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Review

Seaweed Polysaccharides in Agriculture: A Next Step towards Sustainability

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Abstract: The seaweed-based biostimulants available in the market are proven to achieve better results than synthetic commercial fertilizers in plant growth parameters. There are many compounds present in seaweeds that are responsible for the plant bioactivities. Seaweed polysaccharides, such as agar, alginate, and carrageenan, make up most of the seaweed biomass and are proven to achieve excellent results in agricultural crops (in poly- and oligosaccharides formula). These types of compounds are reported to improve seed germination and plant vigor, increase the uptake of soil nutrients, and protect plants against several abiotic and biotic stresses such as salinity, drought, temperature, and pathogens. When applied to the soil directly or sprayed on the foliage, seaweed poly- and oligosaccharides can protect plants against pathogens by stimulating a plant to produce secondary metabolites and manage its defense pathways. Therefore, seaweed poly- and oligosaccharides constitute an important source of potential elicitors in plants and have a particular interest for agriculture. Thus, in this review, the focus is on the potential application of these compounds in the agricultural domain: problems, obstacles, and possibilities.

Keywords: seaweed polysaccharides; biostimulants; bioactivities; plants; agriculture

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1. Introduction

Seaweed extracts include a diverse range of bioactive compounds that stimulate and directly boost plant growth and its defensive responses to pathogens [1]. Some studies have shown that seaweed-based biostimulants can achieve better results in plant growth parameters when compared to commercial fertilizers [2]. Plants grown in soils treated with seaweed extracts, either applied to the soil directly or sprayed on the foliage, show a wide range of responses. When applied to the soil these extracts can stimulate soil microflora and cause soil water retention and remediation. Seaweed extracts alleviate the nutrient deficit in plants and can have a positive impact on the phytohormone balance [2].

Plants serve as biosensors for detecting the presence of bioactive compounds provided by seaweeds, testing them and even evaluating their effects, in general. This is an easy way to guarantee that seaweed extracts have a consistent level of bioactivity [3]. Consequently, seaweed extracts can operate as elicitors in plants by stimulating their defenses, including salicylic acid (SA), jasmonic acid (JA), and ethylene (ET) pathways [4]. These phytoelicitors can improve crop yield [5] and plant vigor [5], increase the uptake of soil nutrients [6], provide longer shelf life of the fruits [5], improve seed germination [7], and protect plants against several abiotic and biotic stresses such as salinity, drought, temperature [2], and pathogens [8].

The active organic compounds responsible for the bioactivity may change depending on the seaweed class and species, as well as the extraction method used. They often include a variety of organic and inorganic bioactive compounds such as polysaccharides (alginate, agar, and carrageenan), polyphenols, phytohormones (auxins, cytokinins, and gibberellins), phytohormone-like (betaine), minerals (potassium, phosphorus, calcium, and some trace elements), and other different components (lipids, peptides, glycoproteins, and proteins) [4]. Seaweed extracts are mainly composed of polysaccharides, sugars known for improving plant growth in a similar way to hormones [9,10] and whose characteristics depend on the species and ecological conditions of the seaweed [1,11]. The extraction procedures have a significant impact on the content of seaweed extracts. During the extraction process, complex compounds such as polysaccharides are often transformed into oligomers that are extremely bioactive in plants.

In a study related to the influence of oligo-alginates and oligo-carrageenans in the resistance of tobacco plants against tobacco mosaic virus (TMV) [12], it was reported that these seaweed oligosaccharides could stimulate the plant's growth and defense against TMV by activating the antioxidant enzyme ascorbate peroxidase (AP), which modulates the level of the antioxidant compound ascorbate (ASC) and docosahexaenoic acid (DHA). In addition, the activation of the defense enzyme phenylalanine ammonia-lyase (PAL) led to the activation of the phenylpropanoid pathway and to the synthesis of secondary metabolites with an antiviral activity.

However, there are many challenges in obtaining seaweed extracts without compromising the biochemical integrity of the bioactive compounds and ensuring the efficacy of their biostimulant potential. Some of the methods used are water-based extraction, acid hydrolysis-based extraction, alkaline hydrolysis-based extraction, microwave-assisted extraction, ultrasound-assisted extraction, pressurized liquid extraction, enzyme-assisted extraction, and super-critical fluid extraction [2].

It is hypothesized that seaweed polysaccharides' bioactivities are affected by the presence and position of sulfate groups in the molecular chain of the polymers. The degree of sulfation, their concentration, and oxidation, all together, have an impact on these bioactivities [13]. Typically, alginophytes show the lowest sulfate group content, whereas carrageenophytes, the highest [14].

However, there is still a lack of information about the biochemical diversity of seaweed poly- and oligosaccharides, and their mechanism of action for specific activities. All the studies familiar with the influence of seaweed poly- and oligosaccharides bioactivities on plants do not mention the correlation between them and specific components, the structure, or the molecular length of basic monomers [13]. Therefore, there is an urgent need to characterize seaweed polysaccharides based on their monosaccharide composition and molecular size to understand their potential bioactivity [14].

2. Seaweed Polysaccharides

The chemical structures of the polysaccharides obtained from seaweeds are different depending on the taxonomic group to which they belong, their species, the season when these seaweeds were harvested, and the respective extraction method. The colloids authorized in the food industry, and widely used worldwide, are alginate (extracted from brown algae), agar, and carrageenan (extracted from red algae) [15–18].

2.1. Alginate

Alginate (Figure 1) is a polysaccharide naturally found in brown seaweed in the form of alginic acid. This anionic polymer is based on monomers of β-D-mannuronic acid (M) and 1,4 α-L-guluronic acid (G) [19]. Depending on the position of the monomeric units in the chain, the molecular weight of the polymer, and the nature of its associated counter ions, the properties of this polysaccharide can differ [1,20].

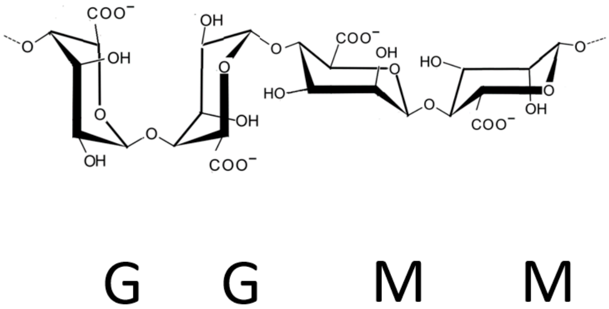

Figure 1. Chemical structure of alginic acid [14] Legend: G—guluronic acid; M—mannuronic acid.

At the level of food certification, the molecular weight of alginate is not considered. However, it is contemplated for good practices in the extractive industry associated with the food industry [21].

The industrial extraction of this polysaccharide involves several steps: washing the seaweed to remove impurities and pre-treatment with heated acid (usually hydrochloric acid for 24 h) to remove pigments, proteins, and lipids [22]. Next, the solid–liquid extraction takes place, where the solid residue is subjected to an alkaline treatment (sodium carbonate) followed by a centrifugation or filtration process. After this process, hydrochloric acid is added to the liquid extract to precipitate the alginate dissolved in the solution in the form of sodium alginate. After precipitation, the solution with the precipitate is centrifuged/filtered to obtain the precipitated alginate. Afterwards, the alginate is dried and milled for later application [23].

Alginate is classified as a non-organic compound and is approved by the Food and Drug Administration (FDA, USA) and the European Food Safety Authority (EFSA, EU) as a food ingredient [24]. In this context, the application and labeling of food products containing alginate are regulated according to the European Union Commission Regulation (1333/2008) as E400 (alginic acid), E401 (sodium alginate), E402 (potassium alginate), E403 (ammonium alginate), E404 (calcium alginate), and E405 (propylene glycol alginate) [21].

The main characteristics of alginate are its high degree of viscosity and absorption, which make it possible to thicken food products, such as jellies, marmalades, sauces (e.g., mayonnaise), syrups, and ice cream [25,26].

The FDA has approved alginate for human consumption after toxicological testing. However, the FDA requires evidence of good practices in alginate extraction and the use of alginate at threshold concentrations, which vary according to the type of food product [24].

2.2. Agar

Agar (Figure 2) is a very important polysaccharide industrially extracted from the red seaweeds genus *Gracilaria* and *Gelidium*, from the phylum Rhodophyta [27–29]. Generally, the industrial extraction method is based on a thermal treatment of the seaweed biomass in an aqueous solution (between 2–4 h at 105–110 °C) for immediate filtration while the extract is hot (as the agar gels very quickly at 50 °C). After the filtration process, the extract either gels or is maintained in a viscous solution due to the amount of agar present in the solution. However, the gel itself is normally yellowish or brown in color because some of its constituents are degraded (proteins, monosaccharides). Therefore, the freezing/thawing technique is used to obtain a concentrated agar with a clear color, as this technique allows the agar to be washed with water, avoiding pre-treatment to reduce impurities during extraction. Finally, the agar obtained is dried in an oven with air circulation and then milled for later application in industry [23,30,31].

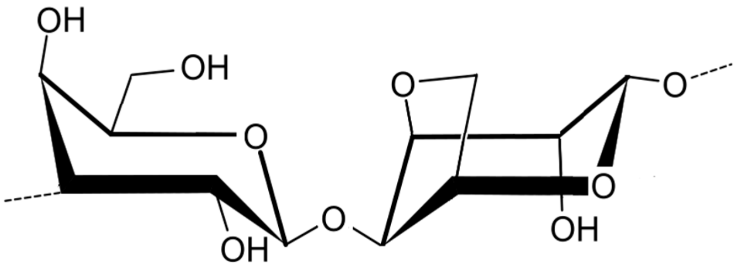

Figure 2. Chemical structure of agar [14].

It is a gel-forming polysaccharide consisting of 70% agarose and 30% agaropectin molecules, composed of residues of (1–4)-3, 6-anhydro-L-galactose and β 9 (1–3)-D-galactose [27]. To date, there is no evidence that its molecular weight has any significance for food safety, and therefore, it is considered safe regardless of its molecular weight [28]. However, the quality of the agar differs greatly between species belonging to these two orders. For example, agar extracted from *Gelidium corneum* (Gelidiales) is considered more suitable for pharmaceutical applications, [29]. On the other hand, agar extracted from *Gracilaria gracilis* (Gracilariales) is normally used, almost exclusively, in the food industry. However, normally, this agar has one more step in the industrial extraction system, which consists of an alkaline pre-treatment with sodium hydroxide, to increase the quality of the rheological properties of the agar obtained [30].

Agar is considered safe for human consumption by regulatory authorities in the United States of America (FDA) and the European Union (EFSA). Despite the inclusion of agar (E406) in the list of approved food additives, its application in food products is regulated and limited. It is estimated that approximately 90% of commercialized agar is destined for the food industry [30].

2.3. Carrageenan

Carrageenan is extracted from red seaweed of the order Gigartinales. The first historical use of carrageenan was for food purposes and occurred in Ireland [32]. Carrageenan is a polysaccharide consisting of alternately linked galactose and 3,6-anhydrogalactose units, by alternating α-1,3 and β-1,4 glycosidic bonds, and whose molecular weight (greater than 100 kDa) is required for safe use in food terms [33,34]. In this case, there are three types of carrageenan (Figure 3) normally marketed: kappa-carrageenan (κ) (Figure 3a), which forms rigid gels with syneresis; iota-carrageenan (ι) (Figure 3b), which is characterized by producing elastic and smooth gels; and finally, lambda-carrageenan (λ) (Figure 3c), which originates viscous solutions without ever gelling [30].

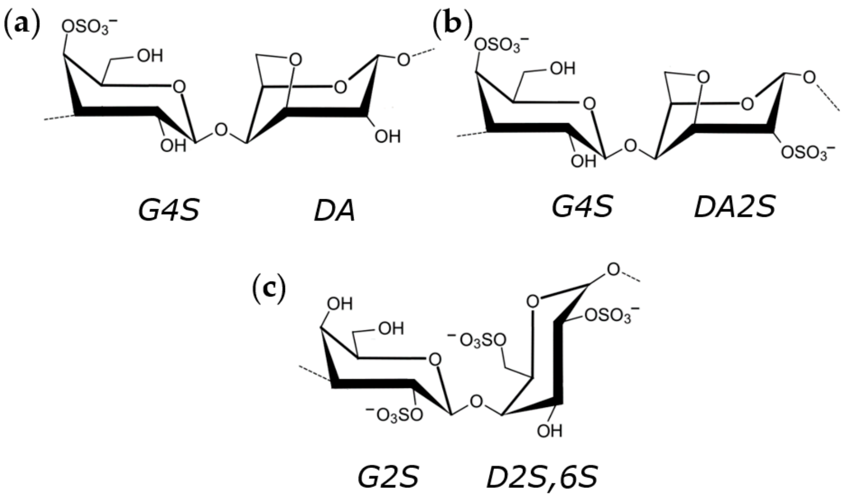

Figure 3. Chemical structure of the different main types of carrageenan: (**a**) kappa-carrageenan; (**b**) iota-carrageenan; (**c**) lambda-carrageenan [14].

In the carrageenan extraction industry, the pre-treatment of seaweed through a depigmentation step is necessary (with sodium hypochlorite or organic solvent) to obtain a clear color in the final product [32,35]. The carrageenan extraction step must be carried out in an alkaline (e.g., sodium hydroxide) or aqueous solution. Subsequently, carrageenan can be recovered by alcoholic precipitation, drum drying, or precipitation in aqueous potassium chloride and subsequent freezing (as in the case of κ-carrageenan). However, only methanol, ethanol, and isopropanol can be used for precipitation and purification of carrageenan [36–38]. To ensure food quality and safety, carrageenan is hot-dried at a temperature above 40 °C in a drying oven with forced ventilation before use [35].

3. Seaweed Poly- and Oligosaccharides Bioactivities on Plants

Unlike phycocolloids in the food area, degraded/hydrolyzed seaweed polysaccharides were the aim of several studies (Tables 1 and 2) with promising results as possible inducers of resistance and as biostimulants. With the emerging need to reduce synthetic-compound use in agriculture in the European Union, polysaccharides and their oligosaccharides are gaining new scientific interest to serve as alternatives. Seaweed extracts have already demonstrated the potential to promote seed germination and plant vigor and improve cultivars [1,3,39–44]. As an advantage, seaweeds do not compete for land space, which allows the exploration of polysaccharides in a sustainable and circular economy way, possibly alleviating the effects of climate change (Figure 4).

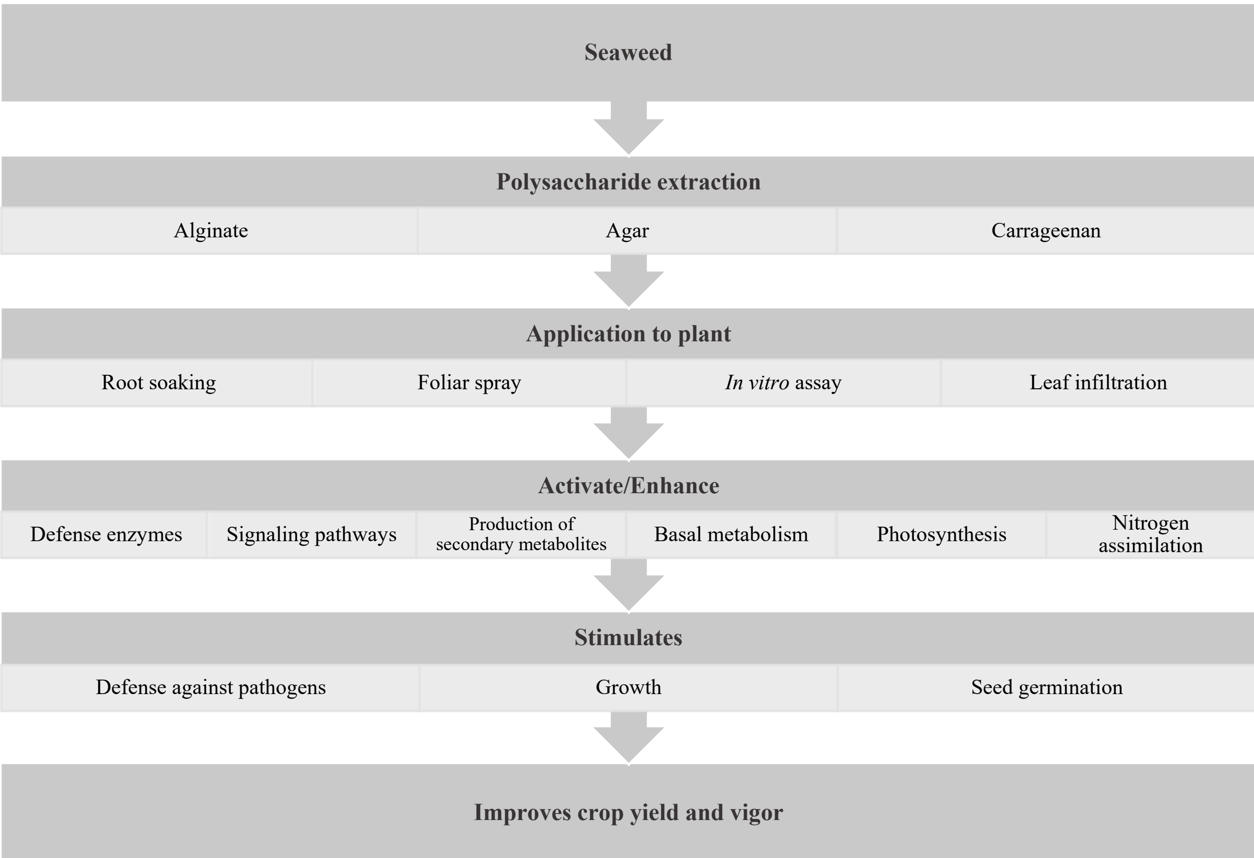

Figure 4. Schematic representation of seaweed polysaccharides action in plants.

3.1. Alginates and Oligo-Alginates

Alginates are biodegradable and non-toxic compounds traditionally used as natural fertilizers due to their superabsorbent or water-retaining properties. The carboxylic acid groups present on the alginic acid chain, combined with the metallic ions in the soil, form high-molecular-weight polymers that can absorb moisture and retain large amounts of water. Generally, water retention is a problem in sandy soils. These soils, when watered, dry up easily and drain away valuable nutrients beyond the plant roots. The use of alginates can improve this problem, stimulating plant root system development and increasing soil microbial activity [1,20].

Seaweed alginates and oligo-alginates, produced by the enzymatic degradation of alginic acid, were reported to activate defense responses against pathogens (Table 1) in wheat plants [45], date palm roots [46], tomato plants [47], olive trees [48], and against TMV [12] by regulating defense-responsive signaling pathways. To induce resistance against viral infections, including TMV, alginates activate different defense enzymes such as phenylalanine ammonia-lyase (PAL), peroxidase (POD), and ascorbate peroxidase (AP), which elicit their metabolic pathways and the synthesis of secondary metabolites, such as phenolic compounds with antiviral activity [12,45,46]. In tomato plants (Table 1), the alginate confers resistance against a fungal infection by inducing antioxidant defense and antifungal pathogenesis-related (PR) protein expression by signaling pathways mediated by salicylic acid (SA), jasmonic acid (JA), and ethylene (ET) [47]. In an experiment with olive trees (Table 1), the alginate induced resistance against a *Verticillium dahliae* fungal infection by restricting the pathogen's growth and strengthening the host defense metabolism [48].

In addition, seaweed alginates and oligo-alginates can stimulate growth, seed germination, and shoot elongation in different plant species [12,14] by enhancing nitrogen assimilation and basal metabolism [49] (Table 1).

Therefore, alginates constitute an important source of potential elicitors in plants and a particular interest in agriculture. The chemical characterization of alginates or oligo-alginates and their mechanism to boost plant growth remains unclear.

3.2. Agar and Agar-Oligosaccharides

Agar is a polysaccharide extracted from the red seaweed genus *Gracilaria* and *Gelidium*. Due to the huge availability of biomass from these seaweeds, it represents an excellent choice for commercial cultivation and to study their bioactive potential. Many species of these genus have been evaluated for their antibacterial, antioxidant, antifungal, antiprotozoal, anti-inflammatory, antiviral, cytotoxic, antihypertensive, spermicidal, and embryotoxic activities [50]. The type and number of substituents on the agar structure are crucial elements for the bioactivities' efficacy. The sulfur content generally correlates with activity, which is why active agars are typically sulfated [51].

In a study about seaweeds' carbohydrate polymers as plant growth promoters, agar extracted from two red seaweeds, *Gracilaria gracilis* and *Asparagopsis armata*, showed positive results in the growth and seed germination of kale plants [14].

Although there are many studies regarding the bioactivities of agarophytes [50], there is still a lack of studies regarding the bioactivities of agar, especially its effect on plants.

3.3. Carrageenans and Oligo-Carrageenans

Carrageenans and their oligomers, extracted from various red seaweeds, present a significant source of bioactive substances that activate plants' defense mechanisms and offer resistance against abiotic and biotic stresses. This can be achieved by modulating various physiological and biochemical processes [52]. Additionally, carrageenans control several metabolic activities in plants, including cell division, purine and pyrimidine synthesis, assimilation of nitrogen and sulfur, and photosynthesis [14,53].

Lemonnier-Le Penhuizic et al. [54] demonstrated that oligosaccharides (of varying molecular weights, but less than 500 Da) of λ-carrageenan act as inducers of embryogenesis. It should be noted that, in this study, both alginate and agar oligosaccharides were also tested, but with less significant results than those obtained by carrageenans. In general, the oligosaccharides obtained from carrageenan promote an increased plant height, greater leaf biomass, and better carbon fixation, as well as superior nitrogen assimilation and greater overall plant growth [53], in addition to promoting plant defenses as elicitors and activating their defense mechanisms against pathogens [55].

Tobacco plants [56] and eucalyptus trees [57] treated with commercially available κ-, ι-, and λ-carrageenans showed positive results in their growth. The oligo-carrageenans enhanced photosynthesis, basal metabolism, and the synthesis of secondary metabolites such as essential oils and polyphenolic compounds (Table 2). In addition, κ-, ι-, and λ-carrageenans were reported (Table 2) to induce long-term protection against viral, bacterial, and fungal infections at a systemic level by activating the phenylalanine ammonia-lyase (PAL) enzyme and enhancing the accumulation of phenylpropanoids with potential antimicrobial activities [58,59].

As said previously, the level of sulfation of the polymer is suggested to influence their bioactivity and, therefore, their targeted applications for plant defenses [13]. The sulfate group content differs depending on the type of carrageenan: κ-carrageenan has 20–30% of sulfate group content, ι-carrageenan has 28–35%, and λ-carrageenan has 32–39% [59,60]. Among the three carrageenans, λ-carrageenan was considered the most potent elicitor due to its high sulfur content, inducing systemic resistance in plants. Plants treated with λ-carrageenan (Table 2), either through leaf infiltration or foliar spray, showed resistance against several pathogens by inducing SA-, JA-, and ET-dependent defense pathways [59,61–64].

I-carrageenan, sprayed on leaves, was reported (Table 2) to stimulate the growth of tobacco plants by enhancing photosynthesis, basal metabolism, and cell cycle, as well as ascorbate (ASC) levels and ascorbate peroxidase (AP) enzyme activity [65]. This oligo-carrageenan can elicit resistance against the moth *Trichoplusia ni* in *Arabidopsis thaliana* by inducing various defense mechanisms, including JA- and SA-dependent pathways, proteinase inhibitors, and an alteration of the products of glycosylate hydrolysis [66].

K-carrageenan, used in leaf spray treatment, was reported (Table 2) to stimulate the growth of chickpea plants, maize plants [67], and pine trees [68] by enhancing the basal metabolism and the production of secondary metabolites. Additionally, κ-carrageenan, applied through leaf infiltration, showed resistance against several pathogens by inducing SA-, JA-, and ET-dependent defense pathways [69–72].

When compared to λ-carrageenan, κ-and ι-carrageenan showed better results in the growth of the roots and leaves in kale by inducing the production of indole-3-acetic acid (IAA), responsible for the plant's development [14].

In sum, carrageenans and oligo-carrageenans can be employed as naturally occurring growth-enhancing, anti-fungal, and anti-viral agents.

In these cases, the mechanisms by which these poly- and oligosaccharides operate are yet unknown, nor is the characterization completed to have a direct correlation between polysaccharides, molecular weight, and the respective bioactivity. Thus, it will be essential to clarify from the biochemical point of view the potential danger of the polysaccharide degradation through the digestive system, or not, and what is the potential of low molecular weight oligosaccharides in plant health.

Table 1. Alginate and Oligo-Alginate bioactivities on plants.

Seaweed/Source	Polymer	Plant Species	Application Method	Bioactivity	Reference
Bifurcaria bifurcata	Alginate	*Phoenix dactylifera* L.	Root soaking	Induces date palm natural defenses by enhancing PAL activity and phenolic compounds content.	[46]
Colpomenia peregrina	Alginate	*Brassica oleracea* L.	In vitro assay	Stimulates seed germination and growth in kale.	[14]
Commercially available	Sodium alginate	*Solanum lycopersicum* L.	Foliar spray	Resistance against *Alternaria solani* fungal infection in tomato plants by inducing antioxidant defense and antifungal PR protein expression by signaling pathways mediated by ET, JA and SA.	[47]

Table 1. *Cont.*

Seaweed/Source	Polymer	Plant Species	Application Method	Bioactivity	Reference
Commercially available	Alginate	*Olea europaea* L.	In vitro assay	Resistance against *Verticillium dahliae* fungal infection in olive trees by restricting the pathogen's growth and strengthening the host defense metabolism.	[48]
Fucus spiralis	Alginate	*Phoenix dactylifera* L.	Root soaking	Induces date palm natural defenses by enhancing PAL activity and phenolic compounds content.	[46]
Lessonia trabeculata	Oligo-Alginates (Poly-Gu)	*Nicotiana tabacum* L.	Foliar spray	Stimulates growth and induces resistance to TMV in tobacco plants by activating the antioxidant enzyme AP, which modulates the level of the antioxidant compounds ASC and DHA. The activation of the defense enzyme PAL leads to the activation of the phenylpropanoid pathway and to the synthesis of secondary metabolites with antiviral activity.	[12]
Lessonia flavicans (formerly *Lessonia vadosa*)	Alginate	*Triticum aestivum* L.	Leaf infiltration	Induces the enzyme activities of PAL and POD.	[45]
Lessonia flavicans (formerly *Lessonia vadosa*)	Oligo-Alginates (Poly-Ma)	*Nicotiana tabacum* L.	Foliar spray	Stimulates growth and induces resistance to TMV in tobacco plants by activating the antioxidant enzyme AP, which modulates the level of the antioxidant compounds ASC and DHA. The activation of the defense enzyme PAL leads to the activation of the phenylpropanoid pathway and to the synthesis of secondary metabolites with antiviral activity.	[12]
Sargassum muticum	Alginate	*Brassica oleracea* L.	In vitro assay	Stimulates seed germination and growth in kale.	[14]
Undaria pinnatifida	Alginate	*Brassica oleracea* L.	In vitro assay	Stimulates seed germination and growth in kale.	[14]

Table 2. Carrageenans and Oligo-Carrageenans bioactivities on plants.

Seaweed/Source	Polymer	Plant Species	Application Method	Bioactivity	Reference
Acanthophora spicifera	λ-carrageenan	*Hevea brasiliensis* L.	Foliar spray	Resistance against *Phytophthora palmivora* fungal infection in *H. brasiliensis* by inducing SA-dependent defense pathways.	[63]
Calliblepharis jubata	κ, λ, and ι-carrageenan	*Brassica oleracea* L.	In vitro assay	Stimulates seed germination and growth in kale. κ- or ι-carrageenan showed best results.	[14]
Chondracanthus teedei var. *lusitanicus*	κ, λ, and ι-carrageenan	*Brassica oleracea* L.	In vitro assay	Stimulates seed germination and growth in kale. κ- or ι-carrageenan showed best results.	[14]

Table 2. *Cont.*

Seaweed/Source	Polymer	Plant Species	Application Method	Bioactivity	Reference
Commercially available	κ, λ, and ι-carrageenan	*Nicotiana tabacum* L.	Foliar spray	Stimulates the growth of tobacco plants by enhancing net photosynthesis and ribulose 1, 5 biphosphate carboxylase/oxygenase (RuBisCO) activity.	[56]
Commercially available	λ-carrageenan	*Arabidopsis thaliana* L. Heynh.	Foliar spray	Resistance against *Sclerotinia sclerotiorum* fungal infection in *A. thaliana* by inducing JA/ET-dependent defense pathways.	[61]
Commercially available	κ, λ, and ι-carrageenan	*Arabidopsis thaliana* L. Heynh.	Foliar spray	Resistance against the moth *Trichoplusia ni* in *A. thaliana* by inducing various defense mechanisms including JA- and SA-dependent pathways, proteinase inhibitors, and an alteration of the products of glycosylate hydrolysis. ι-carrageenan showed best results.	[66]
Commercially available	κ, λ, and ι-carrageenan	*Solanum lycopersicum* cv. Sheyenne	Foliar spray	Resistance against tomato chlorotic dwarf viroid (TCDVd) by inducing JA-dependent defense pathways. κ- or ι-carrageenan did not have an effect.	[62]
Commercially available	κ-carrageenan	*Pinus radiata*	Foliar spray	Stimulates growth and basal metabolism and increases the level of growth-promoting hormones.	[68]
Commercially available	κ, λ, and ι-carrageenan	*Nicotiana tabacum* L.	Foliar spray	Stimulates the growth of tobacco plants by enhancing photosynthesis, basal metabolism, and cell cycle, as well as ASC levels and AP activity. ι-carrageenan showed best results.	[65]
Commercially available	κ, λ, and ι-carrageenan	*Eucalyptus globulus* Labill.	Foliar spray	Stimulates the growth of *Eucalyptus globulus* by enhancing photosynthesis, basal metabolism, total essential oils and polyphenolic compounds with potential antimicrobial activities.	[57]
Commercially available	κ, λ, and ι-carrageenan	*Nicotiana tabacum* L.	Foliar spray	Induces long-term protection against viral, bacterial and fungal infections at systemic level in tobacco plants by activating the PAL enzyme and enhancing the accumulation of phenylpropanoids with potential antimicrobial activities.	[58]
Commercially available	λ-carrageenan	*Triticum aestivum* L.	Foliar spray	Resistance against *Zymoseptoria tritici* fungal infection in wheat plants by inducing SA- and JA-dependent defense pathways.	[64]
Commercially available	Carrageenan	*Olea europaea* L.	In vitro assay	Resistance against *Verticillium dahliae* fungal infection in olive trees by restricting the pathogen's growth and strengthening the host defense metabolism.	[48]

Table 2. *Cont.*

Seaweed/Source	Polymer	Plant Species	Application Method	Bioactivity	Reference
Kappaphycopsis cottonii (formerly *Eucheuma cottonii*)	κ-carrageenan	*Nicotiana tabacum* L.	Leaf infiltration	Resistance against *Phytophthora parasitica* in tobacco plants by inducing defense genes encoding sesquiterpene cyclase, chitinase, and proteinase inhibitor and triggering the signaling pathways mediated by ET, JA and SA. λ-carrageenan showed best results.	[59]
Eucheuma spinosa	ι-carrageenan	*Nicotiana tabacum* L.	Leaf infiltration	Resistance against *Phytophthora parasitica* in tobacco plants by inducing defense genes encoding sesquiterpene cyclase, chitinase, and proteinase inhibitor and triggering the signaling pathways mediated by ET, JA and SA. λ-carrageenan showed best results.	[59]
Chondracanthus acicularis (formerly *Gigartina acicularis*)	λ-carrageenan	*Nicotiana tabacum* L.	Leaf infiltration	Resistance against *Phytophthora parasitica* in tobacco plants by inducing defense genes encoding sesquiterpene cyclase, chitinase, and proteinase inhibitor and triggering the signaling pathways mediated by ET, JA and SA. λ-carrageenan showed best results.	[59]
Gigartina pistillata	λ-carrageenan	*Nicotiana tabacum* L.	Leaf infiltration	Resistance against *Phytophthora parasitica* in tobacco plants by inducing defense genes encoding sesquiterpene cyclase, chitinase, and proteinase inhibitor and triggering the signaling pathways mediated by ET, JA and SA. λ-carrageenan showed best results.	[59]
Grateloupia turuturu	κ, λ, and ι-carrageenan	*Brassica oleracea* L.	In vitro assay	Stimulates seed germination and growth in kale. κ- or ι-carrageenan showed best results.	[14]
Hypnea musciformis	κ-carrageenan	*Cicer arietinum* L. and *Zea mays* L.	Foliar spray or soil drench	Stimulates the growth of chickpea and maize plants by eliciting the production of secondary metabolites. The application by soil drench showed better results than the foliar spray.	[67]
Hypnea musciformis	κ-carrageenan	*Nicotiana tabacum* L.	Leaf infiltration	Resistance to TMV in tobacco plants by inducing SA-, JA-, and ET-dependent defense pathways.	[71]
Kappaphycus alvarezii	κ-carrageenan	*Capsicum annuum*	Foliar spray	Resistance against *Colletotrichum gloeosporioides* fungal infection in *C. annuum* by inducing antioxidant defense and antifungal PR protein expression by signaling pathways mediated by ET, JA, and SA.	[72]

Table 2. *Cont.*

Seaweed/Source	Polymer	Plant Species	Application Method	Bioactivity	Reference
Schizymenia binderi	Oligo-Carrageenans (Poly-Ga)	*Nicotiana tabacum* L.	Foliar spray	Stimulates growth and induces defense in tobacco plants by activating the antioxidant enzyme AP, which modulates the level of the antioxidant compounds ASC and DHA. The activation of the defense enzyme PAL leads to the activation of the phenylpropanoid pathway and to the synthesis of secondary metabolites with antiviral activity.	[12]
Tichocarpus crinitus	κ/β-carrageenan	*Nicotiana tabacum* L.	Leaf infiltration	Resistance to TMV in tobacco plants by interfering with the deproteinization and replication in the cells of binding virions, leading to fewer necrotic lesions on the leaves.	[69]
Tichocarpus crinitus	κ/β-carrageenan	*Datura stramonium* L.	Leaf infiltration	Inhibits the development of the potato virus X (PVX) infection in *D. stramonium*.	[70]

4. Current and Future Perspectives

In agriculture, there are currently various commercial seaweed biostimulants available that are proven to be effective in the stimulation of seed germination, increased plant vigor, fruit production, and defense against pathogens. However, the mechanisms of action in these extracts are still unknown. For example, what pathways these extracts induce and what secondary metabolites are produced are questions that still need an answer.

4.1. Current Perspectives

Seaweed polysaccharides are used as a functional component of conventional fertilizers, facilitating water and nutrient retention in soils. Their primary role in agriculture is as a soil conditioner. They are natural materials capable of absorbing large amounts of water (super-absorbents), up to hundreds of times their own weight. In agriculture, these polysaccharides are commonly referred to as moisture-holding hydrogels for enhancing soil water retention, which is a fundamental soil feature [8,20]. Super-absorbents were researched and developed in agricultural regions to enhance the abiotic qualities of soil. They improve water-retention ability, water-consumption efficiency, soil permeability, infiltration rates, plant performance, and soil aeration. In addition, they can also lower the irrigation frequency and compaction shift, prevent erosion and water drainage, and lower fertilizer dissolution. Consequently, these materials develop a better adsorption capacity, enhancing plant uptake of nutrient elements and stimulating microbial activity. However, because these substances stimulate microbial activity, they can act as substrates for pathogenic microbes, thus, harming the crops. This traditional use can be further exploited as demonstrated by the studies cited above (Tables 1 and 2); however, there is still a long road to obtain the full potential of the seaweed polysaccharides for improving agriculture [73,74].

4.2. Future Perspectives

There is still a lack of knowledge of what specific bioactive compounds from seaweed have an impact on plant metabolism and growth.

Although there is an increased number of studies regarding the use of seaweed extracts or seaweed biomass in agricultural crops, very few are focused on the impact of seaweed polysaccharides. These compounds take up most of all the seaweed biomass and are reported to show valuable results in the protection against plant pathogens.

In the studies regarding the effects of seaweed polysaccharides in crops, many lack an explanation of the polysaccharide extraction process. Furthermore, most of the studies tend to rely more on traditional extraction methods without optimizations and greener protocols. Moreover, the majority were executed in in vitro assays exclusively, without further extension to in vivo assays, such as pot experiments, green house experiments, or in soil experiments, depending on the crop. Nonetheless, in the experiments carried out in the field, many studies [45,56–58,63–66,68] did not grant information about the composition of the soil or substrates where plants were grown, as well as the biochemical composition of the plants after the experiment and a correlation between what the soil absorbed vs what the plant absorbed after the extracts were applied.

This could also be an interesting topic to focus on in the future; seaweed extracts could potentially improve soil quality, aid the soil recovery, and elevate the soil remediation.

As was said previously, there are many studies (Tables 1 and 2) in which seaweed polysaccharides exhibit protection against plant pathogens. Therefore, it would be beneficial to test their impact on plant growth and chemical composition.

The next step in sustainable agriculture is to understand the mechanisms of action of specific bioactive compounds and form a correlation with their molecular weight.

5. Conclusions

In a planet with an increased demand for new and greener alternatives for the agricultural practices, seaweed-based biostimulants gain an important role in our future. Seaweed-based biostimulants can be substituted for the synthetic compounds present in commercial stimulants and fertilizers, used in agriculture to improve crop yield and vigor. Seaweed polysaccharides are commercially important compounds with many regulations in the food industry and well-known extraction procedures. These seaweed compounds can improve plant growth in a similar way to hormones because they operate as elicitors in plants to stimulate their defense pathways. Seaweed polysaccharides' bioactivities are affected by the presence and position of sulfate groups in the molecular chain of the polymers; therefore, their monosaccharide composition and molecular size can help us to understand their potential bioactivity and predict their practical application in the agricultural sector.

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