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Review article

Seaweed extracts: Potential biodegradable, environmentally friendly resources for regulating plant defence

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ABSTRACT

Marine macroalgae or seaweeds are the major components of the marine flora and are used as food, feed and fertilizer. Applications of seaweed extracts (SEs) from certain algae have the potential to improve plant growth and yield. The richness of polysaccharides, oligosaccharides, peptides, proteins and phytohormones in various SEs, favor the deployment of SEs as bio-elicitors for disease tolerance in plants. The SEs from some algae regulate the physiological, biochemical and molecular mechanisms of the plants to enhance defence against pathogens. The SEs also modulate the rhizosphere microbial composition, which contributes to regulation of plant defence responses. The regulation of salicylic acid (SA) and jasmonic acid (JA)-signaling pathways, reactive oxygen species (ROS) homeostasis and defence-related genes/enzymes by applications of SEs play a major role in the molecular regulation of defence response. This review focuses on the bioactive molecules of various SEs, functional mechanism of bio-elicitors, phytohormones, and molecular regulation towards disease tolerance in plants.

1. Introduction

Seaweeds or marine macroalgae are commonly classified in to three major groups on the basis of their brown, red and green pigmentations as: the Phaeophyta, Rhodophyta and Chlorophyta, respectively. These macroalgae are photosynthetically active, serve as food resource for other organisms, possess different mechanisms for carbon acquisition, and important for maintaining the environment quality [1]. Various seaweeds are important sources for human food in many Asian countries such as China, Japan and Korea [2,3], fertilizers and fuels [4]. The importance of various seaweed extracts (SEs) for their utilization in agriculture has been reviewed [5–7]. Plants being sessile, are simultaneously exposed to different environmental challenges, including both abiotic and biotic factors, some of these factors either additively or individually limit their growth and productivity [8]. Plants require complex co-ordination of cellular, developmental and physiological processes in response to adverse environmental conditions. The cellular responses form a complex co-ordination of various signal transduction pathways in order to orchestrate the biochemical and molecular processes required to combat various stresses and adaptation of plants throughout their lifecycle. The abiotic stresses like salinity, drought, cold and heat result in metabolic modulation, membrane disorganization, closure of stomata, decreased photosynthetic activity, imbalance of reactive oxygen species (ROS) homeostasis and disturbances in nutrient uptake [9].

Seaweeds contain different compounds such as proteins, peptides, amino acids, soluble and insoluble fibers, lipids, pigments, phenols and various polysaccharides. Seaweeds are rich in different growth hormones such as auxins, cytokinins and gibberellins and certain SEs are reported as effective bio-stimulants, which can increase the yield of different crops [6,10,11]. Kauffman et al. defined bio-stimulants as materials, promoting plant growth in low quantities and are not consider in fertilizers category [12]. Furthermore, bio-stimulants were classified in to three groups based on their source and content, as the humic

Abbreviations: ABA, Abscisic acid; ACO, ACC oxidase; ANE, *Ascophyllum nodosum* extract; AOS, Alleneoxide synthase; APOX, Ascorbate peroxidase; CAT, Catalase; CHIT, Chitinases; DHAR, Dehydroascorbate reductase; ETI, Effector-Triggered Immunity; GLU, Glucanases; GPOX, Guaiacol peroxidase; GR, glutathione reductase; GST, Glutathione S-transferase; ISR, Induced systemic resistance; JA, Jasmonic acid; LOX, Lipoxygenase; NPR, Non-expressing pathogenesis-related; PAL, Phenylalanine ammonia lyase; PDF, Plant defensin; POD, Peroxidase; PPO, Polyphenol oxidase; PR, Pathogenesis related; PTI, Pathogen triggered immunity; ROS, Reactive oxygen species; SA, Salicylic acid; SAR, Systemic acquired resistance; SEs, Seaweed extracts; SPS, Sulphated polysaccharide; STS, Stilbene synthase; TCDVd, tomato chlorotic dwarf viroid; TMV, Tobacco mosaic virus.

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substances (HS), the hormone containing products (HCP), and amino acid containing products (AACP). The bio-stimulants support agriculture by providing at least one of the following functions; enhance nutrition, impart abiotic stress tolerance and/or improve crop quality traits. Bio-stimulants also regulate plant defence against different pathogens, however, from the regulatory point of view the regulators and stakeholders have kept the bio-stimulation and biocontrol separate [12]. Bio-stimulants produced from various seaweeds help in maintaining good soil health and increase the beneficial microflora [13]. By 2016 the SEs represented 33% (483 million euro) of the total bio-stimulant market and now SEs are estimated to have a value of 894 million Euro by 2022 with extracts from brown seaweeds forming a major group [14]. A number of commercial SEs are available for the improvement of growth and yield of agricultural and horticultural crops [5]. The SEs are reported to improve resistance by predominantly regulating the plant antioxidant pathways in response to different abiotic stresses such as salinity, water deficient and freezing [15–18].

Apart from abiotic stresses, certain biotic agents such as fungi, bacteria and viruses reduce both growth and yield of the plants. Different plants have various defence mechanisms to combat the biotic stresses in response to pathogenic attacks. The plant's innate immune system of has a multi-faceted defence system consisting of pathogen triggered immunity (PTI) and effector-triggered immunity (ETI) against biotrophic, necrotrophic and hemibiotrophic fungal and bacterial pathogens [19]. The PTI and ETI activate local immune responses by activating the systemic acquired resistance (SAR) [20], or induced systemic resistance (ISR). The defence response involve participation of a complex network of signaling molecules such as salicylic acid (SA), jasmonic acid (JA) and ethylene (ET) [21]. Pathogenic fungi causes several diseases in plants such as leaf-spot, rust, wilt, blight, coils, scab, gall, canker, damping-off, root rot, mildew, and die-back. Fungi are responsible for 80% plant diseases, causing major yield loss [22,23]. More than 200 plant pathogenic bacterial species exist in nature [24], and some of them are very harmful, e.g. *Pseudomonas*, *Ralstonia*, *Agrobacterium*, *Xanthomonas*, *Erwinia*, *Xylella*, *Pectobacterium*, and *Dickeya* [25,26]. Plant viruses can be very destructive and cause huge yield damage and sometimes may lead to 100% loss. Approximately, 30 types of viroids have been reported to infect a large number of plants [27]. These biotic stresses are generally controlled by the applications of pesticides, fungicides and anti-microbial chemicals, which eventually enter in the human food chain leading severe toxicity. According to FAO [28], the major pesticide groups (i.e. insecticides, herbicides, fungicides, plant growth regulators and rodenticides) and use of chemicals have been increased at global level from 2.2 million tons in 1990 to 41 million tons in 2017. Therefore, a well-defined strategy should be followed for combating different crop diseases using environmental friendly approaches [24]. The induction of natural defence systems by the applications of SEs can serve as a preferred alternative being environmentally friendly, biodegradable and non-toxic to the flora and fauna [29]. Marine algae serve as a valuable renewable resource of numerous elicitors for inducing varied defence responses. This review discusses the applications of different seaweed constituents and extracts to control plant disease. The composition, mechanism and function of different SEs towards regulating the antioxidative pathways, genes expression and hormones synthesis are also discoursed elaborately (Fig. 1).

2. Effect of different seaweeds constituents as bio-elicitors for developing disease tolerance

The bio-elicitors induce the natural defence system of plants in response to various diseases. The induction of the defence mechanisms of plants can be activated by the elicitors from pathogens or the host itself in order to acquire the SAR [30]. Elicitors have been isolated from bacteria, fungi, oomycetes [31], algae [32], and can be broadly categorized as proteins, peptides, fatty acids, glycoproteins, lipids, oligosaccharides, and polysaccharides [31–33]. Different marine algae are rich source of nutrients and bioactive compounds, which can improve the cellular metabolism, growth and also disease tolerance in plants [6]. In some studies pure forms of polysaccharides (Table 1), whereas, in others crude SEs (Table 2) have been analyzed for their efficacies towards disease management in plants in order to control fungal, bacterial and viral pathogens. The role of different algal polysaccharides such as carrageenans, fucans, laminarans and ulvans is further discussed as defence molecules to protect plants against various diseases in this review.

3. Carrageenans

Carrageenans are linear, partially hydrophilic sulphated galactans composed by alternate units of D-galactose and 3,6-anhydrogalactose

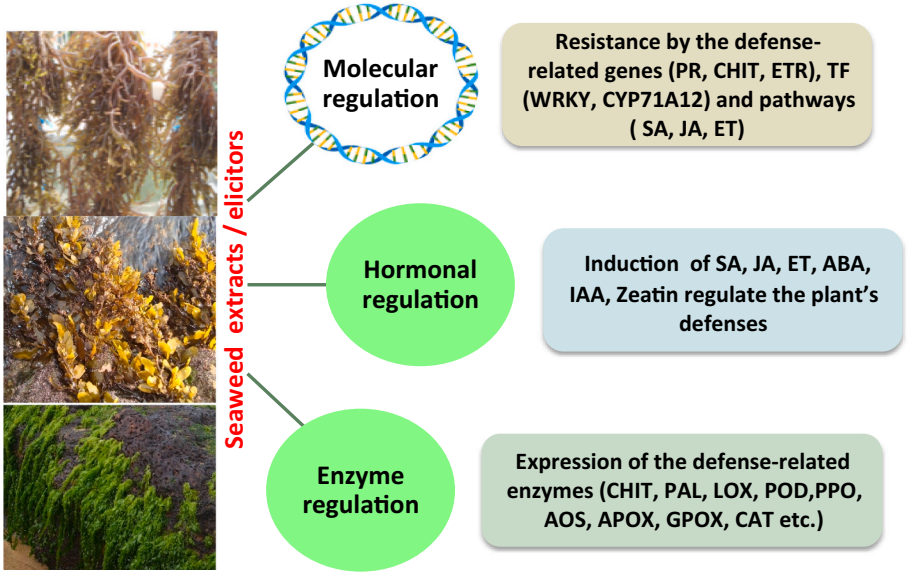

Fig. 1. Mechanism of disease resistance in plants, ABA: Abscisic acid, AOS: alleneoxide synthase, APOX: ascorbate peroxidase, CHIT: chitinases, CYP: cytochrome P450, ET: ethylene, ETR: ethylene receptor, GPOX: guaiacol peroxidase, IAA: indole-3-acetic acid, JA: Jasmonic acid, LOX: Lipoxygenase, PAL: Phenylalanine ammonia lyase, POD: peroxidase, PPO: Polyphenoloxydase, PR: Pathogenesis related, SA: Salicylic acid, TF: Transcription factors.

Table 1
Effect of different algal bio-elicitors on the defence response of different plant spp.

S. no.	Elicitor	Algal species	Casual organisms	Host plant	Application	Response of plants	References
Red algae							
1.	κ, λ, and ι-carrageenans	–	*Trichoplusia ni*	Arabidopsis	Sprayed two times on fully expanded plants at 5 d intervals and after 48 h of second spray infestation was performed	Increased expression of defence-related genes isothiocyanates and nitriles	[46]
2.	κ-carrageenan	*Hypnea musciformis*	TMV	Tobacco	Infiltration in mesophyll cells and after 4–8 d TMV inoculation was performed	Increased expression of defence-related hormones and metabolites. Increased strengthening of cell walls	[45]
3.	κ-carrageenan	*Kappaphycus alvarezii*	*Colletotrichum gloeosporioides* (Penz.) Sacc.	*Capsicum annuum* Linn.	Leaves sprayed once and after 24 h treated with pathogen	Increased expression of defence-related genes and proteins	[101]
4.	κ/β-carrageenan	*Tichocarpus crinitus*	TMV	Tobacco	Leaves inoculated/rubbed 24 h before or after infection	Interfering cell replication	[43]
5.	κ/β-carrageenan	*T. crinitus*	Potato Virus-X	*Datura stramonium*	Leaves sprayed and after 24 h infected with pathogen	Stimulation of lytic processes resulted in the destruction of viral particles	[44]
6.	λ-Carrageenan	–	*Sclerotinia sclerotiorum*	Arabidopsis	Two sprays on fully expanded plants at 5 d intervals and after 48 h of second spray infestation was performed	Increased expression of defence-related genes and enzymes	[40]
7.	λ-Carrageenan	–	TCDVd	Tomato	Sprayed on leaves then after 48 h infestation was performed	Increased expression of defence-related genes and enzymes	[27]
8.	λ-Carrageenan	*Acanthophora spicifera*	*Phytophthora palmivora*	Rubber tree	Leaves sprayed once and after 24 h treated with pathogen	Increased expression of defence-related genes and enzymes	[102]
9.	λ-Carrageenan	–	*Zymoseptoria tritici*	Wheat	Sprayed once then after 5 d infestation was performed	Increased expression of SA- and/or JA-dependent signaling pathways	[103]
10.	Oligo-carrageenans	–	TMV, *Botrytis cinerea* and *Pectobacterium carotovorum*	Tobacco	Leaves sprayed once a week for three times, and after 45 d treated with pathogen	Increased expression of defence-related enzymes	[41]
Brown algae							
11.	β-1,3 Glucan	*Laminaria digitata*	*Erwinia carotovora*	Tobacco	Infiltration of elicitor was done and after 5 d pathogen was applied	Increased expression of defence-related enzymes, SA and PR proteins	[59]
12.	β-1,3 Glucan	*L. digitata*	*B. cinerea*, *Plasmopara viticola*	Grapevine	Leaves incubated with elicitor and after 24 h inoculated with pathogen	Increases expression of defence-related genes and enzymes	[60]
13.	β-1,3 Glucan	*L. digitata*	*P. visticola*	Grapevine	Sprayed with elicitor and after 2 d pathogen was applied	Increased expression of defence-related genes, hormones, callose, phenol depositions, and cell death	[62]
14.	Fucan	*Pelvetia canaliculata*	TMV	Tobacco	Infiltrated	Increased expression of defence-related enzymes, hormones, phytoalexin, scopoletin and PR proteins	[53]
15.	Fucoidan	*Fucus evanescens*	TMV	Tobacco	Leaves infiltrated with elicitor and after 5 d inoculated with TMV	Increased expression of defence-related genes	[54]
16.	Fucoidan	*Lessonia vadosa*	–	Tobacco	Sprayed whole plant	Increased expression of defence-related enzymes	[52]
17.	Galactan	*Schizymenia binderi*	TMV	Tobacco	Sprayed once a week, for 1 month and after 15 d inoculated with TMV	Increased expression of defence-related enzymes and secondary metabolites	[92]
18.	Guluronic acid	*L. trabeculata*	TMV	Tobacco	Sprayed once a week, for 1 month and after 15 d inoculated with TMV	Increased expression of defence-related enzymes and secondary metabolites	[92]
19.	Laminarin	*L. digitata*	TMV	Tobacco and Arabidopsis	Leaves infiltrated with elicitors and after 3 and 8 d inoculated with TMV	Induced expression of PR1 genes and PR proteins	[56]
20.	Laminarin	*L. digitata*	TMV	Tobacco	Leaves infiltrated and after 8 d inoculated with TMV	Increased the expression of genes encoding *O*-methyltransferases of the phenylpropanoid pathway	[104]
21.	Laminarin	*L. digitata*	*Blumeria graminis*	Wheat	Sprayed and after 2 d treated with pathogen	Increased expression of defence-related enzymes	[105]
22.	Laminarin	*L. digitata*	*B. cinerea, Sphaerotheca macularis* and *Mycosphaerella fragariae*	Strawberry	Sprayed during blooming and twice before harvest	Reduced infection by 50–70%	[106]
23.	Laminarin	*L. digitata*	*P. viticola*	Grapevine	Leaves sprayed and after 2 d infected with pathogen	Increased expression of defence-related genes	[107]
24.	Laminarin	*L. digitata*	*P. viticola*	Grapevine		Increased defence response	[108]

(*continued on next page*)

Table 1 (*continued*)

S. no.	Elicitor	Algal species	Casual organisms	Host plant	Application	Response of plants	References
					Sprayed and after 2 d inoculated with pathogen		
25.	Laminarin	*L. digitata*	*P. viticola*	Grapevine	Leaf disc treated and after 48 h inoculated with pathogen	Increased expression of metabolic pathway	[109]
26.	Laminarin	*L. digitata*	*Stethynium empoasca*	Tea plant	Leaves were sprayed and then treated with leafhopper	Increased expression of defence-related genes, enzymes and secondary metabolites	[110]
27.	Mannuronic acid	*L. vadosa*	TMV	Tobacco	Sprayed once a week, for 1 month and after 15 d inoculated with TMV	Increased expression of defence-related enzymes and secondary metabolites	[92]
28.	Oligo-sulphated-galactan	*S. binderi*	TMV	Tobacco	Sprayed with elicitor once per week for 2 weeks and then infected with TMV in a single leaf	Increased expression of defence-related enzymes	[47]
Green algae							
29.	Glucuronan and Ulvan	*Ulva lactuca*	*Fusarium oxysporum*	Tomato	Internodes infiltrated and after 24 h treated with pathogen	Increased expression of defence-related enzymes	[30]
30.	Glucuronan and oligoglucuronans	*U. lactuca*	*Penicillium expansum* and *B. cinerea*	Apple fruit	Treated at wounded zone and after 24 h inoculated with pathogen	Increased expression of defence-related enzymes, lignins and phenolics	[111]
31.	Ulvan	*U. lactuca*	*A. brassicicola* and *Colletotrichum higginsianum*	Arabidopsis	Sprayed once then after 3 d infestation was performed	Increased resistance against pathogen	[112]
32.	Ulvan	*U. lactuca*	*Verticillium dahliae*	Olive	Twigs soaked in elicitor and after 24 h soaked in pathogen solution	Stimulated phenolic metabolism	[75]
33.	Ulvan	*U. lactuca*	*F. oxysporum f.* sp. *phaseoli* (*Fop*)	Common bean	Plants sprayed thrice at 12, 15 and 18 d after seeds sowing on pre-infested soil	Reduced fungal colonization	[113]
34.	Ulvan	*U. fasciata*	*C. lindemuthianum*	Bean	Sprayed twice at 2 d intervals and then after 2 d treated with pathogen	Reduced anthracnose severity	[50]
35.	Ulvan	*U. fasciata*	*B. graminis*	Rice, wheat and barley	Sprayed twice and then after 24 h treated with pathogen	Increased chitin-elicited oxidative burst	[72]
36.	Ulvan	*U. fasciata*	*Uromyces appendiculatus*	Bean	Sprayed once or twice with elicitor and then after 3 d and 6 d treated with pathogen	–	[69]
37.	Ulvan	*U. fasciata*	*C. lindemuthianum*	Bean	Sprayed twice at 3 d and 6 d and after inoculated with pathogen	Increased expression of defence-related enzymes	[70]
38.	Ulvan	*U. fasciata*	*A. brassicicola*	Arabidopsis	Sprayed once then after 3 d treated with pathogen	Increased expression of NADPH oxidase activity, hydrogen peroxide	[114]
39.	Ulvan and Oligoulvans	*U. lactuca*	*B. cinerea and P. expansum*	Apple	Treated at wounded zone and after 12 h inoculated with pathogen	Increased expression of defence-related enzymes and metabolites	[74]
40.	Ulvan	*U. armoricana*	*C. gloeosporioides*	Papaya fruit	Treated at wounded zone and after 2 h inoculated with pathogen	Increased expression of defence-related enzymes	[115]
41.	Ulvan	*Ulva* sp.	–	Barrel clover	Sprayed either once at 3 d or twice at 3 d and 6 d before inoculation with pathogen	Increased expression of defence-related hormones	[116]

PR: pathogenesis related, SA: salicylic acid, TCDVd: tomato chlorotic dwarf viroid, TMV: tobacco mosaic virus.

joined by α-1,3 and β-1,4-glycosidic linkage [34]. These polysaccharides have six basic types of carrageenans viz., iota (ι), kappa (κ), lambda (λ), mu (μ), nu (ν), and theta (θ) [35]. The κ, ι and λ-carrageenans dimers have one, two and three sulphated groups, respectively, possessing 20%, 33% and 41% sulphate content, respectively [36]. The κ, ι and λ-carrageenans have been reported as elicitors to control disease in a few crops. Carrageenan ratios, differ according to the algal species, and in some red algae carrageenans are found to be >40%, by dry weight. The *Kappaphycus alvarezii* and *Hypnea musciformis* are sources of κ-carrageenan, whilst *Eucheuma denticulatum* and *Gigartina pistillata* have a greater preponderance of ι- in particular and some λ-carrageenan, respectively [36,37].

Applications of carrageenans and their oligosaccharides have been shown to activate defence system in some plants and animals and their efficacy may depend on the level of sulphation [26]. The λ-carrageenans have the highest levels of sulfphation followed by κ and ι carrageenans. The use of λ-carrageenan has been shown to have benefits for the management of disease control caused by different microorganisms [38]. λ-Carrageenan was found to be active against *Phytophthora parasitica* in tobacco cells and its application led increased expression of defence-related genes encoding for sesquiterpene cyclase, chitinase and proteinase inhibitor. The expression of lipoxygenase (*LOX*) and ACC oxidase (*ACO*), whose gene expressions lead to JA and ET biosynthesis, were highly induced, and the amount of cellular SA was increased in presence of the polysaccharide elicitor [39]. An increase in activity of oxalate oxidase and the expression of JA-signaling associated genes, e.g., alleneoxide synthase (*AOS*), plant defensin (*PDF1.2*) and pathogenesis related (*PR-3*) were observed with the application of highly sulphated λ-carrageenan (35% sulphation) in *Arabidopsis thaliana*. The λ-carrageenan treatment produced resistance against *Sclerotinia sclerotiorum* infection, whereas the less sulphated ι-carrageenan (30% sulphation) exhibited enhanced susceptibility [40].

Table 2
Effect of different seaweed extracts on the disease tolerance in different plant spp.

S. no.	Algal species (extract/ commercial name)	Host plant	Disease	Organism	Application	Response of plants	References
Red algae							
1.	*Acanthophora spicifera* (SWC)	Rice	Fungal blast	*Pyricularia oryzae*	Sprayed one time	Increased expression of defence-related enzymes	[98]
2.	*A. spicifera*	Tomato and sweet pepper	Early blight, bacterial spot	*Alternaria solani* and *Xanthomonas campestris*	Sprayed 4 times at 2 w interval and after 6 h of first spray treated with pathogen	Increased expression of defence-related genes, hormones and enzymes	[117]
3.	*Corallina mediterranea* and *Corallina officinalis*	Tomato	Root-knot	*Meloidogyne incognita*	Soil drenched twice after inoculation	Increased expression of defence-related genes and enzymes	[118]
4.	*Gelidium serrulatum*	Tomato	Early blight and bacterial spot/ blight	*A. solani and X. campestris*	Sprayed twice at 15 d interval and after 6 h treated with pathogens	Increased expression of defence-related enzymes and genes	[119]
5.	*Gracilaria confervoides*	Cucumber	–	*Rhizoctonia solani, Fusarium solani* and *Macrophomina phaseolina*	7 d pre-infested soil was amended with dry algae powder and after that seeds were sown	–	[120]
6.	*Kappaphycus alvarezii* (K-sap)	Tomato	Charcoal rot	*M. phaseolina*	Sprayed one time	Increased expression of defence-related genes and hormones	[85]
7.	*Kappaphycus alvarezii* (BFIICaB®)	Tomato	–	*F. oxysporum*	Spayed twice at 5 d interval after inoculation with pathogen	Increased expression of defence-related enzymes	[121]
8.	*Melanothamnus afaqhusainii*	Eggplant	Root rot and root knot	*M. phaseolina, F. solani* and *F. oxysporum*	Dry powder application		[122]
9.	*Melanothamnus afaqhusainii*	Watermelon	Root rot and root knot	*M. phaseolina, R. solani* and *F. oxysporum*	Dry powder application		
10.	*Solieria robusta*	Soybean	Root rot	*F. solani*	Dry powder application	–	[123]
11.	BKPSGII® (*K. alvarezii* X *Sargassum* sp.)[a]	Tomato	–	*F. oxysporum*	Spayed twice at 5 d interval after inoculation with pathogen	Increased expression of defence-related enzymes	[121]
Brown algae							
12.	*Ascophyllum nodosum* (Maxicrop)	Strawberry	Red spider infestation	*Tetranychus urticae*	Sprayed seven times twice-weekly	Reduced red spider mite incidence	[124]
13.	*A. nodosum* (ANE)	Strawberry	Powdery mildew	*Podosphaera aphanis*	Sprayed twice 1st and 5th d	Increased expression of defence-related enzymes and secondary metabolites	[95]
14.	*A. nodosum* (SW)	Carrot	Black rot and botrytis blight	*A. radicina* and *Botrytis cinerea*	Sprayed with SW then inoculated 6 h later with the pathogens, again sprayed with SW at 10 and 20 d after inoculation	Increased expression of defence-related genes, proteins and enzymes	[76]
15.	*A. nodosum* (Stimplex™)	Cucumber	Alternaria blight, gummy stem blight, fusarium rot, stem rot and botrytis blight	*A. cucumerinum, Didymella applanata, F. oxysporum* and *B. cinerea*	Sprayed or drenched twice at 10 d interval and after 6 h treated with pathogens	Increased expression of defence-related genes, enzymes and secondary metabolites	[77]
16.	*A. nodosum* (Marmarine®)	Cucumber	Damping-off	*Phytophthora melonis*	Sprayed or drenched twice at 5 d intervals	Increased expression of defence-related genes and enzymes	[80]
17.	*A. nodosum* (ANE)	Arabidopsis	Bacterial speck and stem rot	*Pseudomonas Syringae* and *Sclerotinia Sclerotiorum*	Irrigated and sprayed	Increased expression of JA-related genes	[79]
18.	*A. nodosum* (Stella Maris®)	Arabidopsis	Bacterial disease	*P. syringae* and *X. campestris*	Seedlings were treated one time	Increased expression of defence-related genes	[83]
19.	*A. nodosum* (ANE)	Tomato	Alternaria blight and bacterial leaf spot	*A. solani* and *X. campestris*	Sprayed or root-drenched at 15 d intervals in the field	Increased expression of JA/ET pathway genes, defence-related enzymes and phenols	[81]
20.	*A. nodosum* (Dalgin®)	Tomato	Damping-off	*P. capsici*	Sprayed one time	Increased expression of genes and defence-related enzymes	[94]
21.	*A. nodosum* (Stimplex®)	Tomato and sweet pepper	Bacterial spot and early blight	*X. campestris* and *A. solani*	Sprayed 3 times at 10-d intervals	Increased expression of defence-related gene and enzymes	[82]
22.	*A. nodosum* (AMPEP) (Acadian Seaplants)	*Kappaphycus*	*Neosiphonia apiculate* endophyte infection	*Neosiphonia apiculata*	Dipped for 45 min in AMPEP	Increased expression of H_2O_2	[125]
23.	*A. nodosum* (AMPEP)	*Kappaphycus*	Ice-ice, goose bumps	*Polysiphonia subtilissima*	*Kappaphycus* treated for a period of 1 h and then incubated for growth	Activation of natural defence against pathogens	[126,127]

(*continued on next page*)

Table 2 (*continued*)

S. no.	Algal species (extract/ commercial name)	Host plant	Disease	Organism	Application	Response of plants	References
24.	*A. nodosum* (AMPEP)	*Kappaphycus*	Epiphyte infection	*Neosiphonia* sp.	Pre-infected seedling was soaked for 30 min	Reduced infection	[128]
25.	*A. nodosum* (Acadian®)	Grapevine	Bunch rot	*A. cinerea*	Sprayed six times between the pea-size fruit stage and harvest	Increased expression of defence-related genes	[84]
26.	*A. nodosum* and *Ecklonia maxima* (Kelpak®, OSMO®)	Tomato	Root-knot	*M. chitwoodi* and *M. hapla*	Root drenched for 9 times at 5 d intervals and after 2 w of 1st treatment inoculated with pathogen	Reduced hatching, and sensory perception	[129]
27.	*A. nodosum* (LSE)	Wheat	Fusarium head blight	*F. graminearum*	Seedlings were drenched and after 48 h sprayed with pathogen	Increased expression of defence-related gene and enzymes	[130]
28.	*A. nodosum* (Dalgin Active®)	Wheat and durum wheat	*Septoria tritici* blotch	*Zymoseptoria tritici*	Sprayed one time and after 48 h inoculated with pathogen	Increased expression of defence-related PR protein, antioxidant metabolism, phenylpropanoid, and octadecanoid-based pathways	[131]
29.	*A. nodosum* (Maxicrop Original®)	Arabidopsis	Root-knot	*M. javanica*	Applied in culture medium and after 10 d of germination inoculated with nematode	Decreased number of females nematodes	[132]
30.	*Cystoseira myriophylloides, Laminaria digitata,* and *Fucus spiralis* (used separately)	Tomato	Wilting and crown gall	*Verticillium dahlia* and *Agrobacterium tumefaciens*	Seed imbibition and seedlings sprayed two times at 3 and 7 d and after that inoculated with pathogen	Increased expression of defence-related enzymes	[99]
31.	*C. myriophylloides*, *L. digitata* and *F. spiralis* (SE) (used separately)	Tobacco	Wild fire	*P. syringae*	Seed soaked	Increased expression of defence-related enzymes	[100]
32.	*Durvillaea potatorum* and *A. nodosum* (Seasol®)	Broccoli	Clubroot	*Plasmodiophora brassicae*	Soil drenched and after 28 d infected with pathogen	Decreased the number of plasmodia on root hairs	[133]
33.	*Durvillaea potatorum* and *A. nodosum* (Seasol®)	Arabidopsis	–	*P. cinnamomi*	Root drenched and after 7 d inoculated with pathogen	Increased expression of defence-related genes and ROS-based signaling pathways	[134]
34.	*Ecklonia maxima* (Kelpak®)	Tomato	Root-knot nematodes infestation	*M. incognita*	Sprayed or soil drenched	–	[135]
35.	*Ecklonia maxima* (Kelpak®)	Pepper	*Verticillium* Wilt	*V. dahliae*	Soil drenched and after 3 d inoculated with pathogen	–	[136]
36.	*L. digitata*	Grapevine	Gray mould and downy mildew	*B. cinerea* and *P. viticola*	In cell suspensions and sprayed on both leaf surfaces	Increased expression of defence-related genes	[59]
37.	*Padina pavonia* (SWC)	Rice	Fungal blast	*Pyricularia oryzae*	Sprayed one time	Increased expression of defence-related enzymes	[98]
38.	*Padina gymnospora* and *Sargassum liebmannii* (used separately)	Tomato	Early blight	*A. solani*	Sprayed one time	Increased expression of defence-related enzymes and genes	[93]
39.	*Sargassum filipendula*	Tomato	Early blight and bacterial spot/ blight	*A. solani* and *X. campestris*	Sprayed twice at 15 d interval and after 6 h treated with pathogens	Increased expression of defence-related enzymes and genes	[122]
40.	*S. fusiforme* (AP)	Tomato	Powdery mildew, late blight and gray mould	*Oidium* spp., *P. infestans* and *B. cinerea*	Sprayed one time	Induced hypersensitive cell death and $O_2^{\bullet-}$ production	[137]
41.	*S. polycystum*	Rubber tree	Leaf fall	*P. palmivora*	Seedlings were sprayed one time	Increased expression of defence-related enzymes, hormones and phytoalexin scopoletin	[90]
42.	*S. tenerrimum*	Cotton	Red cotton pest	*Dysdercus cingulatus*	Seeds were soaked	Insecticidal activity might be due to cytotoxic oxysterol and hydroper 24 cholesterol	[138]
43.	*S. tenerrimum* (S-extract)	Tomato	Charcoal rot	*M. phaseolina*	Sprayed twice at vegetative and reproductive stage	Increased expression of defence-related enzymes and hormones	[91]
44.	*S. wightii* (Dravya)	Cotton	Bacterial blight	*X. campestris*	Seed soaked followed by 3 foliar sprays at the intervals of 10 d	Increased defence-related enzymes	[97]
45.	*S. tenerrimum, S. wightii* and *S. swartzii*	Sunflower	Root rotting	*M. phaseolina* and *F. solani*	Seeds showing on amendment soil	–	[139]
46.	*S. vulgare*	Potato	Pythium leak	*Pythium aphanidermatum*	Wounded tuber treated and after 2 h inoculated with pathogen	–	[140]
47.	*S. vulgare*	Potato	Fusarium dry rot	*F. oxysporum*		–	[141]

(*continued on next page*)

Table 2 (*continued*)

S. no.	Algal species (extract/ commercial name)	Host plant	Disease	Organism	Application	Response of plants	References
					Wounded tuber treated and after 2 h inoculated with pathogen		
48.	*S. vulgare*	Tomato and sweet pepper	Early blight, bacterial spot	*A. solani* and *X. campestris*	Sprayed 4 times at 2 w interval and after 6 h of first spray treated with pathogen	Increased expression of defence-related genes, hormones and enzymes	[117]
49.	*Spatoglossum variabile*	Eggplant and watermelon	Root rotting and Root knot	*M. phaseolina, F. solani, F. oxysporum* and nematodes	Dried powder application	Significant suppressive effect on root rotting fungi *F. solani*, *M. phaseolina* and root knot	[122]
50.	*Stokeyia indica*	Eggplant and watermelon	Root rotting and Root knot	*M. phaseolina, R. solani, F. oxysporum* and nematodes	Dried powder application	–	[122]
51.	*Turbinaria conoides*	–	Root rot	*F. oxysporum*	Poisoned food technique	–	[142]
Green algae							
52.	*Caulerpa sertularioides* and *Ulva lactuca* (used separately)	Tomato	Early blight	*A. solani*	Sprayed one time and after 24 h treated with pathogen	Increased expression of defence-related enzymes and genes	[93]
53.	*U. armoricana*	Common bean, grapevine and cucumber	Powdery mildew	*Erysiphe polygoni, E. necator* and *Sphareotheca fuliginea*	Sprayed either once at 3 d or twice at 3 and 6 d and after that inoculated with pathogen	Increased expression of a reporter gene regulated by a defence-gene promoter	[86]
54.	*U. fasciata*	Tomato	Root-knot	*M. incognita*	Soil drenched twice directly after inoculation	Increased expression of defence-related genes and enzymes	[118]
55.	*U. lactuca*	Banana	Root knot	*Meloidogyne* spp.	Dried powder added to the soil	–	[143]
56.	*U. lactuca*	Tomato	Early blight and bacterial spot/ blight	*A. solani* and *X. campestris*	Sprayed twice at 15 d interval and after 6 h treated with pathogens	Increased expression of defence-related enzymes and genes	[119]
57.	*U. lactuca* (SWC)	Rice	Fungal blast	*P. oryzae*	Sprayed one time	Increased expression of defence-related enzymes	[98]
58.	*U. lactuca*	Apple	Blue and gray mould	*Penicillium expansum* and *B. cinerea*	–	Increased expression of antioxidant enzyme and phenylpropanoid metabolism	[66]
59	*Ulva* spp. (UE)	Barrel clover	Anthracnose	*Colletotrichum trifolii*	Leaves were infiltrated or sprayed	Increased expression of defence-related genes and phytoalexins, PR proteins and cell wall proteins	[73]

SWC - seaweed concentrate, ANE - *Ascophyllum nodosum* extract, SW - Seaweed *Ascophyllum nodosum*, AMPEP - *Ascophyllum* marine plant extract Powder, SE - seaweed extracts, AP - algal product, UE - *Ulva* extract.

[a] Combined treatment of red and brown algae.

The effects of κ-, ι- and λ-oligo-carrageenans against tobacco mosaic virus (TMV), *Botrytis cinerea* and *Pectobacterium carotovorum* were demonstrated by Vera et al. [41]. In this study, all of the oligo-carrageenans induced protection against *P. carotovorum* with similar efficiencies, whereas ι- and λ-oligo-carrageenans provided protection against *B. cinerea* and only λ-oligo-carrageenan provided protection against TMV. The oligo-carrageenans application induced phenylalanine ammonia lyase (PAL) activity and accumulation of phenolics. PAL helps in the synthesis of phenylpropanoid, a precursor of different phenolic compounds such as, flavonoids, isoflavanoids, anthocyanins, plant hormones, phytoalexins, and lignins leading to plant defence [42]. Similarly, κ-, ι- and λ carrageenans were tested on tomato plants against the tomato chlorotic dwarf viroid (TCDVd) [26]. Tomato plants treated with λ- carrageenan showed a higher resistance against TCDVd by controlling the viroid replication as well as by up-regulation of JA-mediated genes expression of LOX, AOS and pathogenesis-related proteins [26]. The application of κ/β-carrageenan from *Tichocarpus crinitus* reduced TMV levels on tobacco leaves [43]. The κ/β- carrageenan application on *Datura stramonium* displayed an increased size of nucleoli, mitochondrial counts and membranes of rough endoplasmic reticulum. They have also stimulated several lytic processes in *D. stramonium*, preventing the intracellular accumulation and translocation of Potato Virus X particles [44].

The sulphated polysaccharide 4 (SPS4, containing 98% κ-carrageenan) from the red alga *H. musciformis*, provided anti-viral activity against TMV by activation of SA-dependent pathogenesis-related genes *PR-1a*, *PR-2* and *PR-5* and JA-dependent *PR-3* and *Def1.2* (member of PR12 genes group and encoding defensin protein) [45]. The κ-carrageenan was also found to act as an elicitor of defence responses in *A. thaliana* against the insect *Trichoplusia ni*, whereas, no significant effect was observed with λ- and ι-carrageenans [46]. Thus, λ-carrageenans can be used a potential defence-primer or priming agent, possibly due to its high sulphate content compared to other carrageenans. The oligo-sulphated galactans poly-GA from *Schyzimenia binderi*, structurally related to lambda oligo-carrageenan, elicited the reduced number of necrotic lesions caused by TMV and provided long term tolerance to protection. The decrease in TMV-capsid protein gene expression in the distant leaves reflected the systemic protection against the TMV. The treated plants also elicited higher activity of PAL and increased accumulation of conjugated phenylpropanoid compounds. All together this study revealed that a systematic resistance was acquired by using the Poly-GA from *S. binderi* against the TMV [47].

4. Fucans

Fucans form the major constituent of brown seaweed cell walls, comprising 5–20% of the dry weight [48,49]. Fucans are structurally ramified heterogeneous sulphated polysaccharides composed of a

central backbone of fucose. Structural differences exist in fucans in different algal species and also within the same species. Fucans have been classified into two groups [50], viz., the first group includes the fucans from *Saccharina latissima* (formerly *Laminaria saccharina*), *Laminaria digitata*, *Analipus japonicus*, *Cladosiphon okamuranus*, and *Chorda filum* having central chains composed of (1 → 3)- linked α-L-fucopyranose residues. The second group of fucans isolated from *Ascophyllum nodosum* and Fucus species possessed central chains comprising repeating (1 → 3) and (1 → 4)-linked α-L-fucopyranose residues [51]. These fucans are reported to function as elicitors having different biological properties such as anti-viral, anti-inflammatory and anticoagulant. However, very limited studies have been carried out using the application of pure fucans on disease tolerance in plants, as compared to other polysaccharides. The native and the partially depolymerized fraction of fucoidan extracted from *Lessonia vadosa* imparted significant activation of PAL, LOX and glutathione S-transferase (GST) defence enzymes in tobacco plants [52]. The oligoflucan from the *Pelvetia canaliculata* induced alkalinization and oxidative burst in the culture medium of tobacco suspension cells followed by induction of PAL and LOX activities. Interestingly, the infiltration of the same oligoflucan in tobacco leaves caused accumulation of SA, phytoalexin scopoletin and PR proteins (PR-1, PR-2, PR-3 and PR-5), indicated the potential role towards eliciting the tobacco defence signaling pathway. Its application strongly reduced the number and size of lesions induced by TMV, thus suggest its potential role in imparting local resistance and SAR against TMV [53]. The application of fucoidan from *Fucus evanescens* in combination with virus particles on tobacco plant revealed reduced necrotic lesions and more agglutination of virus particles as compared to leaves inoculated with virus alone [54].

5. Laminarans

The laminarin polysaccharides are found in brown algae and is a linear homopolysaccharide with linkages β (1 → 3): β(1 → 6) in a ratio of 3:1. Three simple ramifications of β-glucose at C-6 position makes for an average polymerization degree of 25 glucose units represented by laminaran [55,56]. Structural analyses of laminarin demonstrated that the chain length and the presence of sulphate residues determined its elicitation activity [57]. Laminarins are found in the brown algae as *Laminaria hyperborea* and L. *digitata* and to a lesser extent in *Fucus serratus* and *F. vesiculosus* [58]. Stimulation of defence response by laminarins were studied in cell suspension cultures of tobacco [59], grapevine [60] and rice [61]. Activation of protein kinase, Ca^{2+} influx, oxidative burst, alkalinization of extracellular media, increase in chitinase and β-1, 3-glucanase activities and phytoalexins production were observed by the applications of laminarin. The application of laminarin on tobacco, elicited phytoalexin accumulation and expression of PR-proteins when treated with *Erwinia carotovora* [59]. Similarly, the application of laminarin induced PR-protein expression on the treatment of *B. cinerea* and *Plasmopara viticola* [60].

The β-1, 3-glucan laminarin from the brown algae L. *digitata* was found as an effective elicitor in reducing the disease response caused by *B. cinerea* and *P. viticola* by more than 50% in grape plants. The application of laminarin to grape plants revealed higher expression of different genes such as *LOX*, *GST*, *PAL*, stilbene synthase 1 (*STS1*), polygalacturonase-inhibiting protein (*PGIP*) and chitinases (*CHIT1b*, *CHIT3*, *CHIT4c*) [60]. Ménard et al. observed that β-1, 3-glucan sulphate induced SA-dependent signaling in *Nicotiana tabacum* and *A. thaliana* [56]. In *N. tabacum* an oxidative burst by laminarin sulphate PS3 was Ca^{2+} dependent but partially kinase independent, whereas the laminarin induced strictly kinase-dependent oxidative burst. Interestingly, laminarin induced the expression of ethylene- dependent protein, while PS3 activated the expression of SA-dependent proteins. The sulphated laminarin also induced resistance in grapevine cultivar (*Vitis vinifera*) against downy mildew caused by *P. viticola.* This resistance in grapevine was associated with H_2O_2 production at the infection sites, upregulation of defence-related genes, depositions of callose and phenol, and hypersensitive response-like cell death [62].

6. Ulvans

Ulvans are complex heteropolysaccharides which contain rhamnose (16.8–45.0%, p/p), xylose (2.1–12.0%), glucose (0.5–6.4%), uronic acid (6.5–19.0%), iduronic acid (1.1–9.1%) and sulphate (16.0–23.2%). Mannose and galactose also have been found in ulvans from some *Ulva* spp. [63]. These sugars are structurally grouped by two main repeating disaccharides, which are: the ulvabiuronic acid type A (β-DGlcA (1 → 4) α-L-Rha 3S → 1) and type B (α-L-IdoA (1 → 4) α-L-Rha 3S → 1), which serve as elicitors in controlling the disease tolerance in the plants [64,65]. Ulvan was extracted from *Ulva fasciata* and oligo-ulvans were derived by depolymerization of cell wall polysaccharides from other Ulva species, such as *U. armoricana*, *U. rigida*, *U. lactuca*, *U. compressa* and *U. intestinalis* [66,67]. The application of ulvans for disease tolerance in different plants has been reported by many researchers (Table 1). Treatment of plants with ulvan has shown the tolerance in the common bean plants against *Uromyces appendiculatus* [68,69]. The sulphated polysaccharides from the *U. fasciata* reduced the anthracnose (caused by *Colletotrichum lindemuthianum*) severity in bean plants [50,70]. The ulvan from *U. fasciata* also provided disease resistance against Glomerella leaf spot (*Colletotrichum gloeosporioides*) on apple [71], and powdery mildew (*Blumeria graminis*) on wheat and barley [72]. The prior application of Ulva extract on *Medicago truncatula* plants reported biosynthesis of phytoalexins and PR protein after the treatment of *Colletotrichum trifolii* spores [73]. The application of Ulvan from *U. lactuca* to tomato [29], apple [74], and olive plants [75] provided tolerance to different fungal diseases by increasing different enzymes activities such as PAL, peroxidase (POD) and polyphenol oxidase (PPO). The *U. lactuca* bio-elicitors helped in reducing the impacts of infections in tomato plants caused by *Fusarium oxysporum* in an SA-dependent manner. It was quite interesting to see that the two polysaccharides, i. e. the glucuronan (un-sulphated homopolymer) and the ulvan (sulphated heteropolymer) produced differential responses in the accumulation of SA. The glucuronan had no significant elicitor effect, whereas the ulvan induced higher elicitor activity [29]. Different polysaccharides like guluronic acid (Poly-Gu), mannuronic acid (Poly-Ma) and sulphated galactan (Poly-Ga) from brown and red algae showed differential responses against TMV and with reduced number of lesions (9, 22 and 74%, respectively) in tobacco by varied activities of different stress-related antioxidative enzymes, e.g. APOX (ascorbate peroxidase), DHAR (dehydroascorbate reductase), GR (glutathione reductase), PAL and GST [92].

7. Effect of different crude seaweed extracts on the disease tolerance

In addition to the role of pure constituents derived from different seaweeds, as discussed earlier in this review, the role of crude SEs from different algae for disease management of plants have also been studied (Table 2). The proposed mechanisms of plant disease tolerance attributed to the applications of various SEs involves, up-regulation of various defence-related genes, plant hormones and defence enzymes, and these components interact and cross-talk to form a complex network facilitating disease tolerance in plants. Detailed transcriptomic and microarray analyses revealed the differential regulation of network of genes and transcription factors orchestrating the plant defence signaling pathway. The application of selected SEs (from a variety of brown, red and green algae) enhanced transcript expression of defence-related genes of various pathways such as: antioxidative (*PPO, LOX*), antimicrobial (*β-1, 3-glucanase* and *PPO*), pathogenesis-related (*PRs*), SA-related (*PAL*) and JA-related synthesis, thereby improving plant stress tolerance (Fig. 2). An application of *A. nodosum* extract (SW) to carrot showed a higher expression of *PR-1*, *PR-5*, *chitinase*, lipid transfer

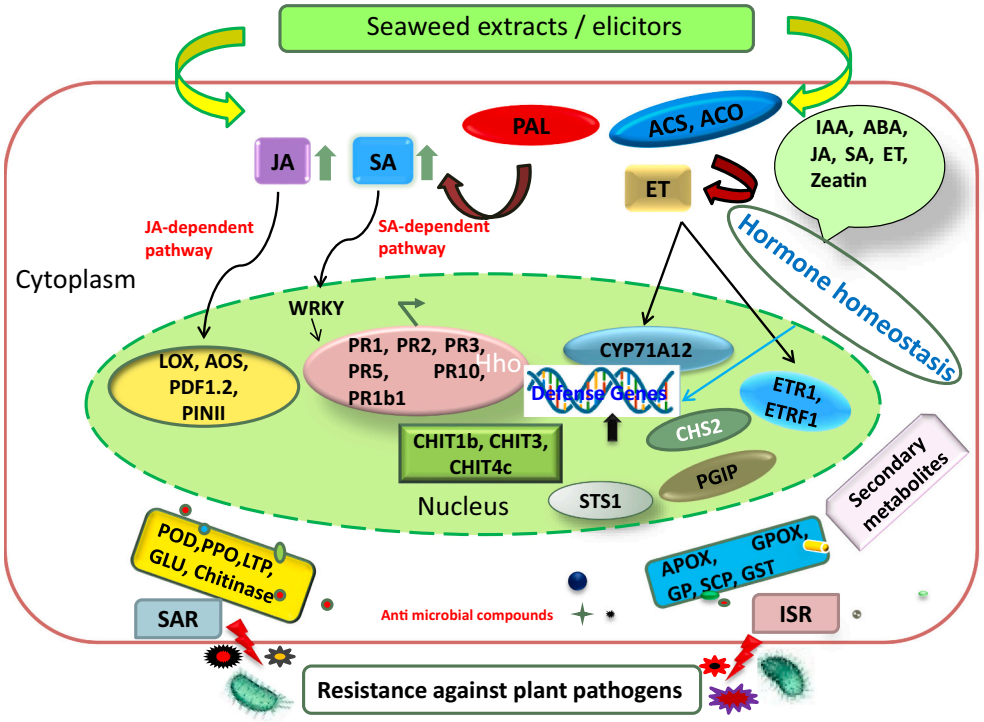

Fig. 2. Molecular and biochemical mechanism of disease tolerance using the algal extract, ABA: Abscisic acid, ACO: 1-aminocyclopropane-1-carboxylate oxidase, ACS: Acetyl-coenzyme A synthetase, AOS: alleneoxide synthase, APOX: ascorbate peroxidase, CHIT: chitinases, CYP: cytochrome P450, ET: ethylene, ETR: ethylene receptor, GLU: glucanases, GP: glutathione peroxidase, GPOX: guaiacol peroxidase, GST: glutathione S-transferase, IAA: indole-3-acetic acid, ISR: induced systematic resistance, JA: Jasmonic acid, LOX: Lipoxygenase, LTP: *lipid transfer protein*, PAL: Phenylalanine ammonia lyase, PDF1.2: plant defensin, PGIP: polygalacturonase-inhibiting protein, PINII: proteinase inhibitor II, POD: peroxidase, PPO: Polyphenoloxydase, PR: Pathogenesis related, SA: Salicylic acid, SAR: Systemic acquired resistance, STS: *stilbenesynthase1*, SCP: phytoalexin scopoletin.

protein (*LTP*), *PAL*, chalcone synthase and non-expressing pathogenesis-related protein (*NPR-1*) genes [76]. The same authors also observed the higher expression of *chitinase*, *LOX*, *POD* and *PAL* genes in cucumber [77]. The hydrolytic activities of chitinases and glucanases (GLU) on pathogen cell wall constituents like, chitin and glucan, respectively, help in releasing oligosaccharides, which act as elicitors to sustain the induction levels of defence reactions [78]. The application of *A. nodosum* extract (ANE) was reported to provide the treated plants with resistance against *Pseudomonas syringae* by increasing the expression of the JA-dependent defence gene *PDF1.2* [79]. Plants treated with 0.5% Marmarine, an *A. nodosum* derived extract (IFTC™, Amman, Jordan) showed a significant reduction in *Phytophthora melonis* infection and enhanced the activities of various defence-related genes in cucumber, e. g. pathogen-induced 4, *LOX*, *PAL* and galactinol synthase [80]. The ANE sprayed on to tomatoes and sweet peppers elicited a significantly higher expression of the *PIN11* gene (i.e., a marker in the JA/ISR defence pathway) and *ETR*-1 gene (i.e., marker gene for the ethylene/ISR defence pathway), which are involved in JA or ET-signaling. The expression of *PR-1* did not increase during the treatments of *Xanthomonas campestris* pv. *vesicatoria* and *Alternaria solani* [81,82]. Another ANE product, i.e. Stella Maris® (Acadian) also enhanced the expression of transcription factors, *WRKY30* and *CYP71A12*, and *PR-1*genes. *WRKY30* is known to respond to H_2O_2 production, and is involved with SA and JA immunity-signaling pathway genes and cytochrome P450 is responsible for the production of phytoalexin (camalexin) having antimicrobial functions [83]. The ANE (Acadian®)-treated vines reported higher expression of the *VvPR-1* and *VvCaS2* genes (for the synthesis of the β-1, 3-glucan callose) [84]. Application of a *K. alvarezii* extract (K-sap) promoted up-regulation of *PR-1b1*, *PR-3* and *PR-5* genes in tomato plants during *Macrophomina* stress [85]. Administration of a crude extract of *U. armoricana* comprising with ulvans having uronic acid and sulphated rhamnose reduced powdery mildew diseases in common bean, grapevine and cucumber as caused by *Erysiphe polygoni*, *E. necator* and *Sphaerotheca fuliginea* pathogens, respectively [86]. An *Ulva* extract up-regulated a broad range of defence-related genes involved in the synthesis of phytoalexins, pathogenesis-related protein, cell wall protein and primary metabolism in *M. trancatula* as evidenced by DNA microarray analysis [73].

Phytohormones SA, JA and ET are synergistically and/or antagonistically regulated in response to different stresses, and are an important component of the plant's stress signaling crosstalk [20]. SA, JA, and ET may act individually, or in combination, towards inducing resistance in plants against various pathogens [87]. The SA-dependent defence system showed activation of the SAR and induced PR proteins [79], whereas, the SA-independent activated the ISR, which was triggered by nonpathogenic microbes and was largely associated with JA and ET-dependent responses [88,89]. In addition to the stress-related hormones, the growth and development-related phytohormones such as abscisic acid (ABA), auxins, cytokinins, brassinosteroids, gibberellins were shown to be involved with regulating plant defence, either alone or together with the primary defence hormones [85,20]. The ANE showed JA-dependent resistance in *A. thaliana* against *P. syringae* [79]. In the same study, the application of ANE was tested on *Arabidopsis* NahG transgenic plants (accumulate little or no SA), and on two mutant *sics1* (defect in SA biosynthesis) and *jar1* (JA resistant). The NahG transgenic plants and *ics1* showed less disease severity on ANE application, whereas *jar1* mutant showed higher disease severity [79]. Enhanced levels of SA accumulation were observed in rubber tree plants further to the application of *Sargassum polycystum* extract [90]. In addition, *Sargsssum tenerrimum* extract (S-extract)-treated tomato plants produced higher levels of accumulation of SA when applied both at the vegetative and reproductive stages of *Macrophomina phaseolina* infection [91]. Applications of K-sap alone and in combination with *M. phaseolina* on tomato plants showed enhanced accumulation of ABA, indole acetic acid (IAA), and SA, facilitating development of SAR [85].

It is very important to study the kind of enzymes activated in the host plant by the application of individual SE during defence response. The ANEs were widely tested for disease tolerance in different crops against various pathogens and it was observed that activation of defence-related enzymes also get expressed during defence mechanism. The applications of different types of commercial extracts or extracts prepared by different researchers from *A. nodosum* on different crop species, i.e. carrot [76], cucumber [77,80], tomato [81,82,94], sweet pepper [82], and strawberry [95], revealed higher activities of certain defence-

related enzymes including POD, PPO, PAL, chitinase and β-1,3-glucanase. These studies reflected that almost identical responses were observed in terms of the kind of enzymes expressed by the application of the *A. nodosum* extract. The PAL, POD and phenolic compounds help in increasing the free phenolic pool which is basically utilized in enzyme activities, polymerization, and eventually synthesize lignin to help in disease tolerance [96]. Jayaraj et al. observed the higher lipoxygenase activity by the treatment of a commercial seaweed extract (SW) formulation containing ANE to cucumber plants which led to generation of ROS and superoxide anion radicals and singlet oxygen [76]. The active oxygen lead to oxidation of membrane lipids, resulted in the production of antifungal compound, e.g. phytoalexins and those involved in cell wall lignification and signal transduction. An extract of the brown alga *Sargassum wightii* (Dravya, a commercial product) application produced a higher accumulation of phenols and PPO in cotton plants against bacterial blight disease [97]. Applications of *S. polycystum* extract on rubber tree increased the activities of catalase (CAT), POD, β-1, 3-glucanase and phytoalexin scopoletin for preventing *Phytophthora* disease [90]. The CAT is a major enzyme that scavenges the H_2O_2 during stress condition, it was observed that CAT activity in rubber plant by applying *S. polycystum* extract was slightly increased compared to untreated plants. An extract of *S. tenerrimum* was applied at the vegetative stage and reproductive stage in tomato plants, which exhibited higher accumulation of antioxidative enzymes (superoxide dismutase, CAT, APOX and POD) with *M. phaseolina* treatment [91]. Flora and Rani, showed that SEs from *Padina pavonia*, *Acanthophora spicifera* and *U. lactuca* significantly reduced the severity of the fungal blast disease of rice caused by *Pyricularia oryzae*, in addition the PAL, POD, sugar, protein and starch also increased in rice in response to the fungi [98]. Extracts of the brown algae, i.e. *Cystoseira myriophylloides*, *L. digitata*, and *F. spiralis* individually applied to tomato plants revealed enhanced activities of PPO and POD against the tomato pathogen *Verticillium dahlia* [99]. The applications of *C. myriophylloides* and *F. spiralis* extracts also showed reduced crown gall disease in tomato plants caused by *Agrobacterium tumefaciens* [99]. Hernández-Herrera et al. had observed differential activity of the PPO, guaiacol peroxidase (GPOX), and trypsin inhibitory enzymes by the application of four different SEs (from *U. lactuca, Caulerpa sertularioides, Sargassum liebmannii* and *Padina gymnospora*) against a challenge by *A. solani* in tomato plants [93]. The PPO activity was found to be highest after applications of the *U. lactuca* extract. The GPOX activity was observed two-fold higher after the *C. sertularioides* treatment and four-fold higher in *P. gymnospora*-treated plants, as compared to their controls (without extract application). The activity of trypsin inhibitory enzymes was found high with all the four extracts. The SEs from *F. spiralis, C. myriophylloides* and L. *digitata* when used for priming the seeds of tobacco plants showed reduced symptoms of wild fire disease and higher H_2O_2 accumulation and enhanced activity of antioxidant enzymes including CAT, APOX, GPOX and PPO [100].

8. Conclusion

The present review revealed the importance of seaweed-based bio-elicitors from red, brown and green algae towards disease management in different crop plants. The usage of SEs can serve as an alternative to commercially available chemicals, which are routinely used for disease management in agriculture, and can also help in ameliorating the environmental problems caused by chemicals for control of disease. Several research papers are now being published which shows the insight mechanism towards disease tolerance. SEs help in activation of the innate immunity of the plants by upregulation of various pathogenic-responsive genes and transcription factors, defence-related enzymes and hormones. Research had been carried out to standardize the various methods for preparation of extracts, time of applications, durations and mode of applications. The SEs have diversity in their constituents composition, thereby, they show differential regulation of tolerance towards different pathogens. To facilitate the increase in use of SEs for sustainable agriculture and moreover to develop the trust that SEs can help as bio-elicitor, different algal extract should be tested for different diseases on different plants and understand that why different source provides stress tolerance better than other. Further, it is very important to analyze and study SEs chemical constituents, also characterize the dosage, mode, duration and number of SE/SEs applications to different crops for sustainable achievement of results. However, on the basis of research carried out in this field, it is evident that the algal extract can induce natural defence in plants and has a great potential in managing the disease tolerance in crops.

CRediT authorship contribution statement

Pradeep K. Agarwal: Conceptualization, draft preparation, reviewing and editing; Mohit Dangariya: Literature collection, writing and presentation; Parinita Agarwal: Writing and editing.

Statement of informed consent, human/animal rights

No conflicts, informed consent, human or animal rights applicable.

Declaration of competing interest

The authors declare no conflict of interest.

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