the enormous advantages that seaweeds possess and their applications. Further exhaustive research is needed to fully understand how seaweed extracts influence plant molecular pathways and gene expression, as well as their role in shaping the plant-associated microbial community. Such insights may enable the development of crop-specific formulations. At the same time, it is essential to ensure that seaweed-based biostimulants are environmentally safe and do not harm soil or aquatic ecosystems.

Conclusion

Global agricultural production must meet the increasing demands of a booming population without compromising the integrity of existing natural resources. This is a difficult challenge to overcome, because this situation is aggravated by rapid urbanization resulting in the shrinkage of arable lands. Therefore, available natural resources must be managed efficiently to maximize crop production while simultaneously sustaining soil health. Both the challenges of increasing agricultural productivity and ensuring sustainable management of natural resources can be addressed using eco-friendly alternative inputs that leave no harmful residues in the environment or in the agricultural produce. One such promising marine resource with the potential to function both as a plant growth promoter and a soil conditioner is seaweed. Compounds derived from seaweeds can also be used to add value to raw materials from agriculture and animal husbandry.

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Authors' contributions

AM and GM conceived the concept and drafted the manuscript. AM also designed the tables and diagrams. SKG, SK and BK reviewed, revised and finalised the manuscript. All authors read and approved the final version of the manuscript.

Compliance with ethical standards

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