Seaweed Extracts

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The use of seaweed-based bioproducts has been gaining momentum in crop production systems owing to their unique bioactive components and effects. They have phytostimulatory properties that result in increased plant growth and yield parameters in several important crop plants. They have phytoelicitor activity as their components evoke defense responses in plants that contribute to resistance to several pests, diseases, and abiotic stresses including drought, salinity, and cold.

Keywords: seaweed extracts ; phytoelicitor components ; phytostimulation ; stress tolerance ; mechanisms of action ; organic inputs ; sustainable agriculture ; biostimulants ; Sargassum ; Caribbean ; Integrated disease management

1. Seaweed Extracts—Methods of Preparation and Application into Plants

Both physical methods (heat, pressure, and microwaves) and chemical methods (solvents, acids, and alkali) are used for the extraction of seaweeds. The choice of extraction metho[1]d should be able to deal with the complexity of the seaweed composition and guarantee the integrity of biologically active molecules that have biostimulant value. The most widely used extraction process involves alkaline extraction at high pressure. This method has been found to be optimally effective, although some hormonal molecules can be degraded. The advantage of this method is the high level of extractability and moderate degradation of polysaccharides into oligomers which are one of the most biologically active components of seaweed extracts [2][3].

The method of application of the seaweed extracts plays an important role in their use and responses by plants. Most application types are either foliar, root application, or a combination of both. The extracts can be applied to soil or growing medium through fertigation, drenching or dripping [4]. However, foliar sprays of less than or equal to 0.05% v/v of the extract have been reported to be optimal for the crop and result in more effective control of disease and higher yields [5]. The better performance of foliar applications has been attributed to the immediate interaction with the plant tissues because foliar absorption happens almost immediately. Further, the adsorption of extracts by soil particles is common, which may reduce its instant mobility [5][6]. Additionally, the optimal application times for these extracts were determined to be around every 10–14 days for provoking the best plant responses [7].

2. Effect of Seaweed Extracts on Plant Growth

Over the decades, seaweed extracts have been highly explored for possible use in crop production for improving biomass yield and produce quality. These extracts have been shown to positively affect seed germination and plant growth at all stages up to harvest and even post-harvest [8][6] (Table 2). Seaweed products have been shown to promote increased germination rates and cause significant increases in seedling vigor by enhancing root size and density [9]. The extracts have also been shown to protect seedlings from transplantation shock in tomato, cabbage, and marigold [10][11]. The improved rooting architecture could be a result of small levels of phytohormones present in the extracts such as auxins as well as various stimulatory processes engaged in the plant system upon treatment with these extracts [12]. The enhancement of root systems of plants treated with seaweed extracts was also observed in vegetatively propagated plants. For instance, cuttings from floricultural plants such as marigold treated with an extract from *E. maxima* led to an increase in root density [13]. This was also reported in stone pine cuttings treated with *E. maxima* extract which is otherwise very difficult to root [14]. Treatment with *A. nodosum* extract was able to increase the number of propagules per plant in daylilies [15]. Extracts of *A. nodosum* and *K. alvarezii* also improved water uptake and nutrients, which ultimately led to the promotion of overall vigor and the growth of plants [16][17]. Application of *A. nodosum* and *Laminaria* spp. extracts in maize showed that leaves were able to significantly absorb more Zn, Fe, B, Cu, Mo, S, Mg, Ca, and Mn than the controls [18]. Applications of *A. nodosum* on cottonwood significantly increased potassium uptake in the leaves [19]. A similar increase in potassium levels was also observed in the leaves of mustard treated with *E. maxima* [20].

Seaweed extracts are also reported to have or influence phytohormonal activity. Results of a study in spinach treated with *E. maxima* extracts showed the increase of plants' endogenous cytokinins, isopentyladenine, dihydrozeatin, and cis-zeatin which have all been linked to positive plant growth [21]. At the plant's vegetative stage, application of *A. nodosum* in tomato and sweet pepper led to the increased chlorophyll content of leaves which was probably due to inhibition of chlorophyll degradation caused partly by betaines present in the extract [22][23]. These betaine compounds in the seaweed extracts suspend photosynthetic activity loss by the inhibition of chlorophyll degradation [24]. Similarly, a significant increase in chlorophyll content, stomatal conductance, photosynthetic rate, and transpiration rates were recorded in asparagus plants treated with *A. nodosum* [25]. Treatment of willow plants with an extract of *E. maxima* enhanced the electron transfer rates of both photosystems [26]. Tomato plants treated with red, brown, and green species of seaweed extracts resulted in increased plant height, increased leaf numbers, increased root width and root length, and an overall increase in biomass [8][27].

Seaweed extracts also triggered early flowering and increased fruit set in a variety of crop plants, for example, tomato, pepper, and snap bean [8][5][28][29]. These increases in flower numbers and fruit set inevitably led to an improvement in yields. For instance, the application of seaweed extracts in tomatoes caused a significant increase in flower number, inflorescence number, flower to fruit ratio, and increased fruit number and size [20][22]. This yield increase was thought to be as a result of various levels of phytohormones present in the extracts such as cytokinins and induction of host hormonal synthesis [30]. Recent studies have shown that seaweed extracts and their components can modulate the expression of genes responsible for the endogenous biosynthesis of growth hormones including auxin, cytokinin, and gibberellin [8]. This was reported in tomato and sweet pepper plants treated with extracts of *A. nodosum*, *S. vulgare*, and *A. spicifera* [8][6]. Apart from increasing harvestable crop yield, extracts have been reported to enhance the nutrient quality of crops such as tomato, pepper, lettuce, spinach, cucumber, and strawberry [31][5][32][33][34]. Treatment of cucumber with an extract of *Macrocystis pyrifera* led to significant increases in total phenols, antioxidant capacity, and vitamin C in the fruits [34]. Applications of *A. nodosum* lead to increases in anthocyanins and total phenolic contents in the grapevines and berries [35]. Strawberry plants treated with *A. nodosum* seaweed extract improved the edible quality of the fruit by enhancing total soluble solids, sucrose, and fructose. The same study also reported an increase in a health compound, quercetin, which has been highly documented as a cardiovascular promoter and anticancer-reducing agent [31]. Application of an extract of *Codium tomentosum* as a postharvest spray to apples resulted in a reduced browning index coupled with inhibition of peroxidase and polyphenol oxidase, enzymes linked to browning which can reduce the shelf life of the produce [36]. These booster effects have been shown to accumulate in the plant irrespective of the type of application done, i.e., foliar, soil root drench, or a combination of both [5][37][38]. Ashing of the seaweed extract product leads to the loss of biostimulant activity which confirmed the role of organic fraction of these seaweed extracts in eliciting positive growth responses in plants [37]. Though seaweed extract biostimulants contain minimum levels of minerals that plants can readily assimilate, the main contribution of the extracts is their ability to stimulate various processes in the plant system which would eventually allow for enhanced growth and productivity of plants [8][39][40].

3. Effect of Seaweed Extracts on Plants' Tolerance to Biotic Stresses

The ever-changing climate and the extensive overuse of chemical pesticides have increased the emergence of infectious and resistant pests and pathogens in major crops, thus substantially reducing agricultural outputs [41][42]. Nematode parasites cause serious infestation and damage to plants; however, seaweed extracts have been shown to reduce the infestation of nematodes in plants such as *Arabidopsis thaliana* [38], sunflower [39], and tomato [40]. However, this nematocidal activity is largely a part of the plant's defense response, possibly by cytokinin: auxin ratio adjustments as it was shown that seaweed extracts had no direct nematicidal properties [43]. Furthermore, extracts of *Sargassum wightii* and *Padina pavonica* showed significant insecticidal activity against the red cotton stainer (*Dysdercus cingulatus*) which is a serious pest harming cotton crops [44]. The infestation of greenfly aphid (*Aphis gossypii*) and serpentine leafminer (*Liriomyza trifolii*) was also significantly reduced in cotton upon mixed treatments with S*argassum* spp., *A. nodosum*, *Laminaria* spp. [45]. On the other hand, citrus greening was also reduced by a reduction of the pest *Diaphorina citri* upon treatment with extracts of *Caulerpa sertularioides*, *Laurencia johnstonii* and *Sargassum horridum* [46]. Additionally, seaweed extracts were able to significantly reduce infestation caused by borers, aphids, and thrips in sugarcane thus preventing great economic loss [47][48]. This reduction in infestation can be due to the antifeedant effects, growth inhibition, and also cytotoxicity on ovarian tissue cells of the pests. For example, an acyclic diterpenoid isolated from *Sargassum* had growth repellent effects against pink bollworm [49].

Seaweed extracts also serve as elicitors to plant defense responses against harmful bacterial, fungal, and even viral pathogens thereby protecting crops from major economic damage from diseases [50][19]. Extracts of various brown, red, and green macroalgae (Table 2) were recorded to have great eliciting effects against some harmful bacterial and fungal pathogens. There were several fungal and bacterial diseases that were controlled by the application of seaweed extracts. The reduction of infection levels is due to a general improvement of vigor of seaweed extract treated plants, preformed resistance, induced systemic or systemic acquired resistance, or enhanced soil suppressiveness due to altered microbial dynamics.

Apart from eliciting defense towards bacterial and fungal pathogens, seaweed extracts have shown the potential to control the harsh symptoms of viroid and viruses of plants [51]. Symptoms of the tomato chlorotic dwarf viroid were significantly decreased when pre-treated with a λ-carrageenan polysaccharide from a seaweed extract. Similarly, the severity of tobacco mosaic virus (TMV) in tobacco was significantly reduced when treated with sulfated galactans which are a major component of some of the seaweed extracts [51]. Furthermore, treatment of plants with oligosaccharides derived from seaweeds showed a significant reduction of symptoms caused by tobacco mosaic virus in tobacco plants [52][53].

4. Effect of Seaweed Extracts on Plants' Tolerance to Abiotic and Environmental Stresses

In addition to stresses caused by pests and diseases, various environmental stresses such as drought, high temperature, salt, and freezing conditions can hamper crop productivity. It is also estimated that by the year 2050, approximately 50% of arable lands will be plagued by high salt and drought conditions. These abiotic stresses can lead to the build-up of reactive oxygen species (ROS) which will ultimately cause damage to the plant system [52][53]. Interestingly, plants treated with seaweed extracts such as *A. nodosum* and *Sargassum* spp. were able to withstand the damaging effects of these abiotic stresses (Table 2). For example, a significant reduction was recorded in leaf osmotic potential when grapevines and tomato plants were treated with seaweed extracts thus preventing extensive damage [54]. *Kappaphycus alvarezzi* extract treatment on various wheat varieties under salinity and drought stress resulted in plants with increased root length, enhanced chlorophyll content and carotenoids, and tissue water content. The extract also caused a significant reduction in electrolyte leakage and lipid peroxidation, decreased Na^+/K^+ ratio, and increased Ca content, thereby reducing ionic disparity. Further, treated wheat plants accumulated osmoprotectants including proline, amino acids, and total protein [55]. Seaweed extracts also promote freezing tolerance in barley [56] and *A. thaliana* [57] with an increase in winter hardiness when treated with seaweed extract sprays. Seaweed extract-induced attenuation of the harsh effects of drought, cold, and salinity stress has shown to be mediated through enhanced root morphology, a build-up of non-structural carbohydrates which improved storage of energy, enhanced metabolism, and water adjustments, as well as the build-up of proline [56][57].

The enhancement and priming effects of seaweed extracts on the plant's defenses against both abiotic and biotic stresses can be attributed to the chemical composition of the extracts as well as its eliciting properties [1]. In the subsequent sub-sections, we will reveal the proposed modes of action of seaweed extracts in eliciting growth and defense responses as well as discuss their compositional features in relation to the varying responses recorded [2].

Table 1. Effect of seaweed extract biostimulants on major crops.

Crop	Seaweed Extract	Observed Effects	Reference
Tomato (*Solanum lycopersicum*)	- *Ascophyllum nodosum* - *Sargassum* spp. - *Cystoseira myriophylloides* - *Gelidium serrulatum* - *Ulva lactuca* - *Laminaria digitata* - *Fucus spiralis* - *A. spicifera*	- Increased germination rate and seedling vigor - Increased shoot and root growth - Increased chlorophyll content (Soil Plant Analysis Development—SPAD index) - Increased flowering - Fruit yield increase - Fruit quality improvement - Improved resistance to pathogens: Verticillium wilt (*Verticillium dahliae*), early blight (*Alternaria solani*), crown gall (*Agrobacterium tumefaciens*), and bacterial spot (*Xanthomonas campestris* pv. *vesicatoria*) - Increased tolerance to salinity, drought, and cold stress	[58][4][25][26][59][60][61][62][63][64]
Sweet pepper (*Capsicum annuum*)	- *A. nodosum* - *Sargassum* spp. - *A. spicifera*	- Increased shoot and root growth - Increased chlorophyll content (SPAD index) - Increased flowering - Fruit yield increase - Fruit quality improvement - Improved resistance to pathogens: early blight (*Alternaria solani*), blight and fruit rot (*Phytophthora capsica*) and bacterial spot (*Xanthomonas campestris* pv. *vesicatoria*) - Increased tolerance to salinity and drought stress	[58][4][56][57][60][65]
Lettuce (*Lactuca sativa*)	- *A. nodosum* - *Durvillaea potatorum* - *Durvillaea antarctica* - *Ecklonia maxima*	- Increased root and shoot - Increased chlorophyll content - Increased photochemical efficiency and increased activity of photosystem II - Marketable yield increase	[32][65]
Cauliflower (*Brassica oleracea*)	- *A. nodosum*	- Increased heart size - Increased curd diameter	[66]
Soybean (*Glycine max*)	- *A. nodosum* - *Kappaphycus alvarezii*	- Improved nutrient uptake - Enhanced yield parameters - Improved drought tolerance	[67][68][69]

Crop	Seaweed Extract	Observed Effects	Reference
Strawberry (*Fragaria x ananassa*)	- *A. nodosum* - *Sargassum* sp. - *Laminaria* sp. - *Duvillaea potatorum*	- Increased vegetative growth - Increased crown carbohydrate, leaf phosphorus, and potassium contents - Increased yield - Enhanced fruit quality and taste - Increased resistance to powdery mildew (*Podosphaera aphanis*), grey mold (*Botrytis cinerea*), leak (*Rhizopus* and *Mucor* spp.), anthracnose (*Colletotrichum acutatum*), leather rot (*Phytophthora cactorum*), and stem end rot (*Gnomonia comari*)	[31][69][70][71][72]
Cucumber (*Cucumis sativus*)	- *A. nodosum* - *Macrocystis pyrifera* - *Ulva armoricana*	- Increased fruit yield - Enhanced nutritional fruit content - Reduced fungal infections by leafspot (*Alternaria cucumerinum*), blight (*Didymella applanata*), wilt (*Fusarium oxysporum*), grey mold (*Botrytis cinerea*), and powdery mildew (*Erysiphe polygoni*, *E. necator* and S*phareotheca fuliginea*)	[73][74][75]
Onion (*Allium cepa*)	- *A. nodosum*	- Increased germination rate and seedling vigor - Increased bulb diameter and weight - Increased mineral content - Increased ascorbic acid - Disease reduction caused by downy mildew (*Peronospora destructor*) - Aided in water stress resistance and increased N, P, K uptake	[76][77][78][79]
Potato (*Solanum tuberosum*)	- *A. nodosum* - *K. alvarezii* - *Gracilaria edulis* - *E. maxima*	- Growth improvement - Increased yield and tuber quality - Increased resistance to drought stress	[80][81][82][83][84]
Broccoli (*Brassica oleracea* var. *italica*)	- *A. nodosum*	- Increased biomass - Increased nutritional value	[84][85]

Crop	Seaweed Extract	Observed Effects	Reference
Spinach (*S. oleracea*)	- *A. nodosum* - *E. maxima* - *Codium liyengarii*	- Increased fresh yield, dry biomass and leaf area - Increased SPAD index - Increased micro/macronutrient profile - Increased resistance to drought stress	[28][86][87][88]
Carrot (*Daucus carota*)	- *A. nodosum* - *E. maxima*	- Increased harvest index (HI) - Improved nutritional content - Reduction of fungal disease severity caused by black rot (*Alternaria radicina*) and grey mold (*B. cinerea*)	[89][90][91][92][93]
Wheat *(Triticum aestivum*)	- *A. nodosum* - *E. maxima* - *K. alvarezii* - *G. edulis* - *G. dura* - *Sargassum latifolium* - *Ulva lactuca*	- Increased chlorophyll content (>SPAD) - Increased yield - increased micro/macronutrients in root, leaves, and grains - Increased protein content - Improved drought and salinity tolerance	[38][94][95][96][97][98][99]
Rice (*Oryza sativa*)	- *A. nodosum* - *Kappaphycus* sp. - *Gracilaria* sp. - *Hydroclathrus* sp. - *Sargassum* sp.	- Greater germination % and seedling vigor - Improved yield - Improved nutrient uptake	[100][101][102][103]
Apple (*Malus domestica*)	- *A. nodosum* - *Codium tomentosum*	- Decreased alternate bearing - Greater chlorophyll content - Increased photosynthesis and respiration rates - Increased fruit set and fruit yield - Increased anthocyanin content - Improved red color intensity - Minimized fruit browning post-harvest	[34][104][105][106][107]

Crop	Seaweed Extract	Observed Effects	Reference
Maize (*Zea mays*)	- *A. nodosum* - *Laminaria* sp. - *Gracilaria edulis* - *K. alvarezii*	- Increased germination % and rate - Increased seedling vigor - Increased shoot and root growth - Increased net carbon assimilation - Total grain yield	[16][108][109][110][111][112]
Orange (*Citrus* spp.)	- *A. nodosum* - *E. maxima* - *Sargassum horridum* - *Laurencia johnstonii* - *Caulerpa sertularioides*	- Increase in maturity index (MI) - Lessened fruit drop - Increased yield - More vitamin C - Increased TSS - Significant control of the Asian citrus psyllid, *Diaphorina citri*	[7][44][113][114][115]
Sugarcane (*Saccharum officinarum*)	- *A. nodosum*	- Increased biomass in plantlets - Increased plant growth parameters (SPAD, height and leaf area index) - Increased yield - Improved sugar content - Enhanced water retention capacity and water content - Lowered risk of wilting - Significant control of borers, aphids, and thrips	[48][115][116]

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