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Interaction of seaweed metabolites with plants to enhance protection against biotic and abiotic stresses

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Abstract: Biotic and abiotic stresses severely compromise economically important food crops' nutritional quality, growth, and yield. Conversely, the conventional reliance on chemical fertilisers and pesticides has generated substantial environmental and health risks, necessitating the development of sustainable alternatives. Seaweeds are rich sources of bioactive primary and secondary metabolites, and also promising natural biostimulants for enhancing plant resilience and productivity. Specific seaweed-derived metabolites function as molecular elicitors, mimicking pathogen-associated molecular patterns (PAMPs) and activating multi-layered plant defence mechanisms. This review aims to capture recent literature on the biological efficacy of seaweed extracts and their constituent metabolites, such as polysaccharides, phenolic compounds, and fatty acids, against diverse biotic stressors (e.g., bacteria, viruses, oomycetes, fungi (ascomycetes and basidiomycetes), nematodes, and herbivorous insect pests) and abiotic stressors (such as salinity, drought, extreme temperatures, and heavy metals). The biochemical, physiological, and molecular mechanisms by which seaweed-derived bioactive compounds modulate plant defence responses and stress tolerance pathways are also discussed in detail. In conclusion, seaweed extracts and derived metabolites show promising stress-type-specific effects against biotic and abiotic stresses through diverse mechanisms. However, field validation, dosage optimisation, and the discovery of novel bioactives are essential to harnessing their potential fully in sustainable agriculture.

Keywords: seaweed extracts; metabolites; biotic stress; abiotic stress; plant protection; plant resilience

The rapid climate changes negatively impact agricultural productivity by increasing soil salinity levels, elevating temperatures, and intensifying drought conditions (Deolu-Ajayi et al. 2022). These abiotic stress factors have affected plant growth by disrupting biochemical, physiological, and molecular processes (Asif et al. 2023; Oyebamiji et al. 2024). For example, in rice, the accumulation of Na^+ due to long-term salinity exposure causes a Na^+/K^+ imbalance and impairs photosynthetic efficiency, including nutrient uptake (Chen et al. 2022). Activating compensatory ion transport systems mitigates salinity-induced ion toxicity and inadvertently enhances the uptake and translocation of heavy metals, such as cadmium (Nosek et al. 2020). Besides salinity stress, extremely high and low temperatures affect agricultural productivity and food security. High temperatures can cause a 10–17%

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decline in yields at various growth stages, while extremely low temperatures may lead to a 60–70% decline in total yields of legumes such as chickpeas and soybeans (Oyebamiji et al. 2024). Under abiotic stress conditions, plants overproduce reactive oxygen species (ROS), including superoxide anion (O_2^-), hydrogen peroxide (H_2O_2), hydroxyl radical (·OH), and singlet oxygen ($^1O_2$) (Sachdev et al. 2021). The predominant ROS types and their cellular localization vary depending on the specific organelle involved (such as chloroplasts, mitochondria, or peroxisomes) and the abiotic stress encountered (Sachdev et al. 2021). To counteract this oxidative damage, plants utilise enzymatic and non-enzymatic antioxidants that can scavenge ROS to prevent cellular damage (Oyebamiji et al. 2024). Simultaneously, this ROS-mediated stress response triggers the transcriptional upregulation of protective genes and metabolic pathways. For instance, wheat seedlings under water shortage conditions were observed with upregulated gene expression levels of antioxidant enzymes, catalase (CAT), the stress-signalling kinase Mitogen-Activated Protein Kinases (MAPK), and osmoprotectant proline biosynthesis-related enzymes (P5CS and P5CR) (Dudziak et al. 2019). Similarly, tomato plants under salt stress show enhanced expression of sodium/hydrogen antiporter genes (NHX1), while maize plants under heat stress upregulate heat shock protein (HSP) and dehydrin (DHN) genes (Qi et al. 2022; Cavusoglu et al. 2023). This oxidative stress causes direct cellular damage and increases plant susceptibility to biotic attacks by compromising the pathogen defence mechanism (Dixit et al. 2024).

Likewise, biotic stress, caused by diverse pathogens, including viroids, viruses, bacteria, oomycetes, fungi (ascomycetes, basidiomycetes), nematodes, and herbivorous insects, results in substantial crop losses worldwide. Particularly, fungi-like and fungi are reported to cause roughly 80% of crop diseases, such as late blight (*Phytophthora infestans*) and downy mildews (*Plasmopara*, *Peronospora* spp.), and they are responsible for billions in annual losses globally (El Hussein 2014; Dudziak et al. 2019). Plants respond to pathogen invasion through sophisticated pattern recognition systems that detect pathogen-associated molecular patterns (PAMPs) or damage-associated molecular patterns (DAMPs), subsequently triggering complex defence signalling cascades involving salicylic acid (SA) and jasmonic acid (JA) pathways (Hou et al. 2019). This pathogen recognition triggers comprehensive transcriptional reprogramming characterised by coordinated upregulation of pathogenesis-related proteins (PRs), antioxidant enzyme systems [peroxidase (POD), superoxide dismutase (SOD), glutathione peroxidase (GPX)], secondary metabolite biosynthetic enzymes [such as phenylalanine ammonia-lyase (PAL), chalcone synthase (CHS), flavonol synthase (FLS)], and structural fortification genes governing callose deposition and cell wall reinforcement (Ali et al. 2018; Sachdev et al. 2021; Wang et al. 2023a). Importantly, certain metabolites can act as elicitors through functioning as PAMP-like molecules and activating both induced systemic resistance (ISR) and systemic acquired resistance (SAR) pathways (Shukla et al. 2019). This metabolite-mediated activation primes plants for enhanced defence responses even before pathogen encounter (Rasul et al. 2021; Velho et al. 2022).

The world population is predicted to reach 9.7 bil. by 2050 (UNDESA 2019), and global food demand is projected to increase by up to 56% between 2010 and 2050 according to a meta-analysis (Van Dijk et al. 2021). Accordingly, continuous growth in crop production is required to ensure food security (Alexandratos & Bruinsma 2012). Considering the increasing demand, unavailability of land, and climate change, there is an urgent need to reduce crop losses due to biotic and abiotic stresses (Schneider et al. 2022; Palmgren & Shabala 2024). Despite the beneficial roles of pesticides and chemical fertilisers in enhancing crop production, their excessive and long-term usage has raised serious concerns regarding health risk and environmental sustainability (Lin et al. 2019). For example, humans are exposed to pesticides through direct agricultural activities and indirect contact via contaminated air, water, soil, and food. This continuous exposure may contribute to both acute toxicity and the development of chronic diseases (Tudi et al. 2022). Therefore, there is a need to explore alternative ways to decrease or eventually avoid using these chemicals in agriculture. One approach to improve agricultural productivity under unfavourable environmental conditions would be cultivating crops capable of combating biotic and abiotic stresses. This has been traditionally achieved through breeding programs; however, these techniques are laborious and time-consuming (Deolu-Ajayi et al. 2022; Oyebamiji et al. 2024). Recently, plant biostimulants have gained immense

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attention for improving plant growth by improving stress resilience, plant growth, and development. These non-fertiliser substances derived from natural sources, such as microorganisms, plant or animal by-products, or seaweed extracts, stimulate plant growth and increase defence against various environmental stresses (Deolu-Ajayi et al. 2022). Among different sources of biostimulants, seaweed extracts have gained growing attention as promising natural substances based on their unique advantages (Ali et al. 2021).

While numerous reports have demonstrated the bioactive efficacy of seaweed extracts through *in vitro* antimicrobial assays, a comprehensive understanding of their molecular mechanisms and effectiveness *in vivo* (*in planta*) remains limited (Agarwal et al. 2021; Ali et al. 2021; El Khattabi et al. 2023; Raja & Vidya 2023). Furthermore, studies utilising isolated compounds from diverse chemical classes of seaweeds to elucidate their impact on specific molecular and biochemical pathways in plants, irrespective of plant stress status, are even more scarce, which represents a significant knowledge gap in the field (Rengasamy et al. 2016; de Borba et al. 2021; Lopes et al. 2021; Emad et al. 2022). Therefore, this article aims to review recent literature, mainly from 2012–2024, on crude extracts, well-characterised and purified compounds from seaweed, and their interactive efficacy against various biotic and abiotic stressors in plants. This comprehensive analysis links specific metabolites to their molecular targets and signalling pathways, which can contribute to the development of targeted applications and optimal formulations for specific stress conditions. We particularly emphasise: *(i)* plant and seaweed metabolite interactions under specific stress conditions with their context-dependent responses, *(ii)* molecular mechanisms of action underlying stress mitigation, and *(iii)* integrative cross-tolerance mechanisms by which seaweed metabolites may confer broad-spectrum stress resilience.

SEAWEEDS: PROMISING BIOSTIMULANTS

Rhodophyta (red), Phaeophyta (brown), and Chlorophyta (green) are the three main classes of seaweed, which are marine macroalgae (Belghit et al. 2017). They are valuable sources of a wide spectrum of primary and secondary metabolites, including polysaccharides (e.g., agar, carrageenan, alginate, fucoidan, laminarin, and ulvan), polyphenols, terpenoids, alkaloids, phytohormones (such as, cytokinin, gibberellin, auxin, abscisic acid, ethylene, and jasmonic acid), lipids, amino acids, and proteinaceous substances such as peptides and glycoproteins (Belghit et al. 2017; Uribe et al. 2019; Cotas et al. 2020; Park et al. 2023; Olaetxea et al. 2024; Xie et al. 2024). Regardless of their structural similarity to endogenous plant metabolites, previous studies demonstrate the remarkable capacity of these seaweed-derived compounds to modulate diverse biochemical pathways within plant systems, thereby enhancing growth performance and stress tolerance mechanisms (Shukla et al. 2016; Ahmed et al. 2022; Aina et al. 2022). These diverse biological activities have consequently driven increasing research interest in agriculture. In agricultural applications, various types of methods, including seed priming, foliar spraying, soil drenching, fertigation, biochar, and biopellets, have been adopted to improve soil and delivery efficiency of bioactive compounds derived from seaweed extracts (Rengasamy et al. 2016; Abd El-Basir et al. 2020; Rasul et al. 2021; Ahmed et al. 2022; Nanda et al. 2022). Furthermore, seaweed extracts positively improve plant performance under challenging environmental conditions. For example, watermelon seeds were primed in the aqueous seaweed extracts (ASE) of *Ulva lactuca*, resulting in enhanced seed germination and crop growth with increased tolerance to salt stress (Radwan et al. 2023). Another study has shown that aqueous extracts of *Ascophyllum nodosum* promoted early seedling performance of pea plants while also reducing root rot disease severity after inoculation with *Rhizoctonia solani* (Esserti et al. 2016; Rashad et al. 2022).

TYPES OF SEAWEED METABOLITES

Various studies have investigated the biocontrol efficacy of diverse seaweed extract fractions, including alkaline, aqueous, methanol, ethanol, and water extracts, against plant pathogens and demonstrated their effectiveness (Esserti et al. 2016; Ramkissoon et al. 2017; Rashwan & Hammad 2020). Additionally, the effects of isolated seaweed metabolites, primarily polysaccharides, phenolic compounds, and fatty acid derivatives, have

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been examined through both *in vitro* and *in vivo* (*in planta*) applications (Rengasamy et al. 2016; Velho et al. 2022; Chanthini et al. 2024).

Polysaccharides and their derivatives. Previous studies have reported several bioactivities of seaweed-derived polysaccharides, including their potential in improving plant resilience against diverse types of biotic stresses (Wu et al. 2016; Mani et al. 2021; Mamede et al. 2023). Green seaweeds (Chlorophyta), particularly *Ulva* species (sea lettuce), produce ulvan as their major water-soluble sulfated polysaccharide, which is characterised by rhamnose-3-sulfate containing disaccharide units and contributes to the structural and functional properties of these algae (Li et al. 2023). Ulvan, isolated from *U. lactuca*, has been reported to exert antiviral and antibacterial properties against various pathogen types, including *Staphylococcus aureus*, under *in vitro* conditions (de Borba et al. 2019; de Borba et al. 2021; Velho et al. 2022; Maray et al. 2023). Similarly, brown seaweed (Phaeophyceae) synthesises structurally unique polysaccharides, such as fucoidan, laminarin, and alginate (Li et al. 2021). Fucoidan is a sulfated polysaccharide composed of α-L-fucose with variable sulfate content (Zayed et al. 2020). Laminarin is a beta-glucan with a primarily β-(1–>3)-glucopyranose backbone and occasional β-(1–> 6) branches (Cheong et al. 2025). Alginate consists of linear chains of β-(1,4)-D-mannuronic acid and α-(1,4)-L-guluronic acid (Uysal et al. 2023). These sulfated and unsulfated polysaccharides also possess antimicrobial activities against oomycete (Paris et al. 2019). Notably, the biocontrol efficacy of fucoidan and alginate was found to be primarily associated with their oligosaccharide or hydrolysate forms, rather than the native high-molecular-weight polysaccharides (Zhang et al. 2019; Wang et al. 2023b). Red seaweeds (Rhodophyta) are particularly abundant in sulfated galactans. They are structurally distinct from those present in brown and green algae. Among these, carrageenans are classified into three principal types: κ-, ι-, and λ-carrageenan based on the number and position of sulfate groups present on each disaccharide unit (Rupert et al. 2022; Hossain et al. 2024). This variation in sulfation underlies their distinct gelling behaviours and functional properties (Rupert et al. 2022). Similarly, polysaccharides, including carrageenans, from red seaweeds have also been reported to exhibit antiviral, antibacterial, and antifungal activities (Vera et al. 2012; Mani & Nagarathnam 2018; Mani et al. 2021).

Phenolic compounds. In seaweed, polysaccharides constitute the primary structural components of their cell walls. At the same time, phenolic compounds represent one of the most complex and abundant components that act as potent antioxidants and defence-related metabolites in seaweed extracts. It has been reported that brown seaweeds are especially rich in phlorotannins, whereas red and green seaweeds are more enriched in bromophenols and flavonoids (Cotas et al. 2020). In addition to these predominant phlorotannins, brown seaweeds contain other phenolic compounds, such as flavonoids, bromophenols, and phenolic terpenoids (Cotas et al. 2020). In the case of red seaweed, the *Gracilaria genus* is characterised by its abundance of bromophenols (2-bromophenol and 4-bromophenol) along with phenolic acids (benzoic and protocatechuic acid). Similarly, green seaweeds, including *Ulva*, *Capsosiphon*, and *Chaetomorpha* species, are known for their bromophenols and flavonoids (Cotas et al. 2020). These seaweed-derived phenolic compounds demonstrate broad-spectrum bioactive properties, including antiviral, antibacterial, antifungal, and insecticidal activities, as extensively documented across multiple research investigations (Vimaladevi et al. 2012; Scania & Chasani 2021; Emad et al. 2022; Maheswari & Babu 2022). Eckol, a phlorotannin from *Ecklonia maxima*, has demonstrated efficacy in improving both growth and aphid resistance in cabbage (*Brassica oleracea* L.) (Rengasamy et al. 2016). Despite the wide variety of phenolic compounds present in seaweeds and their efficacy *in vitro* tests against plant pathogens, including experimental evidence for their role in enhancing plant biotic stress tolerance through *in planta* mechanisms, they remain limited.

Fatty acids and lipids. Seaweed lipids and fatty acids are another crucial class of bioactive metabolites, alongside polysaccharides, and phenolic compounds. Algal lipids in seaweed range from 0.12% to 6.73% of dry weight, primarily including phospholipids, glycolipids, and neutral lipids such as triacylglycerols (Perez et al. 2016). Seaweed contains primarily even-numbered carboxylic acids with aliphatic chains, which can be unsaturated or saturated. These fatty acids include monounsaturated (MUFA) and polyunsaturated (PUFA) types, categorised as n-3 or n-6 based on the position of the first double bond. Common PUFAs found

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in seaweed are omega-3 (n-3) and omega-6 (n-6) fatty acids, such as linoleic acid (LNA), docosahexaenoic acid (DHA), α-linolenic acid (ALA), arachidonic acid (ARA), and eicosapentaenoic acid (EPA) (Xie et al. 2024). Despite the potential biological activities of seaweed lipids, most earlier studies have focused on profiling crude fractions rather than investigating their biological properties, including individual purified lipid compounds (Lopes et al. 2021). Fatty acids in seaweed extracts have been shown to exhibit antibacterial and antifungal activities against phytopathogenic bacteria. For example, the chloroform extracts from *Hormophysa cuneiformis* exerted antifungal activity against eight pathogenic fungi likely through membrane disruption mechanisms, and oleic and arachidonic acids were identified as the main peaks among 45 compounds via GC-MS analysis (El-Fallal et al. 2019). While *in vitro* studies have demonstrated the antimicrobial efficacy of seaweed fatty acids, translating these findings to *in planta* applications requires further investigation. However, unlike the well-characterised biocontrol mechanisms of seaweed polysaccharides and phenolic compounds, fatty acid-mediated plant protection remains largely limited to *in vitro* antimicrobial assays, representing a critical knowledge gap, especially regarding systematic *in planta* experiments and rigorous compound purification studies. The following sections describe the major types of seaweed-derived metabolites and their roles in plant defence mechanisms against pathogens and pests.

INTERACTION OF SEAWEED METABOLITES WITH PLANTS UNDER BIOTIC STRESS CONDITIONS

Types of biotic stressors and agricultural impact

Plants encounter numerous biotic stressors in their environment, including attacks from various pathogens [viroids, viruses, bacteria, fungi-like and fungal pathogens (oomycetes, ascomycetes, basidiomycetes), nematodes] and insect pests, resulting in 10–40% annual yield reductions in major food crops, such as wheat, rice, maize, potato, and soybean, worldwide (Savary et al. 2019). Notably, the diversity of these disease-causing agents represents one of agriculture's most persistent challenges, and their distinct evolutionary lineages with unique infection mechanisms make management strategies more complicated.

First, viroids are unique RNA pathogens consisting of small, circular, single-stranded RNA molecules lacking protein coats, causing diseases such as potato spindle tuber viroid and citrus exocortis viroid (Nicaise 2014). Furthermore, Potyviridae (mosaic virus), Closteroviridae (tristeza virus), Geminiviridae (leaf curl virus), and Luteoviridae (yellowing virus) represent the major economically important viral families (Nicaise 2014). It has been reported that plant viral diseases cause approximately 30 bil. USD in annual global losses (Jones 2021). In addition, these pathogens cannot be controlled chemically and require integrated management approaches, including certified pathogen-free materials, vector control, resistant cultivars, and strict quarantine measures due to their obligate intracellular nature (Kumar et al. 2021).

Second, plant bacterial pathogens also represent a major threat to global agricultural productivity by major genera, causing severe diseases, including *Ralstonia* (wilt), *Erwinia* (fire blight), *Xanthomonas* (blight and canker), *Pseudomonas* (speck and spot), and *Xylella* (leaf scorch), and these are considered mainly responsible for economic losses exceeding 1 bil. USD annually worldwide (Mansfield et al. 2012; Savary et al. 2019). Particularly, fire blight caused by *Erwinia amylovora* on apple and pear, and bacterial wilt caused by *Ralstonia solanacearum* on over 200 plant species are ranked as the most destructive bacterial diseases globally (Mansfield et al. 2012; Rupert et al. 2022). Despite the severity of damage across various crop types, controlling bacterial pathogens remains challenging due to the limited effectiveness of copper-based bactericides and concerns about antibiotic resistance development (Mansfield et al. 2012).

Next, oomycete pathogens present unique challenges in plant disease management based on their distinct phylogenetic position as fungal-like eukaryotic microorganisms (Judelson & Ah-Fong 2019). The main pathogenic genera include *Pythium*, *Plasmopara*, and *Peronospora*, encompassing over 120 species that collectively threaten a vast array of agriculturally crucial crops and cause devastating diseases, such as late blight (*Phytophthora*), downy mildews (*Plasmopara*, *Peronospora*, *Pseudoperonospora*), and root rot complexes (*Phytophthora*, *Pythium*) (Derevnina et al. 2016; Dudziak et al. 2019). Notably, these pathogens have demonstrated their

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remarkable host versatility. For example, *P. infestans* alone is responsible for annual losses surpassing 10 bil. USD in potato and tomato production globally (Rhouma et al. 2024). Crops susceptible to downy mildews represent a substantial economic sector worth at least 7.5 bil. USD within the United States (Crandall et al. 2018). However, managing oomycete pathogens has been challenged because their symptoms often resemble those caused by other pathogens or abiotic factors, making accurate detection and diagnosis difficult (Wang et al. 2020).

Moreover, fungal pathogens dominate the plant disease landscape, accounting for approximately 80% of all documented cases and representing the most economically significant group (El Hussein 2014; Khedia et al. 2020). These plant pathogen species primarily belong to the phyla ascomycetes and basidiomycetes, demonstrating distinct biological characteristics and disease mechanisms. Ascomycetes are known as the largest fungal phylum. The major pathogenic genera include *Magnaporthe*, *Zymoseptoria*, *Blumeria*, *Venturia*, and *Fusarium*, which collectively threaten critical food crops through diseases, such as rice blast, wheat septoria tritici blotch, powdery mildews, apple scab, and various wilt diseases (Dean et al. 2012; Fones & Gurr 2015). Remarkably, powdery mildews are reported to affect approximately 10 000 species of angiosperms across 200 countries and 6 continents (Bradshaw et al. 2024). Basidiomycetes are estimated to include about 30 000 species and contain two of the most destructive groups of plant pathogens: rusts (Pucciniomycetes) (7 000 species) and smuts (Ustilaginomycotina) (14 000 species), serious threats to global cereal production (Morrow & Fraser 2009; Lorrain et al. 2019). The obligate biotrophic nature and complex heteroecious, macrocyclic life cycles of these pathogens require multiple host species, challenging both fundamental study and practical control efforts (Singh et al. 2015).

In addition, plant-parasitic nematodes are considered a devastating constraint on global agriculture. Several critical genera, including *Meloidogyne* (root-knot), *Heterodera* and *Globodera* (cyst), *Pratylenchus* (lesion), and *Radopholus* (burrowing), are reported to infect numerous types of cultivated crops (Pires et al. 2022; Kantor et al. 2024). These soil-dwelling nematodes cause approximately 173 bil. USD in crop damage annually worldwide, while developing countries experience worse losses due to inadequate control options (Phani et al. 2021). Nematode management remains challenging due to their microscopic size, symptom similarity to abiotic stress factors, and remarkable survival capacity under adverse conditions (Dutta & Phani 2023).

Lastly, the primary economically important insect pest families include Lepidoptera (armyworms, stemborers, and cutworms), Coleoptera (Colorado potato beetle, weevils), Diptera (fruit flies), Hemiptera (aphids, whiteflies), and Orthoptera (locusts, grasshoppers) collectively attack most crops, and cause characteristic symptoms including defoliation, stunting, wilting, and direct consumption of plant tissues (Deutsch et al. 2018). The fall armyworm (*Spodoptera frugiperda*) represents one of the most destructive invasive pest species globally, causing annual losses exceeding 13 bil. USD worldwide (Overton et al. 2021). The management of insect pests presents significant challenges due to their high reproductive rates, mobility, ability to develop resistance to control measures, and capacity to rapidly adapt to new host plants and environmental conditions under climate change scenarios (Deutsch et al. 2018).

Traditional reliance on chemical pesticides faces increasing limitations as pathogen populations develop resistance and environmental concerns mount. Therefore, intensifying research efforts toward sustainable alternatives, including seaweed-derived biostimulants and elicitors as environmentally friendly disease management tools, would be essential for developing resilient agricultural systems (Ramkissoon et al. 2017; Khedia et al. 2020). Tables 1–4 summarise studies examining the effects of seaweed-derived compounds (well-characterised and purified), crude extracts, and commercial products on various biotic stress factors affecting plants.

Seaweed metabolite efficacy against plant biotic stressor types

Viroids and viruses. Several purified seaweed polysaccharides have demonstrated potent antiviral activities against plant viroids and viruses in greenhouse and controlled plant growth conditions (Table 1). For instance, λ-carrageenan from *Chondrus crispus* showed remarkable efficacy against tomato chlorotic dwarf viroid (TCDVd) when applied as a foliar spray (1 g/L) to tomato plants (Sangha et al. 2015). The symptoms were dramatically reduced by 66% in treated plants. Similarly, oligo-sulfated-galactan (Poly-Ga) from

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Table 1. Antiviral and anti-viroid properties of seaweed extracts

Extract type (crude/ compound/ product)	Seaweed species (Phylum)	Target pathogen (disease)	Host crop	Effective concentration	Application mode	Experimental condition	Efficacy results	Mechanism / mode of action	References
λ-Carrageenan (purified polysaccharide)	*Chondrus crispus* (Rhodophyta)	Tomato chlorotic dwarf viroid (TCDVd)	Tomato	1 g/L	Foliar spray	Growth chamber	Symptom incidence: 28% in treated plants vs. 82% in control	JA-dependent resistance (↑ LOX, AOS); upregulation of 17 defence genes; suppression of viroid replication (no direct effect)	Sangha et al. 2015
Oligo-sulphated-galactan (Poly-Ga)	*Ahnfeltiaopsis devillei* (Rhodophyta)	Tobacco mosaic virus (TMV)	Tobacco (*Nicotiana tabacum* var. Xanthi)	0.5 mg/L	Foliar spray	Greenhouse	Lesion number ↓ up to 80%, suppression of systemic TMV spread (RT-PCR confirmed)	PAL enzyme activation, phenylpropanoid compound accumulation, systemic resistance, SA accumulation (not LOX)	Vera et al. 2011
Oligo-carrageenan kappa	– (Rhodophyta)	Tobacco mosaic virus (TMV)	Tobacco (*N. tabacum* var. Xanthi)	1 mg/mL	Foliar spray (upper/lower, weekly × 3)	Growth chamber, 45 days	TMV infection partial suppression	PAL activity ↑; phenylpropanoids ↑; PR proteins ↑; broad-spectrum	Vera et al. 2012
Oligo-carrageenan lambda	– (Rhodophyta)	Tobacco mosaic virus (TMV)	Tobacco (*N. tabacum* var. Xanthi)	1 mg/mL	Foliar spray (upper/lower, weekly × 3)	Growth chamber, 45 days	Strong & durable TMV suppression (most effective)	PAL activity ↑; phenylpropanoids ↑; PR proteins ↑; broad-spectrum	Vera et al. 2012
Oligo-carrageenan iota	– (Rhodophyta)	Tobacco mosaic virus (TMV)	Tobacco (*N. tabacum* var. Xanthi)	1 mg/mL	Foliar spray (upper/lower, weekly × 3)	Growth chamber, 45 days	TMV infection partial suppression	PAL activity↑; phenylpropanoids↑; PR proteins↑; broad-spectrum	Vera et al. 2012
κ/β-carrageenan (purified polysaccharide)	*Tichocarpus crinitus* (Rhodophyta)	Tobacco mosaic virus (TMV)	Tobacco (*N. tabacum* var. Xanthi-nc)	1 mg/mL	Leaf rub-inoculation	Lab (detached leaf, *in vivo*)	Lesion number ↓ 87% (virus-polysaccharide mix); lesion ↓ in pre-/post-treatment	Induced resistance via host genome activation; virus binding & replication interference (direct virion interaction)	Nagorskaya et al. 2008

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Table 2. Antibacterial efficacy of seaweed extracts

Extract type (crude/ compound/ product)	Seaweed species (Phylum)	Target pathogen (disease)	Host crop	Effective concentration	Application mode	Experimental condition	Efficacy results	Mechanism / mode of action	References
Alkaline extract	*Ulva lactuca* (Chlorophyta)	*Xanthomonas campestris* pv. *vesicatoria* (bacterial spot)	Tomato (*Solanum lycopersicum*, Hybrid 61)	0.5% (*w/v*)	Foliar spray (6h pre-inoculation, 3 applications, 15-day intervals)	Greenhouse (25–30 °C, 70–85% RH, 40 days)	Disease index ↓48.3% (65.25% control → 33.71% treated)	JA/ET pathway activation (↑PIN II, ↑ETR-1); ↑defence enzymes (PAL, POD, PPO, CHI, GLU)	Ramkissoon et al. 2017
Alkaline extract	*Gelidium serrulatum* (Rhodophyta)	*X. campestris* pv. *vesicatoria* (bacterial spot)	Tomato (*Solanum lycopersicum*, Hybrid 61)	0.5% (*w/v*)	Foliar spray (6h pre-inoculation, 3 applications, 15-day intervals)	Greenhouse (25–30 °C, 70–85% RH, 40 days)	Disease index ↓55.6% (65.25% control → 28.98% treated); ↑plant height (35%), ↑leaf number (83%), ↑biomass (2×)	Sequential SA (↑PR-1a) and JA/ET (↑PIN II, ↑ETR-1) pathway activation; ↑defense enzymes; ↑total phenolics	Ramkissoon et al. 2017
Alkaline extract	*Sargassum filipendula* (Phaeophyceae)	*X. campestris* pv. *vesicatoria* (bacterial spot)	Tomato (*Solanum lycopersicum*)	0.5% (*w/v*)	Foliar spray (6h pre-inoculation, 3 applications, 15-day intervals)	Greenhouse (25–30 °C, 70–85% RH, 40 days)	Disease index reduction (moderate, < 48.3%);↑plant growth	JA/ET pathway activation (↑PIN II, ↑ETR-1); ↑defense enzymes; no SA pathway induction	Ramkissoon et al. 2017
Aqueous extract (ASE)	*Cystoseira myriophylloides* (Phaeophyceae)	*Agrobacterium tumefaciens* (crown gall)	Tomato (*Solanum lycopersicum*)	3.0% (*w/v*)	Foliar spray (2–4 days pre-inoculation)	Greenhouse (4 weeks)	Tumor diameter ↓48–57% (3%, 2–4 days pre-treatment)	Induced resistance; ↑POX, ↑PPO, ↑H_2O_2; priming effect; no direct antibacterial activity	Esserti et al. 2016
Aqueous extract (ASE)	*Fucus spiralis* (Phaeophyceae)	*A. tumefaciens* (crown gall)	Tomato (*Solanum lycopersicum*)	0.5% (*w/v*)	Foliar spray (2-4 days pre-inoculation)	Greenhouse (4 weeks)	Tumor diameter ↓33–35% (0.5%, 2–4 days pre-treatment)	Induced resistance; ↑POX, ↑PPO, ↑H_2O_2; priming effect; no direct antibacterial activity	Esserti et al. 2016
Aqueous extract (ASE)	*Laminaria digitata* (Phaeophyceae)	*A. tumefaciens* (crown gall)	Tomato (*Solanum lycopersicum*)	0.5–3.0% (*w/v*)	Foliar spray (2–4 dayspre-inoculation)	Greenhouse (4 weeks)	No significant reduction	No induced resistance or direct effect observed	Esserti et al. 2016
Methanolic extract (MSE)	*C. myriophylloides* (Phaeophyceae)	*A. tumefaciens* (crown gall)	–	100 µg/mL	Disk diffusion assay	*In vitro* (24h evaluation)	↓Bacterial growth (zone of inhibition)	Direct antimicrobial activity	Esserti et al. 2016
Methanolic extract (MSE)	*L. digitata* (Phaeophyceae)	*A. tumefaciens* (crown gall)	–	100 µg/mL	Disk diffusion assay	*In vitro* (24h evaluation)	↓Bacterial growth (zone of inhibition)	Direct antimicrobial activity	Esserti et al. 2016
Methanolic extract (MSE)	*F. spiralis* (Phaeophyceae)	*A. tumefaciens* (crown gall)	–	100 µg/mL	Disk diffusion assay	*In vitro* (24h evaluation)	No inhibition observed	No direct antibacterial effect	Esserti et al. 2016

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Table 2. To be continued...

Extract type (crude/ compound/ product)	Seaweed species (Phylum)	Target pathogen (disease)	Host crop	Effective concentration	Application mode	Experimental condition	Efficacy results	Mechanism / mode of action	References
Stella Maris® (alkaline commercial extract)	*Ascophyllum nodosum* (Phaeophyceae)	Pseudomonas aeruginosa	*Arabidopsis thaliana*	50% (inhibition), 1% (priming)	Seedling immersion (24h) → pathogen inoculation	Laboratory (MS liquid medium)	*In vitro*: ↓58% (50%); *In vivo*: ↓20% (media), ↓47% (tissue) at 1%	Direct antimicrobial at high concentration; ↑ROS burst (H_2O_2); ↑defense genes (WRKY30, CYP71A12, PR-1); SA/JA pathway activation; ↑camalexin synthesis; SAR induction	Cook et al. 2018
Stella Maris® (alkaline commercial extract)	*A. nodosum* (Phaeophyceae)	*P. syringae* DC3000 (bacterial blight)	*Arabidopsis thaliana*	50% (inhibition), 1% (priming)	Seedling immersion (24h) → pathogen inoculation	Laboratory (MS liquid medium)	*In vitro*: ↓58% (50%); *In vivo*: ↓28% (media), ↓22% (tissue) at 1%	Direct antimicrobial at high concentration; ↑ROS burst; ↑WRKY30, ↑CYP71A12, ↑PR-1; moderate SAR activation	Cook et al. 2018
Stella Maris® (alkaline commercial extract)	*A. nodosum* (Phaeophyceae)	*X. campestris* (bacterial canker)	*Arabidopsis thaliana*	50% (inhibition), 1% (priming)	Seedling immersion (24h) → pathogen inoculation	Laboratory (MS liquid medium)	*In vitro*: ↓43% (50%); *In vivo*: ↓41% (media), no tissue reduction	Direct antimicrobial at high concentration; partial ROS and immune priming; limited systemic protection	Cook et al. 2018
Fucoidan enzymatic hydrolysate (FEH)	*S. hemiphyllum* (Phaeophyceae)	*P. syringae* pv. *tomato* DC3000 (bacterial speck)	*Arabidopsis thaliana*	400 µg/mL	Leaf infiltration (24h pre-treatment)	Growth chamber (22°C, 12h photoperiod, 60% RH)	Significant ↓bacterial growth (log-scale CFU $cm^{↓2}$ reduction)	↑ROS burst (H_2O_2); ↑MAPK3/6 activation; ↑immune genes (NHL10, OXI1, WRKY30); callose deposition; stomatal closure; 651 immune genes upregulated	Wang et al. 2023b
Alginate oligosaccharide (AOS)	– (Phaeophyceae)	*P. syringae* pv. *tomato* DC3000 (bacterial speck)	*Arabidopsis thaliana*	25 mg/L	Foliar spray (3 days pre-inoculation)	Growth chamber	Disease index ↓35.62%; bacterial CFU ↓78.88%	SA-mediated pathway activation; ↑PR1 expression; ↑SA content; ↑ROS/NO	Zhang et al. 2019
κ-Carrageenan oligomers	– (Rhodophyta)	*Pectobacterium carotovorum* (soft rot)	Tobacco (*N. tabacum* var. Xanthi)	1.0 mg/mL	Foliar spray (weekly × 3 applications)	Growth chamber (45 days)	Lesion diameter ↓74%; viable colonies ↓87%	↑PAL activity (5×); ↑phenylpropanoids (3.5×); ↑PR proteins; broad-spectrum defense activation	Vera et al. 2012

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Table 2. To be continued...

Extract type (crude/ compound/ product)	Seaweed species (Phylum)	Target pathogen (disease)	Host crop	Effective concentration	Application mode	Experimental condition	Efficacy results	Mechanism / mode of action	References
λ-Carrageenan oligomers	– (Rhodophyta)	*P. carotovorum* (soft rot)	Tobacco (*N. tabacum* var. Xanthi)	1.0 mg/mL	Foliar spray (weekly × 3 applications)	Growth chamber (45 days)	Lesion diameter ↓77%; viable colonies ↓98%	↑PAL activity (5×); ↑phenylpropanoids (3.5×); ↑PR proteins; broad-spectrum defense activation	Vera et al. 2012
ι-Carrageenan oligomers	– (Rhodophyta)	*P. carotovorum* (soft rot)	Tobacco (*N. tabacum* var. Xanthi)	1.0 mg/mL	Foliar spray (weekly × 3 applications)	Growth chamber (45 days)	Lesion diameter ↓83%; viable colonies ↓99%	↑PAL activity (5×); ↑phenylpropanoids (3.5×); ↑PR proteins; broad-spectrum defense activation	Vera et al. 2012
Tomatough® (LBD3)	*Kappaphycus alvarezii* (Rhodophyta)	*P. syringae* pv. *tomato* DC3000 (bacterial speck)	*Arabidopsis thaliana*	4.0 mL/L	Foliar spray (24h pre-infection)	Greenhouse	↓95% (25-fold reduction)	↑SA, ↑PR1, ↑JA, ↑CK; strong SA pathway activation; immune gene upregulation	Roy et al. 2022
AgFort® (LBD12)	*K. alvarezii* (Rhodophyta)	*P. syringae* pv. *tomato* DC3000 (bacterial speck)	*Arabidopsis thaliana*	1.0 mL/L	Foliar spray (24h pre-infection)	Greenhouse	↓96% (25-fold reduction)	↑SA, ↑PR1, ↑JA, ↑CK; stronger, more durable SA/PR1 response than LBD3	Roy et al. 2022
AgFort® (LBD12)	*K. alvarezii* (Rhodophyta)	*X. oryzae* pv. *oryzae* (bacterial leaf blight)	Rice (*Oryza sativa*, TN-1)	1.0 mL/L	Foliar spray (24h post-infection)	Greenhouse	↓63% (2.7-fold lesion reduction)	↑SID2/ICS1, ↑PR1a, ↑SA, ↑CK; immune gene upregulation; suppresses pathogen exploitation	Roy et al. 2022

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Table 3. Oomyceticidal and fungicidal activities of seaweed extracts

Extract type (crude/ compound/ product)	Seaweed species (Phylum)	Target pathogen (disease)	Host crop	Effective concentration	Application mode	Experimental condition	Efficacy results	Mechanism / mode of action	References
Alkaline hydrolysate (AN)	*A. nodosum* (Phaeophyceae)	*Phytophthora cinnamomi* (root rot)	*Arabidopsis thaliana*	1 : 400 dilution of 16% (w/w) soluble solids	Soil drench (sand tube system)	Growth chamber	Pathogen DNA ↓at 24–72 hpi (qPCR); root growth ↑	Priming of SAR (PR1, PR5, NPR1 ↑), JA/SA/auxin signalling, ROS burst (H_2O_2 ↑), cell wall reinforcement, antibiotic/secondary metabolite biosynthesis, upregulation of defence-related TFs (WRKY42, CML8), proteolysis, energy metabolism pathways activated	Islam et al. 2020
Alkaline hydrolysate (DP)	*Durvillaea potatorum* (Phaeophyceae)	*P. cinnamomi* (root rot)	*Arabidopsis thaliana*	1 : 400 dilution of 16% (w/w) soluble solids	Soil drench (sand tube system)	Growth chamber	Pathogen DNA ↓at 24–72 hpi (qPCR); root growth ↑	Priming of SAR (PR1, PR5, NPR1 ↑), JA/SA/auxin signalling, ROS burst (H_2O_2 ↑), cell wall reinforcement, antibiotic/secondary metabolite biosynthesis, upregulation of defence-related TFs (WRKYs, BZIP), proteolysis, energy metabolism pathways activated	Islam et al. 2020
Commercial extract (Marmarine)	*A. nodosum* (Phaeophyceae)	*P. melonis* (damping-off)	Cucumber (*Cucumis sativus*)	0.5% (most effective)	Foliar spray, root drench, spray+drench (30 mL/ plant, twice at 5–10 day intervals)	Greenhouse	Disease incidence ↓58–68% (spray + drench 0.5%); biomass ↑; complete control with Marmarine + fungicide; 1% phytotoxicity ↑	Induced systemic resistance: ↑β-1,3-glucanase, peroxidase, PPO activities; ↑total phenolics; ↑defense gene expression (Cupi4, LOX, PAL, GolS)	Abkhoo & Sabbagh 2016
Crude polysaccharide (CPS, sulphated, incl. λ-carrageenan)	*Acanthophora spicifera* (Rhodophyta)	*P. palmivora* (leaf fall)	Rubber tree (*Hevea brasiliensis*)	0.5 mg/mL	Leaf spraying (24h pretreatment)	*In vivo* (with pathogen)	Reduced infected leaves (~50%), reduced disease severity (2× less), increased SA and scopoletin accumulation (48–96h), increased PR gene expression (HbPR-1, HbGLU), decreased HbASI expression	Activation of SA pathway (↑salicylic acid, ↑scopoletin, ↑PR-protein genes), suppression of JA pathway (↓HbASI), modulation of defence enzymes (↑peroxidase, ↓catalase), no phytotoxicity	Pettongkhao et al. 2019

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Table 3. To be continued...

Extract type (crude/ compound/ product)	Seaweed species (Phylum)	Target pathogen (disease)	Host crop	Effective concentration	Application mode	Experimental condition	Efficacy results	Mechanism / mode of action	References
S. polycystum extract (SWE)	*S. polycystum* (Phaeophyceae)	*P. palmivora* (leaf fall)	Rubber tree (*Hevea brasiliensis*)	0.25 mg/mL	Foliar spray (24h before pathogen inoculation, 10 mL/ seedling)	Greenhouse	Disease index ↓42.3% (16.9 vs. 29.3 in control); SA accumulation ↑2.09-fold in distal leaves	Induction of antioxidant enzymes (CAT ↑, POD ↑); β-1,3-glucanase (GLU) ↑; phytoalexin scopoletin (Scp) ↑; SAR activation via SA signaling; lignin deposition ↑	Khompatara et al. 2019
Laminarin	*L. digitata* (Phaeophyceae)	*Plasmopara viticola* (downy mildew)	Grapevine (*Vitis vinifera* cv. Marselan)	1.0 g/L	Foliar spray (upper/lower leaf surfaces, 48h before inoculation)	Greenhouse (24/18°C day/night, 16h photoperiod, 70±10% RH)	Moderate disease reduction; no zoospore mobility effect; ↑MAPK activation (2 bands: 49 kD and 45 kD); ↑H_2O_2 production; weak callose deposition	Plant defense elicitation (↑MAPK activation, ↑H_2O_2, weak callose deposition); no direct antimicrobial activity	Paris et al. 2019
Alkaline extract	*U. lactuca* (Chlorophyta)	*Alternaria solani* (early blight)	Tomato (*Solanum lycopersicum*)	0.5% (*w/v*)	Foliar spray (6h before inoculation, 3× at 15-day intervals)	Greenhouse (25–30 °C, 70–85% RH, 40 days)	Disease index ↓45.8% (29.66% vs 54.74% control)	Induced resistance; ↑JA pathway, ↑defence enzymes (PAL, POD, PPO, CHI, GLU), ↑PIN II, ↑ETR-1; ↑total phenols	Ramkissoon et al. 2017
Alkaline extract	*S. filipendula* (Phaeophyceae)	*A. solani* (early blight)	Tomato (*Solanum lycopersicum*)	0.5% (*w/v*)	Foliar spray (6h before inoculation, 3× at 15-day intervals)	Greenhouse (25–30 °C, 70–85% RH, 40 days)	Disease index ↓28.9% (38.90% vs 54.74% control)	Induced resistance; ↑JA pathway, ↑defence enzymes (PAL, PPO, CHI), ↑PIN II, ↑ETR-1; ↑total phenols	Ramkissoon et al. 2017
Alkaline extract	*G. serrulatum* (Rhodophyta)	*A. solani* (early blight)	Tomato (*Solanum lycopersicum*)	0.5% (*w/v*)	Foliar spray (6h before inoculation, 3× at 15-day intervals)	Greenhouse (25–30 °C, 70–85% RH, 40 days)	Disease index ↓56.4% (23.86% vs 54.74% control)	Induced resistance; sequential ↑SA and JA pathways; ↑defence enzymes (CHI, GLU, PPO, PAL, POD), ↑PR-1a, ↑PIN II, ↑ETR-1; ↑total phenols	Ramkissoon et al. 2017
Aqueous extract (ASE)	*C. myriophylloides* (Phaeophyceae)	*Verticillium dahliae* (Verticillium wilt)	Tomato (*Solanum lycopersicum*)	0.5%	Foliar spray (2×, 7 and 3 days before inoculation)	Greenhouse (21–60 days)	Foliar alteration index ↓41–46%; stunting index ↓63–80%; vessel browning ↓87–96%; fruit yield ↑2.5× (0.5%)	Induced resistance; POX ↑, PPO ↑, H_2O_2 ↑; priming effect; no direct antifungal effect (ASE)	Esserti et al. 2016

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Table 3. To be continued...

Extract type (crude/ compound/ product)	Seaweed species (Phylum)	Target pathogen (disease)	Host crop	Effective concentration	Application mode	Experimental condition	Efficacy results	Mechanism / mode of action	References
Aqueous extract (ASE)	*F. spiralis* (Phaeophyceae)	*V. dahliae* (Verticillium wilt)	Tomato (*Solanum lycopersicum*)	0.5%	Foliar spray (2×, 7 and 3 days before inoculation)	Greenhouse (21–60 days)	Foliar alteration index ↓41–46%; stunting index ↓63–80%; vessel browning ↓87–96%; fruit yield ↑(0.5%)	Induced resistance; POX ↑, PPO ↑, H_2O_2 ↑; priming effect; no direct antifungal effect (ASE)	Esserti et al. 2016
Aqueous extract (ASE)	*L.digitata* (Phaeophyceae)	*V. dahliae* (Verticillium wilt)	Tomato (*Solanum lycopersicum*)	0.5%, 1.5%	Foliar spray (2×, 7 and 3 days before inoculation)	Greenhouse (21–60 days)	Foliar/stunting/ browning index: moderate reduction (less than *C. myriophylloides*, *F. spiralis*); no yield effect reported	Induced resistance; POX ↑, PPO ↑, H_2O_2 ↑; priming effect; no direct antifungal effect (ASE)	Esserti et al. 2016
Cold water extract (CWE)	*S. tenerrimum* (Phaeophyceae)	*Macrophomina phaseolina* (charcoal rot)	Tomato (*Solanum lycopersicum*)	10% (w/v, foliar spray, as part of S-extract)	Foliar spray	Greenhouse (vegetative & reproductive), hydroponics	Shoot length ↑1.2×, root length ↑1.17× (vs control); SA ↑1.4–1.8×, ABA ↑1.55× (vegetative), O_2^- ↑2.2× (vegetative); CAT, APX, POX ↑(stage-specific); fruit number, weight, girth ↑(vs control); all effects as part of S-extract combined application	Induces defence phytohormones (↑SA, ABA), enhances antioxidative enzymes (↑CAT, APX, POX), improves growth and yield under pathogen pressure	Khedia et al. 2020
Hot water extract (HWE)	*S. tenerrimum* (Phaeophyceae)	*M. phaseolina* (charcoal rot)	Tomato (*Solanum lycopersicum*)	10% (*w/v*, foliar spray, as part of S-extract)	Foliar spray	Greenhouse (vegetative & reproductive), hydroponics	Shoot/root length ↑, SA/ABA/ROS/ antioxidant enzymes ↑, fruit yield ↑(all as part of S-extract combined application, individual effect unknown)	Same as above (all effects measured as part of the combined S-extract)	Khedia et al. 2020

Table 3. To be continued...

Extract type (crude/ compound/ product)	Seaweed species (Phylum)	Target pathogen (disease)	Host crop	Effective concentration	Application mode	Experimental condition	Efficacy results	Mechanism / mode of action	References
Aqueous alkaline extract (AAE)	*S. tenerrimum* (Phaeophyceae)	*M. phaseolina* (charcoal rot)	Tomato (*Solanum lycopersicum*)	10% (*w/v*, foliar spray, as part of S-extract)	Foliar spray	Greenhouse (vegetative & reproductive), hydroponics	Shoot/root length ↑, SA/ABA/ROS/ antioxidant enzymes ↑, fruit yield ↑(all as part of S-extract combined application, individual effect unknown)	Same as above (all effects measured as part of the combined S-extract)	Khedia et al. 2020
Methanolic extract (MSE)	*C. myriophylloides* (Phaeophyceae)	*V. dahliae*	–	50, 100, 500 µg/mL (500 µg/mL)	Amended PDA (mycelial growth assay)	*In vitro* (5 days)	Mycelial growth inhibition: max ↓< 50% (500 µg/mL, only at the highest concentration)	Direct antifungal activity at high concentration	Khedia et al. 2020
Methanolic extract (MSE)	*F. spiralis* (Phaeophyceae)	*V. dahliae*	–	50, 100, 500 µg/mL (500 µg/mL)	Amended PDA (mycelial growth assay)	*In vitro* (5 days)	Mycelial growth inhibition: max ↓< 50% (500 µg/mL, only at the highest concentration)	Direct antifungal activity at high concentration	Khedia et al. 2020
Methanolic extract (MSE)	*L. digitata* (Phaeophyceae)	*V. dahliae*	–	50, 100, 500 µg/mL	Amended PDA (mycelial growth assay)	*In vitro* (5 days)	No significant inhibition observed	No direct antifungal effect	Khedia et al. 2020
Methanol extract (active fraction CA-F8)	*Chaetomorpha antennina* (Chlorophyta)	*A. solani* (early blight)	Tomato (*Solanum lycopersicum*)	50–100 ppm	Disc diffusion, broth dilution, spore germination, and mycelial dry weight	Laboratory (*in vitro*)	Spore germination ↓92.13% (100 ppm); mycelial dry weight ↓44.71%; MIC 3.27 µg/mL, MFC 12.5 µg/mL; inhibition zone up to 14.5 mm (100 ppm, vs. 14.8 mm for chemical control)	Direct antifungal activity (fatty acids, terpenoids, antioxidants); inhibits spore germination and mycelial growth	Chanthini et al. 2023

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Table 3. To be continued...

Extract type (crude/ compound/ product)	Seaweed species (Phylum)	Target pathogen (disease)	Host crop	Effective concentration	Application mode	Experimental condition	Efficacy results	Mechanism / mode of action	References
Methanol extract (active fraction CA-F8)	*C. antennina* (Chlorophyta)	*A. solani* (early blight)	Tomato (*Solanum lycopersicum*)	3.0 g/L (internodal injection)	Internodal injection, pathogen challenge	Greenhouse (*in vivo*)	Disease incidence ↓58.9%; disease severity ↓67.4%; disease control 63.8%; PPO activity ↑78.8%; PO activity ↑54.6%; foliar phenols ↑67.5%; SA detected only in treated plants (3.5 µg/mg FW); phenols peaked at 4 µg GAE/ mg FW (day 3); JA/ SA pathway activation	Induced resistance via SA/JA pathway, increased phenolics and defence enzymes (PPO, PO)	Chanthini et al. 2023
Oligo-carrageenan kappa	– (Rhodophyta)	*Botrytis cinerea* (gray mold)	Tobacco (*N. tabacum* var. Xanthi)	1.0 mg/mL	Foliar spray (upper/lower, weekly ×3)	Growth chamber (45 days)	*B. cinerea* infection: partial suppression	PAL activity ↑; phenylpropanoids ↑; PR proteins; broad	Vera et al. 2012
Oligo-carrageenan lambda	– (Rhodophyta)	*B. cinerea* (gray mold)	Tobacco (*N. tabacum* var. Xanthi)	1.0 mg/mL	Foliar spray (upper/lower, weekly ×3)	Growth chamber (45 days)	*B. cinerea* infection: complete suppression (most effective)	PAL activity ↑; phenylpropanoids ↑; PR proteins; broad	Vera et al. 2012
Oligo-carrageenan iota	– (Rhodophyta)	*B. cinerea* (gray mold)	Tobacco (*N. tabacum* var. Xanthi)	1.0 mg/mL	Foliar spray (upper/lower, weekly ×3)	Growth chamber (45 days)	*B. cinerea* infection: complete suppression (most effective)	PAL activity ↑; phenylpropanoids ↑; PR proteins; broad	Vera et al. 2012
κ-carrageenan (sulfated polysaccharide)	*K. alvarezii* (Rhodophyta)	*Septoria lycopersici* (leaf spot)	Tomato (*Solanum lycopersicum*, cv. PKM 1)	0.3% (*w/v*, foliar spray)	Foliar spray (until runoff, upper/lower leaf surface)	Greenhouse	Disease severity ↓32%; symptom onset delayed; pathogen colonization ↓	Induces ROS burst (↑H_2O_2, ↑O_2^-); enhances antioxidant enzymes (↑POD, ↑SOD); increases calcium oxalate crystals; upregulates chloroplast defense proteins (↑acid phosphatase, ↑CP12-1, ↑PSAK, ↑cytochrome proteins, ↑GATA TFs); restricts pathogen colonization	Mani et al. 2021

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Table 3. To be continued...

Extract type (crude/ compound/ product)	Seaweed species (Phylum)	Target pathogen (disease)	Host crop	Effective concentration	Application mode	Experimental condition	Efficacy results	Mechanism / mode of action	References
κ-carrageenan (sulfated polysaccharide)	*K. alvarezii* (Rhodophyta)	*Colletotrichum gloeosporioides* (anthracnose)	*Capsicum annuum*	0.5% (*in vitro*)	Added to PDA/PDB medium	Laboratory	Mycelial growth inhibition up to 100% ↓	Plasma membrane permeability of pathogen ↑→ fungal growth ↓	Mani & Nagarathnam 2018
κ-carrageenan (sulfated polysaccharide)	*K. alvarezii* (Rhodophyta)	*C. gloeosporioides* (anthracnose)	*C. annuum*	0.3% (*in vivo*)	Foliar spray at 40-day-old stage (24 h before inoculation)	Greenhouse	Disease severity reduced from 91.3% to 24% at day 10 ↓	Peroxidase (GPX) activity ↑; new peroxidase isoform ↑; PR1, PR5, NPR1 (SA pathway) ↑; PDF1.2 (JA pathway) ↑; new defense proteins (dehydroascorbate reductase I/II, NAD(P)H quinone oxidoreductase, eIF5A) ↑; immune priming ↑	Mani & Nagarathnam 2018
Laminarin (β-1,3-glucan)	*L. digitata* (Ochrophyta)	*Fusicladium oleagineum* (olive leaf spot)	*Olea europaea*	Not specified	Foliar spray at 4 weeks before inoculation (single) or at 4 and 2 weeks before inoculation (dual)	Greenhouse	Disease severity ↓up to 100% (dual application at 12 wpi); control efficacy ↑100%	Defence-related gene expression ↑(Pal, Lox, Cuao, Mpol, Bglu, Phely, Aldh1), rapid induction at 3 days post-application; PRR priming; eco-friendly copper alternative	Tziros et al. 2021
Ulvan (sulfated polysaccharide)	*U. fasciata* (Chlorophyta)	*F. oxysporum* f. sp. *phaseoli* (Fusarium wilt)	Common bean (*Phaseolus vulgaris*)	10 mg/mL	Seed soaking (4h, 25 °C)	Greenhouse	Seedling emergence ↑55% (Fop-infested), ↑30% (non-infested), ↑44% (sterilised substrate); no effect on disease severity	Promotes seedling emergence, likely via biostimulation, improved nutrient uptake, and/or oligosaccharide signalling	de Borba et al. 2019
Ulvan (sulfated polysaccharide)	*U. fasciata* (Chlorophyta)	*F. oxysporum* f. sp. *phaseoli* (Fusarium wilt)	Common bean (*P. vulgaris*)	10 mg/mL	Soil irrigation	Greenhouse	No significant effect on seedling emergence or disease severity	Not effective for disease suppression by this method	de Borba et al. 2019

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Table 3. To be continued...

Extract type (crude/ compound/ product)	Seaweed species (Phylum)	Target pathogen (disease)	Host crop	Effective concentration	Application mode	Experimental condition	Efficacy results	Mechanism / mode of action	References
Ulvan (sulfated polysaccharide)	*U. fasciata* (Chlorophyta)	*F. oxysporum* f. sp. *phaseoli* (Fusarium wilt)	Common bean (*Phaseolus vulgaris*)	10 mg/mL	Foliar spray (1–3 times, until runoff)	Greenhous	Disease severity ↓38% (CIAT scale); area under disease progress curve (AUDPC) ↓27%; fungal colonisation in epicotyls ↓70% (up to 20 days); delayed symptom onset (by 4-8 days); no effect after 38 days	Induces resistance (↑PAL, ↑phenolics, ↑lignin); blocks/delays xylem colonisation by pathogen; effect is transient/early stage	de Borba et al. 2019
Ulvan	*U. fasciata* (Chlorophyta)	*Blumeria graminis* f. sp. *Tritici* (Powdery mildew)	–	1.0 mg/mL	Agar medium	*In vitro*	Non-germinated conidia ↓34%, multiple germ tubes ↑81%	Altered germination pattern (no direct inhibition; ↑multiple germ tubes, ↓non-germinated conidia)	Velho et al. 2022
Ulvan	*U. fasciata* (Chlorophyta)	*B. graminis* f. sp. *Tritici* (Powdery mildew)	Wheat (*Triticum aestivum*)	1.0 mg/mL	Foliar spray	*In vivo*	Disease incidence ↓42%, fluorescent papillae ↑13%, localised H_2O_2 ↑90% (24 hai), POX ↑60% (24 hai), LOX ↑45% (24 hai), PAL ↑2.5-fold (48 hai)	Induced plant defence (↑papillae, ↑H_2O_2, ↑phenolics, ↑POX/LOX/PAL activity, ↑phenylpropanoid & PR genes: PAL, CHS, COMT, ANS, FLS, PR1, PR9, PR15, LOX)	Velho et al. 2022
Ulvan	*U. fasciata* (Chlorophyta)	*Zymoseptoria tritici* [Septoria tritici blotch (STB)]	–	10 mg/mL	PDA medium	*In vitro*	No effect on spore germination or mycelial growth	No direct antifungal activity	de Borba et al. 2021
Ulvan	*U. fasciata* (Chlorophyta)	*Z. tritici* [Septoria tritici blotch (STB)]	Wheat (*T. aestivum*)	10 mg/mL	Foliar spray	*In vivo*	Disease severity ↓45%, pycnidia ↓50%, substomatal colonization ↓51%	Induced resistance (↑PR-2, ↑PR-3, ↑OXO, ↑LOX, ↑AOS; no change in PAL/CHS; no major metabolome alteration)	de Borba et al. 2021

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Table 3. To be continued...

Extract type (crude/ compound/ product)	Seaweed species (Phylum)	Target pathogen (disease)	Host crop	Effective concentration	Application mode	Experimental condition	Efficacy results	Mechanism / mode of action	References
A. nodosum extract (ANE)	*A. nodosum* (Phaeophyceae)	*Podosphaera aphanis* (Powdery mildew)	Strawberry (*Fragaria* × *ananassa*)	0.2% (*w/v*)	Foliar spray	Detached leaf, chamber	Spore germination ↓75%, infected leaf area ↓29.1%, disease severity ↓65.7% (7 dpi) and ↓71% (15 dpi)	↑PAL, PPO, PO activity, ↑phenolic (51.5%) and flavonoid (47.2%) content, PRR-mediated defence, acts as (PAMPs)-like elicitor	Bajpai et al. 2019
Water extract (WE)	*Ecklonia* sp. (Phaeophyceae)	*B. cinerea* (gray mold)	–	5.0 mg/mL (plateau)	*In vitro* (colony plug)	*in vitro*	Colony growth ↓18.2→16.8 mm/day (7.7% reduction)	Direct antifungal activity	Righini et al. 2019
Water extract (WE)	*Jania* sp. (Rhodophyta)	*B. cinerea* (gray mold)	–	5.0 mg/mL (plateau)	*In vitro* (colony plug)	*in vitro*	Colony growth ↓18.7→16.8 mm/day (10.2% reduction)	Direct antifungal activity	Righini et al. 2019
Polysaccharide (POL)	*E.* sp. (Phaeophyceae)	*B. cinerea* (gray mold)	–	0.5–3.5 mg/mL	*In vitro* (colony, spores, CFU)	*in vitro*	Colony growth ↓15.4–25.6%; EC_{50} spore 0.096 mg/mL; EC_{50} CFU 1.201 mg/mL	Direct broad-spectrum antifungal	Righini et al. 2019
Polysaccharide (POL)	*Jania* sp. (Rhodophyta)	*B. cinerea* (gray mold)	–	0.5–3.5 mg/mL	*In vitro* (colony, spores, CFU)	*in vitro*	No colony/CFU effect; EC_{50} spore 0.202 mg/mL only	Selective spore inhibition only	Righini et al. 2019
Polysaccharide (POL)	*E.* sp. (Phaeophyceae)	*B. cinerea* (gray mold)	Strawberry (*Fragaria* × *ananassa*)	3.5 mg/mL (highest)	Pre-harvest fruit dip	Greenhouse	Infected area ↓~19.7%; sporulation up to 79.2%	Direct antifungal + plant defence	Righini et al. 2019
Polysaccharide (POL)	*Jania* sp. (Rhodophyta)	*B. cinerea* (gray mold)	Strawberry (*Fragaria* × *ananassa*)	2.0–3.5 mg/mL (plateau at 2.0)	Pre-harvest fruit dip	Greenhouse	Infected area ↓~92.9%; sporulation 96.7–97.4%	Strong plant defence elicitation	Righini et al. 2019
Ethyl acetate extract (JE)	*Jania* sp. (Rhodophyta)	*F. oxysporum* f. sp. *lycopersici* (Fusarium wilt)	–	1 000 µg/mL	Agar well diffusion	Laboratory (*in vitro*)	Inhibition zone: 20 mm	Direct antifungal activity	Abdelaziz et al. 2024

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Table 3. To be continued...

Extract type (crude/ compound/ product)	Seaweed species (Phylum)	Target pathogen (disease)	Host crop	Effective concentration	Application mode	Experimental condition	Efficacy results	Mechanism / mode of action	References
Ethyl acetate extract (JE)	*Jania* sp. (Rhodophyta)	*F. oxysporum* f. sp. *lycopersici* (Fusarium wilt)	Tomato (*Solanum lycopersicum* variety 023)	10 mg/mL	Foliar spray (7 days before inoculation)	Greenhouse (*in vivo*)	PDI ↓20.83%, protection 77.25%, growth recovery (SL +35%, RL +49.1%, LN +31.6%), Chl a/b recovery ↑	↑Total phenolics, ↑proline, ↑POD/PPO activity, ↑antioxidant enzymes, induced resistance, isozyme diversification	Abdelaziz et al. 2024
Ethyl acetate extract (JE)	*Jania* sp. (Rhodophyta)	*F. oxysporum* f. sp. *lycopersici* (Fusarium wilt)	Tomato (*Solanum lycopersicum* variety 023)	10 mg/mL	Soil irrigation (7 days before inoculation)	Greenhouse (*in vivo*)	PDI ↓33.33%, protection 63.61%, growth recovery (SL +22%, RL +26.83%, LN +12.5%), carotenoid recovery ↑	↑Total phenolics, ↑proline, ↑POD/PPO activity, ↑antioxidant enzymes, induced resistance, isozyme diversification	Abdelaziz et al. 2024
Aqueous extract	*E. maxima* (Phaeophyceae)	*Rhizoctonia solani* (root/ crown rot)	Tomato cv. Marmande	10.0 mg/mL	Seed priming	Greenhouse	Emergence ↑, seedling dry weight ↑, stem calibre ↑, disease index ↓, chitinase activity ↑(all concentrations, but lower than JAN/ANA), total C/N ↑, lignin ↑ (5.0/10.0 mg/mL)	Induced plant defence (chitinase, lignin), direct antifungal effect, nutrient enrichment	Righini et al. 2021
Aqueous extract	*J. adhaerens* (Rhodophyta)	*R. solani* (root/ crown rot)	Tomato cv. Marmande	10.0 mg/mL	Seed priming	Greenhouse	Emergence ↑, seedling dry weight ↑, stem calibre ↑, disease index ↓, chitinase activity ↑(highest at 2.5/5.0 mg/mL), total C/N ↑, lignin ↑(all concentrations, progressive increase)	Induced plant defence (chitinase, lignin), direct antifungal effect, nutrient enrichment	Righini et al. 2021

Table 3. To be continued...

Extract type (crude/ compound/ product)	Seaweed species (Phylum)	Target pathogen (disease)	Host crop	Effective concentration	Application mode	Experimental condition	Efficacy results	Mechanism / mode of action	References
Aqueous extract	*A. nodosum* (Phaeophyceae)	*R. solani* (root rot)	Pea (*Pisum sativum*)	3% (*w/v*)	Seed soaking (3h)	Greenhouse	Shoot/root length ↑, dry weight ↑, leaf area ↑, yield ↑, photosynthetic pigments ↑, phenolics ↑, POD/ PPO ↑, defence gene expression ↑, disease severity ↓	Synergistic immune induction (JERF3, POD, CHI II ↑), antioxidant/phenolic pathway ↑, cell wall strengthening	Rashad et al. 2022
Aqueous extract	*S. vulgare* (Phaeophyceae)	*R. solani* (root rot)	Sugar beet (*Beta vulgaris*)	100 g/L stock solution	Seed coating (8h, with Tween 20)	Greenhouse (2 seasons: 2020/2021, 2021/2022)	Disease severity ↓70.82%, disease incidence ↓44.45%, total weight ↑41%, root length ↑25%, root weight ↑333%, root diameter ↑20%, sucrose ↑40.7%, TSS ↑5.0%	Direct antifungal effect (disease severity/incidence reduction) + growth promotion (enhanced root and plant development) + quality enhancement (improved sucrose and TSS)	Abdelwahab et al. 2023
Aqueous extract	*S. vulgare* (Phaeophyceae)	*Sclerotium rolfsii* (root rot)	Sugar beet (*Beta vulgaris*)	100 g/L stock solution	Seed coating (8h, with Tween 20)	Greenhouse (2 seasons: 2020/2021, 2021/2022)	Disease severity ↓52.00%, disease incidence ↓36.92%, total weight ↑12%, root length ↑300%, root weight ↑167%, root diameter ↑120%, sucrose ↑61.1%, TSS ↑200%	Direct antifungal effect (disease severity/incidence reduction) + growth promotion (enhanced root and plant development) + quality enhancement (improved sucrose and TSS)	Abdelwahab et al. 2023

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Table 4. Nematicidal and insecticidal properties of seaweed extracts

Extract type (crude/ compound/ product)	Seaweed species (Phylum)	Target pathogen (disease)	Host crop	Effective concentration	Application mode	Experimental condition	Efficacy results	Mechanism / mode of action	References
Ethanolic extract	*U. fasciata* (Chlorophyta)	*Meloidogyne incognita* (root-knot)	–	1.0 mg/mL (0.125–1.0 mg/mL)	*In vitro* (egg/J2 soaking)	*In vitro*	Egg hatch ↓81.4–87% (3 days); J2 mortality ↑85% (12h, 1.0 mg/mL)	Direct nematicidal effect (egg hatching inhibition, juvenile mortality)	Ghareeb et al. 2019
Ethanolic extract	*Corallina officinalis* (Rhodophyta)	*M. incognita* (root-knot)	–	1.0 mg/mL (0.125–1.0 mg/mL)	*In vitro* (egg/J2 soaking)	*In vitro*	Egg hatch ↓50–60%; J2 mortality ↑80.4% (12h, 0.5 mg/mL)	Direct nematicidal effect (egg hatching inhibition, juvenile mortality)	Ghareeb et al. 2019
Ethanolic extract	*C. mediterranea* (Rhodophyta)	*M. incognita* (root-knot)	–	1.0 mg/mL (0.125–1.0 mg/mL)	*In vitro* (egg/J2 soaking)	*In vitro*	Egg hatch ↓35-40%; J2 mortality ↑(data not specified, dose-dependent)	Direct nematicidal effect (egg hatching inhibition, juvenile mortality)	Ghareeb et al. 2019
Ethanolic extract	*U. fasciata* (Chlorophyta)	*M. incognita* (root-knot)	Tomato	1.0 mg/mL	Soil drench (2×, 150 mL/pot)	Greenhouse (4-week seedlings, 5 000 eggs + J2 at day 10)	Galls ↓77.5%; egg mass ↓74%; eggs ↓75.6%; J2/soil ↓73.2%; RF ↓75.7%	↑POD, ↑PPO, ↑chitinase gene (defence activation); growth promotion; no phyto-toxicity	Ghareeb et al. 2019
Ethanolic extract	*C. officinalis* (Rhodophyta)	*M. incognita* (root-knot)	Tomato	1.0 mg/mL	Soil drench (2×, 150 mL/pot)	Greenhouse (4-week seedlings, 5 000 eggs + J2 at day 10)	Galls ↓50.3%; egg mass ↓58.5%; eggs ↓62.4%; J2/soil ↓68.6%; RF ↓62.4%	↑POD, ↑PPO, ↑chitinase gene (defence activation); growth promotion; no phytotoxicity	Ghareeb et al. 2019
Ethanolic extract	*C. mediterranea* (Rhodophyta)	*M. incognita* (root-knot)	Tomato	1.0 mg/mL	Soil drench (2×, 150 mL/pot)	Greenhouse (4-week seedlings, 5 000 eggs + J2 at day 10)	Galls ↓34.7%; egg mass ↓39%; eggs ↓40.3%; J2/soil ↓36.4%; RF ↓40.3%	↓POD, ↑PPO, ↑chitinase gene (defence activation); growth promotion; no phytotoxicity	Ghareeb et al. 2019
OSMO® (alkaline extract)	*A. nodosum* (Phaeophyceae)	*M. chitwoodi* (root-knot)	Tomato	10 mL/L	Soil drench (at transplant and every 5 days × 20d)	*In vivo*	J2/g root ↓(ns), root biomass ↑(vs. control), no significant effect on shoot	↓Infectivity when J2 pre-exposed (24 h) weakens the host location and orientation ability	Ngala et al. 2015
OSMO® (alkaline extract)	*A. nodosum* (Phaeophyceae)	M. chitwoodi	–	100%, 50% (100% = 10 mL/L)	Direct egg mass immersion; J2 pre-exposure	*In vitro*	100%/50%: hatching ↓, delayed 8 days; 25%/10%: no effect; pre-exposed J2: infectivity ↓after 24h	↓Egg hatch (100%/50% concentration), ↓infectivity when pre-exposed (24h)	Ngala et al. 2015

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Table 4. To be continued...

Extract type (crude/ compound/ product)	Seaweed species (Phylum)	Target pathogen (disease)	Host crop	Effective concentration	Application mode	Experimental condition	Efficacy results	Mechanism / mode of action	References
OSMO® (alkaline extract)	*A. nodosum* (Phaeophyceae)	*M. hapla* (root-knot)	Tomato	10 mL/L	Soil drench (same as above)	*In vivo*	J2/g root (ns); no effect on nematode number per g root vs. control	No clear effect on reproduction at this dose, but ↑root biomass	Ngala et al. 2015
OSMO® (alkaline extract)	*A. nodosum* (Phaeophyceae)	*M. hapla*	–	100%, 50%, 25%, 10%	Egg mass immersion; J2 pre-exposure	*In vitro*	All concentrations: no effect on hatch; pre-exposure (24h) reduces infectivity	No effect on egg hatching; ↓infectivity when pre-exposed (24 h) – species-specific response	Ngala et al. 2015
Kelpak (cell-burst extract)	*Ecklon maxima* (Phaeophyceae)	*M. chitwoodi*	Tomato	10 mL/L	Soil drench (same as above)	*In vivo*	J2/g root ↓(ns); reduced root damage (vs. control)	No significant effect on nematode population, but ↑plant tolerance	Ngala et al. 2015
Kelpak (cell-burst extract)	*E. maxima* (Phaeophyceae)	*M. chitwoodi*	–	100%, 50%, 25%, 10%	Egg mass immersion; J2 pre-exposure	*In vitro*	No effect on hatch; pre-exposure (24h): ↑root location but ↓infectivity (paradoxical effect)	↑J2 root location, but ↓infectivity when pre-exposed (24 h)	Ngala et al. 2015
Kelpak (cell-burst extract)	*E. maxima* (Phaeophyceae)	*M. hapla*	Tomato	10 mL/L	Soil drench (same as above)	*In vivo*	J2/g root ↓(significant vs. control); reduced root damage	↓Nematode multiplication; ↑plant tolerance	Ngala et al. 2015
Kelpak (cell-burst extract)	*E. ia maxima* (Phaeophyceae)	*M. hapla*	–	100%, 50%, 25%, 10%	Egg mass immersion; J2 pre-exposure	*In vitro*	No effect on hatch; pre-exposure (6h) ↑J2 location to root	↑J2 chemotaxis and ↑infectivity when pre-exposed (6 h)	Ngala et al. 2015
Eckol	*E. maxima* (Phaeophyceae)	*Brevicoryne brassicae* (cabbage aphid)	–	10^{-4}–10^{-7} M	Leaf disc treatment	*In vivo* (insect bioassay)	Aphid mortality ↑(concentration-dependent)	Direct insecticidal toxicity	Rengasamy et al. 2016
Eckol	*E. maxima* (Phaeophyceae)	*B. brassicae* (cabbage aphid)	Cabbage (*Brassica oleracea* var. Drumhead)	10^{-6} M	Foliar spray	*In vivo*	Aphid infestation 0% (treated), severe in control; myrosinase ↑, phenolics/flavonoids/ tannins ↑(stress marker)	Induced resistance (↑myrosinase, glucosinolate pathway)	Rengasamy et al. 2016
Ethanolic extract	*Laurencia johnstonii* (Rhodophyta)	*Diaphorina citri* (Asian citrus psyllid)	Citrus (collected from *Citrus sinensis*)	Repellent: 2.5 mg/mL; Insecticidal: LD_{50} = 284 µg/mL	Foliar spray (choice test & contact bioassay)	*In vivo* (insect bioassay)	Repellency: IBT = 0.240 at 18 h (peak effect); insecticidal: 100% mortality at high concentration, rapid kill within 12 h	Repellent/insecticidal; sesquiterpenes (debromolaurinterol, isolaurinterol, and laurinterol) identified from ethanolic extract	González-Castro et al. 2019

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Table 4. To be continued...

Extract type (crude/ compound/ product)	Seaweed species (Phylum)	Target pathogen (disease)	Host crop	Effective concentration	Application mode	Experimental condition	Efficacy results	Mechanism / mode of action	References
Ethanolic extract	*S. horridum* (Phaeophyceae)	*D. citri* (Asian citrus psyllid)	Citrus (collected from *Citrus sinensis*)	Repellent: 2.5 mg/mL; Insecticidal: LD_{50} = 364 µg/mL	Foliar spray (choice test & contact bioassay)	*In vivo* (insect bioassay)	Repellency: IBT = 0.376 at 24 h (constant effect); insecticidal: 100% mortality at high concentration	Sustained repellent activity	González-Castro et al. 2019
Ethanolic extract	*Caulerpa sertularioides* (Chlorophyta)	*D. citri* (Asian citrus psyllid)	Citrus (collected from *Citrus sinensis*)	Repellent: 2.5 mg/mL; Insecticidal: LD_{50} = 3 703 µg/mL	Foliar spray (choice test & contact bioassay)	*In vivo* (insect bioassay)	Repellency: initial attractant (0–4 h, IBT = 0.610) → repellent after 8h (IBT = 0.297 at 12 h); insecticidal: lower activity than others	Biphasic behavioural response (attractant→repellent)	González-Castro et al. 2019
Fatty acid fraction (CFA)	*C. antennina* (Chlorophyta)	*Spodoptera litura* (tobacco cutworm)	–	100 mg/L	Foliar spray on leaves	*In vivo* (mortality bioassay)	Larval mortality: 97.734% (II instar); 96–98% across II-V instars; dose-dependent mortality (25–100 mg/L)	Direct toxicity; 19 fatty acids identified from CFA by GC-MS; major compounds: hexadecanoic acid (28.32%), octadecatrienoic acid (23.05%), linolenic acid (8.231%)	Chanthini et al. 2024
Fatty acid fraction (CFA)	*C. antennina* (Chlorophyta)	*S. litura* (tobacco cutworm)	Tomato (45-day-old)	20 µL/plant	Stem injection (internodal region)	Greenhouse	Induced resistance: larval weight ↓72.85%, pupal weight ↓60.78%, fecundity ↓58.91%; larval-pupal duration extended to 26-28 days; population survival ↓88% (12% vs 72% control); phenolics ↑4.0 µg GAE/mg FW; PO/PPO enzymes ↑76.75%; deformed adults with malformed wings/legs	Induced systemic resistance via SA pathway (3.5 µg/g FW SA); midgut cell disruption with epithelial damage; reduced nutrient utilisation: RCR ↓84%, ECD ↓38.8%; phosphatase enzymes ↓52.1%; detoxifying enzymes ↑(GST, CarE)	Chanthini et al. 2024

Table 4. To be continued...

Extract type (crude/ compound/ product)	Seaweed species (Phylum)	Target pathogen (disease)	Host crop	Effective concentration	Application mode	Experimental condition	Efficacy results	Mechanism / mode of action	References
Laminarin (β-1,3-glucan)	*L. digitata* (Phaeophyceae)	*Empoasca onukii* Matsuda (tea green leafhopper, TLH)	Tea (*Camellia sinensis* cv. 'Longjing 43')	200 mg/L	Foliar spray at the 2nd fully expanded leaf stage (both upper and lower leaf surfaces)	Growth chamber	TLH preference ↓, oviposition ↓, nymph survival ↓; Parasitoid (*S. empoascae*) attraction ↑; Defense signaling: CsMAPK↑, CsWRKY3↑ (1–2 h); H_2O_2 burst (1 h); SA/ABA↑ (peaked 8 h), JA unchanged; Defense enzymes: PPO↑ (peaked 2 days), chitinase↑ (2 –7 days), PAL↑ (1–5 days); Callose deposition↑ (peaked 2 days); FLS↑; Volatile emissions↑ ; GLVs and terpenes enhanced in Lam+TLH vs TLH treatment (12 compounds: 4 GLVs, 6 terpenes, indole, unknown significantly ↑)	Induced systemic resistance via MAPK cascade and WRKY transcription factor activation; SA/ABA signalling pathways (JA-independent); Direct defence: oxidative burst (H_2O_2), defence enzyme activation, structural barriers (callose), flavonoid biosynthesis; Indirect defence: enhanced volatile emission for tritrophic interactions and natural enemy recruitment	Xin et al. 2019

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Ahnfeltiopsis durvillaei proved highly effective against tobacco mosaic virus (TMV) at a sprayed concentration of 0.5 mg/L. Weekly foliar applications reduced TMV lesion numbers by up to 80% while suppressing systemic viral spread (Vera et al. 2011). Interestingly, Vera and coworkers evaluated the protective efficacy of oligo-carrageenans (κ, λ, and ι) against broad-range pathogens, including viruses, bacteria, and fungi, in tobacco plants (Vera et al. 2012). In the case of the virus test, the λ form of oligo-carrageenans provided the most durable TMV suppression over 45 days when applied weekly at 1 mg/mL. At the same time, oligo-carrageenans (κ and ι) were detected to offer only partial protection (Vera et al. 2012). Furthermore, Nagorskaya and colleagues tested κ/β-carrageenan from *Tichocarpus crinitus* in both *in vitro* and *in planta* conditions. The study confirmed direct antiviral activity. Additionally, when co-applied with TMV via leaf rub-inoculation, it led to an 87% reduction in necrotic lesions compared to virus-only controls (Nagorskaya et al. 2008).

Bacterial pathogens. Studies exploring seaweed-derived compounds and their effects on various biotic stress factors were summarised in Table 2. A variety of diverse chemical compounds derived from seaweed, such as peptides, polysaccharides, alkaloids, diterpenes, polyketides, phlorotannins, sterols, lipids, and quinones, have been shown to possess antibacterial properties (Perez et al. 2016; Zouaoui & Ghalem 2018; Ali et al. 2023). However, in some cases, the specific compounds responsible for these antibacterial effects have not been identified fully, and the bioactivity was attributed generally to crude extracts. Moreover, the antimicrobial activity of seaweed compounds against bacterial phytopathogens has been less studied than the extensive research on antibacterial activity against human pathogens (Asimakis et al. 2022; Vicente et al. 2022). Despite this research gap, recent investigations have revealed that specific compounds derived from seaweed and their extracts possess significant antibacterial properties against phytopathogenic bacteria. Seaweed-derived polysaccharides and their derivatives, including fucoidan enzymatic hydrolysate (FEH), alginate oligosaccharide (AOS), and oligo-carrageenan (κ, λ, and ι), demonstrate significant antibacterial efficacy through induced resistance mechanisms against bacterial pathogens (Vera et al. 2012; Zhang et al. 2019; Wang et al. 2023b). For example, FEH and AOS both enhanced resistance against *Pseudomonas syringae* pv. tomato DC3000 in Arabidopsis (Zhang et al. 2019; Wang et al. 2023b). Leaf infiltration with 400 μg/mL FEH achieved logarithmic reductions in bacterial populations. At the same time, 25 mg/L AOS foliar sprays applied three days pre-inoculation reduced disease severity by 35.6% and bacterial colony-forming unit (CFU) counts by approximately 79% (Zhang et al. 2019; Wang et al. 2023b). Vera and coworkers assessed the biocontrol effect of oligo-carrageenans (κ, λ, and ι) against the bacterial pathogen, *Pectobacterium carotovorum* (soft rot), in tobacco plants (Vera et al. 2012). Notably, the impact of these oligo-carrageenans was found to vary slightly depending on their structural difference. Weekly foliar applications of the ι-type oligo-carrageenans at 1 mg/mL provided excellent efficacy, followed by λ- and ι-types, resulting in lesion diameter reductions ranging from 74–83% and bacterial population suppression in the range of 87% to 99% (Vera et al. 2012).

Fungi-like and fungal pathogens. *Oomycetes.* Research on seaweed extracts' oomyceticidal and fungicidal activities is compiled in Table 3. Paris and associates evaluated that laminarin from *Laminaria digitata* had a moderate effect on reducing disease caused by *Plasmopara viticola* in grapevine (*Vitis vinifera* cv. Marselan). This outcome was achieved by applying a 1 g/L foliar spray to upper and lower leaf surfaces 48 h before pathogen inoculation (Paris et al. 2019). However, limited research has been conducted on the biocontrol efficacy test of seaweed extracts, particularly isolated compounds, against oomycete pathogens. Other studies have investigated crude and commercial seaweed extracts from both Phaeophyceae and Rhodophyta, demonstrating their protective effect through plant defence elicitation mechanisms against oomycete pathogens (Abkhoo & Sabbagh 2016; Khompatara et al. 2019; Pettongkhao et al. 2019; Islam et al. 2020).

Ascomycetes. Investigations on seaweed metabolites against ascomycota plant pathogens have been focused primarily on three major polysaccharide classes: carrageenan, laminarin, and ulvan. Each compound exhibits distinct biocontrol mechanisms and efficacy profiles (Table 3). Oligo-carrageenans (κ, λ, and ι) exhibited differential disease suppression against *Botrytis cinerea* in tobacco (Vera et al. 2012). While oligo-carrageenan (κ) only partially suppressed gray mold infection, both λ- and ι-types achieved

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complete suppression when applied as weekly foliar sprays at 1 mg/mL (Vera et al. 2012). This finding was consistent with earlier research showing that oligo-carrageenan's effectiveness against viruses and bacteria varied based on its structure. In addition to stimulating plant defences, kappa-carrageenan sourced from *Kappaphycus alvarezii* proved highly effective against *Colletotrichum gloeosporioides*. It directly inhibited fungal mycelial growth by disrupting the plasma membrane, and limited disease severity to 24% (versus 91.3% in untreated controls) at 10 days post-inoculation in greenhouse settings (Mani & Nagarathnam 2018). Interestingly, laminarin exhibited remarkable efficacy against *Fusicladium oleagineum*, achieving up to 100% disease control of olive leaf spot when applied as dual foliar sprays (Tziros et al. 2021). A previous study evaluated ulvan's potential for seedling emergence and its effects on inhibiting bean seedlings infected with *Fusarium oxysporum* f. sp. *phaseoli*, which is responsible for fusarium wilt disease. As a result, ulvan greatly improved the seedling growth of beans by 55%, 30%, and 44% on fusarium-infested, non-infested, and sterilised substrates, respectively, at 10 mg/mL (de Borba et al. 2019). This study also revealed that ulvan, a sulfated polysaccharide derived from *U. fasciata*, depended on delivery method (de Borba et al. 2019). In particular, ulvan showed the most effectiveness when foliar spray was applied against *F. oxysporum* by achieving a 38% reduction in disease severity and a 70% decrease in fungal colonisation in epicotyls. However, its protective effect was transient and lasted only until 20 days post-application.

Velho and coworkers demonstrated that treating ulvan reduced disease incidence in wheat against powdery mildew (*Blumeria graminis*) by 42% after foliar spray, while showing no direct inhibitory effect on conidial germination, it increased multiple germ tubes (Velho et al. 2022). In another study, ulvan showed no direct antifungal activity against *Zymoseptoria tritici* but acquired a 45% reduction in disease severity through induced resistance mechanisms when applied as a foliar spray to wheat plants (de Borba et al. 2021). Further investigations on seaweed extracts against various ascomycetous pathogens, including their mechanisms of action and efficacy parameters, are detailed in Table 3.

Basidiomycetes. As previously described, there is a significant paucity of in planta studies specifically examining the efficacy of seaweed-derived compounds against basidiomycota pathogens. However, several studies have assessed the biocontrol potential of seaweed extracts through both *in vitro* and *in planta* evaluations by offering promising insights into their practical applicability for disease management (Table 3). The biocontrol effect of seaweed extracts on *R. solani*, a soilborne plant pathogen for root and crown rot, has been examined tomato, pea, and sugar beet. In tomato systems, seed priming with aqueous extracts of both *E. maxima* and *Jania adhaerens* reduced disease index through induction of plant defence responses, including enhanced chitinase activity and lignin accumulation. Moreover, the treatments promoted plant growth by improving emergence rate and seedling weight (Righini et al. 2021). Similarly, aqueous *A. nodosum* treatment in pea via the seed soaking method elevates the overall growth parameters by enhancing shoot, root, weight, and leaf area values, reducing disease severity indices (Rashad et al. 2022). The most pronounced effects were observed with *Sargassum vulgare* in sugar beet, with seed coating treatments producing substantial improvements in root development metrics and a 70.82% reduction in *R. solani* severity (Abdelwahab et al. 2023). In addition to the *R. solani* data, another study examined *Sclerotium rolfsii*, a soilborne pathogen causing root rot disease. *S. vulgare* (Phaeophyceae) extracts also exhibited dual functionality after seed coating treatment in sugar beet by maintaining protective efficacy with a 52% reduction in disease severity and a 36.92% decrease in disease incidence against *S. rolfsii*. Simultaneously, the treatment enhanced crop quality by increasing sucrose and total soluble solids in sugar beet plants (Abdelwahab et al. 2023). These findings suggest that water-extractable compounds from brown and red algae applied at the seed level may have dual capacity for growth promotion and pathogen resistance activation within a single biostimulant treatment.

Nematodes. Research on the nematicidal properties of seaweed compounds remains limited compared to studies targeting fungal and bacterial pathogens. The available literature on the genus *Meloidogyne* with the controlling mechanism is tabulated in Table 4. Ghareeb and coworkers investigated the direct nematicidal activity of ethanolic extracts from *U. fasciata*, *Corallina officinalis*, and *Corallina mediterranea*. They conducted tests on the impact of these extracts on egg hatching and J2 mortality of *Meloidogyne incognita*. The *U. fas-*

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ciata extract demonstrated superior direct nematicidal efficacy compared to the others. At 1 mg/mL concentrations, it suppressed *M. incognita* egg hatching by 81.4–87% and caused 85% juvenile mortality within 12 h, whereas the remaining extracts showed moderate direct effects (Ghareeb et al. 2019). For the greenhouse pot test, 4-week-old tomato seedlings received dual soil drench applications (150 mL/pot) at a 1 mg/mL concentration 2 days after transplanting. A second application was given immediately after nematode inoculation with 5 000 eggs and freshly hatched J2 on day 10. Substantial treatment effects were observed after 60 days of incubation. Notably, *U. fasciata* significantly reduced gall formation by 77.5%, egg masses by 74%, and reproduction factors by 75.7% compared to the other treatments. Similarly, commercial formulations from *A. nodosum* (OSMO®) and *E. maxima* (Kelpak) showed variable nematicidal effects with primary impacts on nematode behaviour and plant tolerance rather than direct population suppression (Ngala et al. 2015) (Table 4).

Insect. While systematic *in vivo* studies on the insecticidal activity of seaweed-derived metabolites remain relatively limited, Rengasamy and coworkers conducted a detailed investigation on examining a purified metabolite, eckol from *E. maxima*, evaluating its efficacy against the cabbage aphid (*Brevicoryne brassicae*) (Table 4) (Rengasamy et al. 2016). Direct *in vitro* bioassays based on the leaf disc method resulted in 80–90% mortality within 24 h, thereby confirming the dose-dependent (10^{-4} to 10^{-7} M) insecticidal properties of eckol. In addition, foliar spray applications at 10^{-6} M completely prevented aphid colonisation on cabbage plants, while untreated controls suffered from severe infestations (Rengasamy et al. 2016). Similarly, other studies have applied seaweed extracts against Asian citrus psyllid (*Diaphorina citri*) and tobacco cutworms (*Spodoptera litura*) through various *in vivo* methodologies (González-Castro et al. 2019; Chanthini et al. 2024). González-Castro and coworkers reported that the ethanolic extract of *Laurencia johnstonii* exhibited potent inhibitory activity against *D. citri* with LD_{50} = 284 µg/mL. To understand the main components of that extract, GC-MS analysis was performed, and three major sesquiterpenes (debromolaurinterol, isolaurinterol, and laurinterol) were identified, which may be responsible for the observed repellent and insecticidal activities (González-Castro et al. 2019). Meanwhile, *Chaetomorpha antennina* fatty acid fractions exhibited dual-mode efficacy against *S. litura*, achieving 97.7% direct mortality through contact bioassays, and 88% population suppression via stem injection-induced plant resistance (Chanthini et al. 2024). These diverse experimental approaches, such as repellent assays, mortality bioassays, and plant-mediated resistance protocols, revealed species-specific active compounds and multitarget mechanisms, positioning seaweed extracts as promising sustainable alternatives for integrated pest management strategies. Extending beyond direct insecticidal approaches, recent investigations have demonstrated the efficacy of marine-derived elicitors in activating plant-mediated defence responses against piercing herbivores. A comprehensive study examined laminarin against the tea green leafhopper (TLH) (*Empoasca onukii* Matsuda) in tea plants (Xin et al. 2019). Foliar applications at 200 mg/L triggered systemic resistance through dual mechanisms encompassing direct anti-herbivore effects by decreasing TLH preference, reducing oviposition, and lowering nymph survival. Notably, laminarin enhanced volatile emissions, enriching terpenes and green leaf volatiles, which may attract the specialist egg parasitoid *Stethynium empoascae* (Xin et al. 2019). These comprehensive findings demonstrate the significant potential of seaweed-derived compounds and extracts involving both direct pathogen inhibition and enhanced host defence responses in response to a wide range of biotic stresses. This broad-spectrum activity, characterised by concentration-, application-, and timing-dependent efficacy, underscores the value of incorporating seaweed-based products in sustainable agriculture to improve crop resilience and productivity.

Mechanism of action of seaweed metabolites against plant pathogens

Seaweed metabolites confer plant protection against biotic stresses through multiple interconnected mechanisms, including immune priming and pattern recognition receptor activation with upregulation of 651 immune-related genes (NHL10, OXI1, WRKY30) (Tziros et al. 2021; Wang et al. 2023b), modulation of salicylic acid signaling pathways (involving PR1, NPR1, PR5 gene expression) (Mani & Nagarathnam 2018; Zhang et al. 2019) and jasmonic acid pathways (through LOX, AOS enzyme activation and PDF1.2 expression) (Sangha

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et al. 2015; Mani & Nagarathnam 2018), enhancement of phenylpropanoid metabolism (via PAL enzyme with 5-fold activity increases, and CHS, COMT, ANS, FLS gene expression) (Vera et al. 2012; Velho et al. 2022), ROS generation and antioxidant enzyme activation (POD, SOD with 60% activity increases, GPX) (Mani et al. 2021; Velho et al. 2022), MAPK cascade signaling (MAPK3/6 activation) (Wang et al. 2023b), and direct antimicrobial effects through membrane disruption and viral interference (Nagorskaya et al. 2008; Mani & Nagarathnam 2018) (Figure 1).

Immune priming and pattern recognition. Plant innate immune systems initiate primary defence mechanisms by detecting PAMPs by specialised pattern-recognition receptors (PRRs), which trigger microbial recognition and subsequent defensive responses (Zipfel 2009). Beyond microbial sources, certain seaweed-derived metabolites also function as biological elicitors and trigger plant immune responses via PRRs priming mechanisms (Tziros et al. 2021). In a previous study, κ-carrageenan was observed to enhance the immune responsiveness of tobacco plants. However, actinomycin D treatment, a transcriptional inhibitor, significantly decreased this elevated immune response. This result indicates that plant immune priming by seaweed polysaccharides requires transcription-dependent activation of the host genome (Nagorskaya et al. 2008). Similarly, several studies show that the priming effect of seaweed metabolites operates through comprehensive

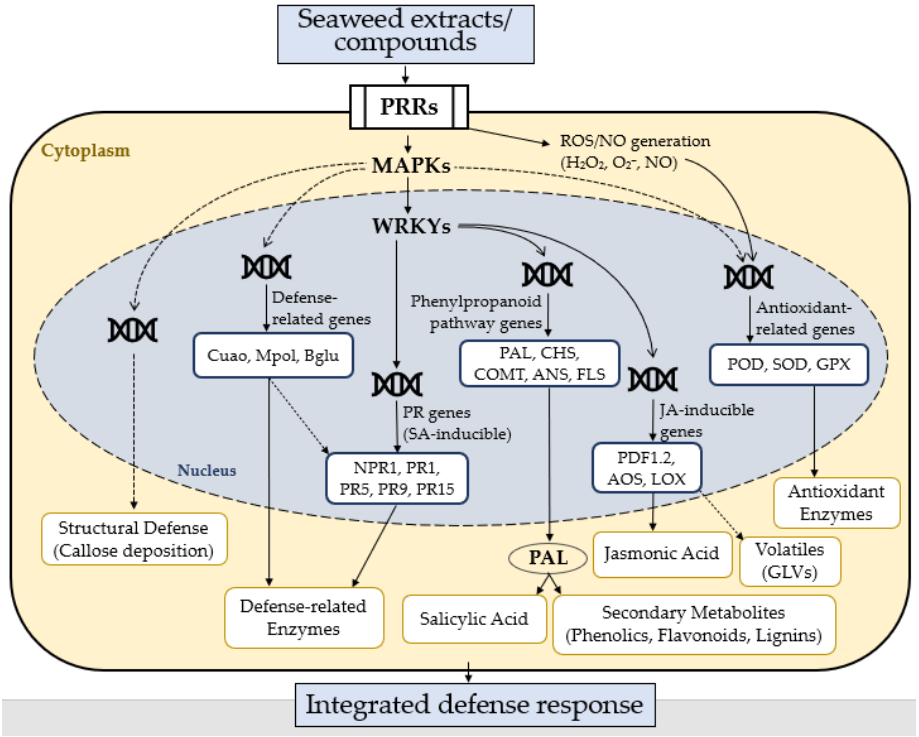

Figure 1. Schematic illustration of the plausible mechanism for seaweed elicitor-induced plant defence responses
Bioactive compounds derived from seaweed extracts are recognised by transmembrane pattern recognition receptors (PRRs), initiating signaling cascades similar to those activated during pathogen-associated molecular pattern (PAMP) recognition. This triggers the activation of various signaling molecules, including salicylic acid (SA) and jasmonic acid (JA), which coordinate the downstream induction of pathogenesis-related (PR) proteins, reactive oxygen species (ROS)-scavenging enzymes, and a variety of secondary metabolites involved in plant defense, ultimately leading to enhanced resistance against a broad spectrum of pathogens and insect pests. Note: SE – seaweed extract; PRRs – pattern recognition receptors; RONS – reactive oxygen and nitrogen species; MAPKs – mitogen-activated protein kinases; CuAO – copper amine oxidase; Mpol – monomeric polyphenol oxidase; Bglu – beta-glucosidase; PAL – phenylalanine ammonia-lyase; CHS – chalcone synthase; COMT – caffeic acid O-methyltransferase; ANS – anthocyanidin synthase; FLS – flavonol synthase; NPR1 – non-expressor of pathogenesis-related protein 1; PR – pathogenesis-related proteins; PDF1.2 – plant defensin 1.2; AOS – allene oxide synthase; LOX – lipoxygenase; POD – peroxidase; SOD – superoxide dismutase; GPX – glutathione peroxidase; GLVs – green leaf volatiles

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transcriptional reprogramming. For instance, FEH treatment triggered upregulation of 651 immune-related genes, including key regulatory elements NHL10, OXI1, and WRKY30 in Arabidopsis plants (Wang et al. 2023b). In another study, the temporal dynamics of defence gene activation in laminarin-treated *Olea europaea* reveal the stimulating expression of core defence-related genes, including Lox, copper amine oxidase (Cuao), polyphenol methyltransferase (MPol), β-glucanase (Bglu), and phenylalanine lyase (Phely) (Tziros et al. 2021). Likewise, tomato plants treated with λ-carrageenan (foliar spray) showed broad proteomic changes and altered expression profiles of 17 defence-associated proteins (Sangha et al. 2015). These seaweed compound-triggered alterations establish priming mechanisms that enable rapid defence mobilisation upon pathogen attack while maintaining metabolic efficiency through selective activation rather than constitutive defence expression (Zipfel 2009).

Signal transduction pathways. Activating plant defence responses by seaweed metabolites involves complex signal transduction networks that coordinate multiple hormonal pathways. Based on the experimental evidence reviewed here, these networks are initiated through MAPK upstream signalling pathways, which activate downstream hormonal responses. Among these downstream mechanisms, SA-mediated signalling represents the most frequently observed response pathway in characterised crop-elicitor combinations. JA pathways and integrated SA-JA crosstalk serve as additional key mechanisms. In the plant immune system, MAPK upstream signalling is the initial signal transduction mechanism that amplifies elicitor recognition events and coordinates downstream hormonal pathway activation (Zhang et al. 2018). For example, FEH treatment in Arabidopsis plants demonstrates this critical upstream role through rapid MAPK3/6 phosphorylation, which functions as a crucial signal amplification step that precedes downstream hormonal responses (Wang et al. 2023b). Similarly, rapidly initiated defence-related signalling through CsMAPK cascade and CsWRKY3 transcription factor activation within 1–2 h was observed after laminarin treatment in tea plant (Xin et al. 2019). Based on these findings, MAPK cascade activation functions as an early-response mechanism for plant recognition of seaweed-derived elicitor signals. SA-mediated defence responses represent a primary mechanism through which seaweed-derived elicitors enhance plant immunity against pathogens. Several studies show that specific marine polysaccharides selectively trigger SA pathway components without concurrent activation of JA signalling networks. For instance, alginate oligosaccharides applied via foliar spray treatments exemplify this selective SA pathway activation in Arabidopsis plants, characterised by enhanced PR1 gene expression and substantial endogenous SA accumulation (Zhang et al. 2019). Similarly, laminarin applications in tea plants (*Camellia sinensis*) resulted in elevated SA and abscisic acid (ABA) levels following pathogen challenge, while JA concentrations remained unchanged relative to control treatments (Xin et al. 2019). The specificity of SA pathway engagement is further demonstrated by oligo-sulphated-galactan treatments in tobacco plants, where sustained PAL enzyme activation drives phenylpropanoid compound biosynthesis and SA accumulation without affecting lipoxygenase (LOX) activity (Vera et al. 2011). These findings suggest that certain seaweed-derived compounds operate a protective system through SA-dependent signalling cascades that activate independently of JA pathway. It has been reported that JA signalling represents a crucial defence mechanism and is particularly effective against necrotrophic pathogens and herbivorous insects (Zhang et al. 2017). Sangha and colleagues reported that λ-carrageenan treatment exemplified selective JA pathway engagement, enabling tomato plants to acquire JA-dependent resistance against TCDVd through coordinated upregulation of allene oxide synthase (AOS) and LOX genes during infection (Sangha et al. 2015). Interestingly, the concurrent activation of both SA and JA signalling pathways was also reported by polysaccharides, κ-carrageenan and ulvan (Mani & Nagarathnam 2018; de Borba et al. 2021; Velho et al. 2022). In the case of κ-carrageenan-treated chilli, simultaneous stimulation of both SA-inducible (NPR1, PR1, and PR5) and JA-mediated (PDF1.2) gene expression was confirmed after foliar spray application (Mani & Nagarathnam 2018). Similarly, ulvan treatment in wheat plants demonstrates integrated responses, concurrently activating JA pathway components through enhanced LOX gene expression while upregulating SA pathway markers, including PR genes (PR1, PR9, and PR15) (Velho et al. 2022). This pattern is consistent with another wheat-ulvan study demonstrating broad-spectrum

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activation based on the upregulated SA-associated (PR2 and PR3) and JA-related (LOX and AOS) gene expression (de Borba et al. 2021). From the studies, structurally similar compounds (e.g., with different numbers of sulfate groups) were observed to trigger distinct pathways (Sangha et al. 2015; Mani & Nagarathnam 2018). For example, λ-carrageenan-treated tomato elicits the JA pathway, while chilli treated with κ-carrageenan activates both SA and JA pathways. Conversely, identical elicitors can show consistent patterns within species. In the case of ulvan, the integrated SA/JA pathways were triggered in wheat (de Borba et al. 2021; Velho et al. 2022). However, an earlier study reported that ulvan-treated dicot plants, such as Medicago and Arabidopsis, activate an immune response via only the JA pathway (Jaulneau et al. 2010). Therefore, developing effective seaweed-based crop protection strategies requires chemical characterisation of elicitors and crop-specific validation of induced signalling pathways to ensure optimal defence activation against target pathogens.

Biochemical defence responses. The phenylpropanoid pathway is one of the predominant defensive responses involved in the biosynthesis of diverse secondary metabolites, such as lignin, phenolics, and flavonoids, in plant species to pathogen challenges (Yadav et al. 2020). Notably, upregulation of genes, enzymes, and metabolites involved in the phenylpropanoid pathway has been identified as a major mechanism through which seaweed-derived polysaccharide compounds activate plant defence systems. For example, oligo-carrageenan applications in tobacco induced five-fold increases in PAL activity alongside 3.5-fold phenylpropanoid accumulation (Vera et al. 2012), while ulvan foliar treatments in wheat resulted in 2.5-fold PAL enhancement accompanied by simultaneous upregulation of downstream biosynthetic genes, including CHS, caffeic acid O-methyltransferase (COMT), anthocyanidin synthase (ANS), and FLS (Velho et al. 2022). The functional significance of phenylpropanoid enhancement was demonstrated in ulvan-treated bean plants (*Phaseolus vulgaris*), as evidenced by stimulated lignin biosynthesis and increased phenolic compound accumulation (de Borba et al. 2019). In contrast, the bioactive efficacy of eckol, a phenolic compound from brown seaweed, in promoting cabbage growth and conferring aphid resistance derives from enhanced myrosinase activity and glucosinolate pathway activation rather than phenylpropanoid accumulation, as evidenced by concurrent decreases in phenolic, flavonoid, and tannin contents (Rengasamy et al. 2016). These findings indicate metabolite-specific targeting of distinct secondary metabolic networks, revealing that pathway activation may depend on compound structure and species-specific metabolic capabilities. In addition to phenylpropanoid-related enhancement, the oxidative defence involves ROS burst coupled with antioxidant enzyme activation to maintain cellular redox homeostasis during defence responses (He et al. 2017). For instance, ulvan treatment of wheat plants resulted in 90% increases in H_2O_2 accumulation and 60% enhancement in POD activity (Velho et al. 2022). Similarly, tea plants treated with laminarin induce a rapid H_2O_2 burst, which is coordinated with the sustained activation of defence enzymes, including polyphenol oxidase (PPO), PAL, and chitinase, over 2–7 days (Xin et al. 2019). The ROS response extends to multiple oxidative species. For instance, κ-carrageenan treatment in tomato plants induced both H_2O_2 and superoxide anion (O_2^-) bursts and also significantly increased antioxidant enzymes, such as POD and SOD activities, which led to a comprehensive oxidative defence environment (Mani et al. 2021). This oxidative response is complemented by enhanced nitric oxide (NO) production, as demonstrated by FEH and AOS treatments generating ROS/NO bursts that contribute to pathogen suppression and defence signal amplification (Zhang et al. 2019; Wang et al. 2023b). Furthermore, enhanced new peroxidase isoforms and GPX activity were observed from the κ-carrageenan-treated chilli plants (Mani & Nagarathnam 2018). Beyond the biochemical responses, plants establish structural reinforcement mechanisms, such as callose deposition, stomatal closure, calcium oxalate crystals, and papillae formation, that provide physical barriers against pathogen invasion and spread (Mani et al. 2021; Velho et al. 2022; Wang et al. 2023b). For example, FEH treatment in Arabidopsis also stimulated callose deposition and stomatal closure, contributing to apoplastic barrier formation and pathogen entry point reduction (Wang et al. 2023b). Similarly, laminarin-treated tea plants demonstrated comparable structural defence enhancement through callose deposition peaking 2 days post-treatment (Xin et al. 2019). The formation of calcium oxalate crystals following κ-carrageenan treatment in tomato plants was observed to establish an additional structural defence mechanism that may interfere with pathogen

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feeding and movement (Mani et al. 2021). Among specialised structural responses, ulvan treatment in wheat induces papillae formation that provides localised cell wall reinforcement at potential pathogen penetration sites (Velho et al. 2022).

While these mechanisms have been discussed as distinct categories, a comprehensive analysis of single studies presents that seaweed metabolite treatments can simultaneously trigger multiple defence layers. For instance, FEH treatment in Arabidopsis concurrently activated immune priming (651 genes including NHL10, OXI1, WRKY30), MAPK cascades (MAPK3/6 phosphorylation), oxidative bursts (ROS/NO generation), and structural barriers (callose deposition, stomatal closure) (Wang et al. 2023b), while ulvan applications in wheat simultaneously enhanced phenylpropanoid pathways (PAL, CHS, COMT, ANS, FLS), hormonal signaling (SA/JA pathways, PR1, PR9, PR15, LOX), ROS responses (H_2O_2, POD), and cell wall reinforcement (papillae formation) (Velho et al. 2022). These findings collectively support seaweed-derived metabolites as potent multi-target elicitors capable of modulating integrated defense networks, rendering them promising candidates for sustainable crop protection strategies that can address the complex challenges caused by diverse biotic stressors.

INTERACTION OF SEAWEED METABOLITES WITH PLANTS UNDER ABIOTIC STRESS

Beyond the challenges caused by pests and diseases, various environmental stresses, such as salinity, drought, temperature extremes, and heavy metal toxicity, can also affect crop productivity. Recent evidence indicates that seaweed extracts can improve plant resilience against these abiotic stresses (Deolu-Ajayi et al. 2022). As summarised in Table 5, several studies have investigated seaweed-derived extracts for mitigating various abiotic stresses in plants through intricate modulation of metabolic pathways.

Seaweed polysaccharides and their derivatives involved in abiotic stress tolerance.

Seaweed polysaccharides involved in biotic stress responses typically function through direct antimicrobial activities and pathogen recognition mechanisms. However, some polysaccharides, such as fucoidan, laminarin, and alginate, or their derivatives, demonstrate distinct mechanisms when applied for abiotic stress tolerance. The reviewed polysaccharides demonstrate diverse molecular weight characteristics ranging from 3.2 kDa (DPP1 from *Pyropia yezoensis*) to 40.2 kDa (LNP-2 from *Lessonia nigrescens*), which exhibit distinct efficacy profiles under different experimental conditions (Salachna et al. 2018; Zou et al. 2018; Zou et al. 2019; Zou et al. 2021; Zuo et al. 2021). In addition to molecular weight, recent studies have revealed distinct structure-activity relationships, where processing methods such as enzymatic hydrolysis, oligomerisation, and chemical modification can substantially alter the biological properties and stress-mitigating capacities of native seaweed polysaccharides. Multiple factors influence the final bioactivity of these compounds, including extraction conditions, sulfate content ranging from 18.97% (*U. prolifera* polysaccharides) to 40.5% (*L. nigrescens* polysaccharides) (Zou et al. 2019; Zuo et al. 2021), and application methods such as foliar spraying (Liu et al. 2013; Zou et al. 2021), root application (Wu et al. 2016), bulb coating (Salachna et al. 2018), and nutrient solution supplementation (Zou et al. 2018; Zou et al. 2019), each optimized for specific stress conditions and plant developmental stages.

Given that the structural characteristics of these compounds have been previously described in the biotic stress section, this section focuses on their modulation mechanisms when mitigating abiotic environmental stressors (Table 5 and Figure 2).

Seaweed metabolite efficacy against abiotic stress types

Salt stress. Salt stress is considered one of the most comprehensively studied abiotic stressors, and according to recent FAO projections (2021), continued soil salinisation trends may render 50% of cultivable land unusable by 2050 (Atta et al. 2023). Utilising seaweed extracts derived from diverse marine algae phyla has been considered a potential strategy for mitigating such stress conditions through multiple physiological and biochemical adaptations (Table 5). Purified polysaccharides have demonstrated comprehensive salt stress mitigation through coordinated enhancement of growth, photosynthetic capacity, and cellular protection mechanisms. Zou and coworkers demonstrated that fucoidan (MW 11.1 kDa, sulfate content 28.6%) extracted from *Macrocystis pyrif-*

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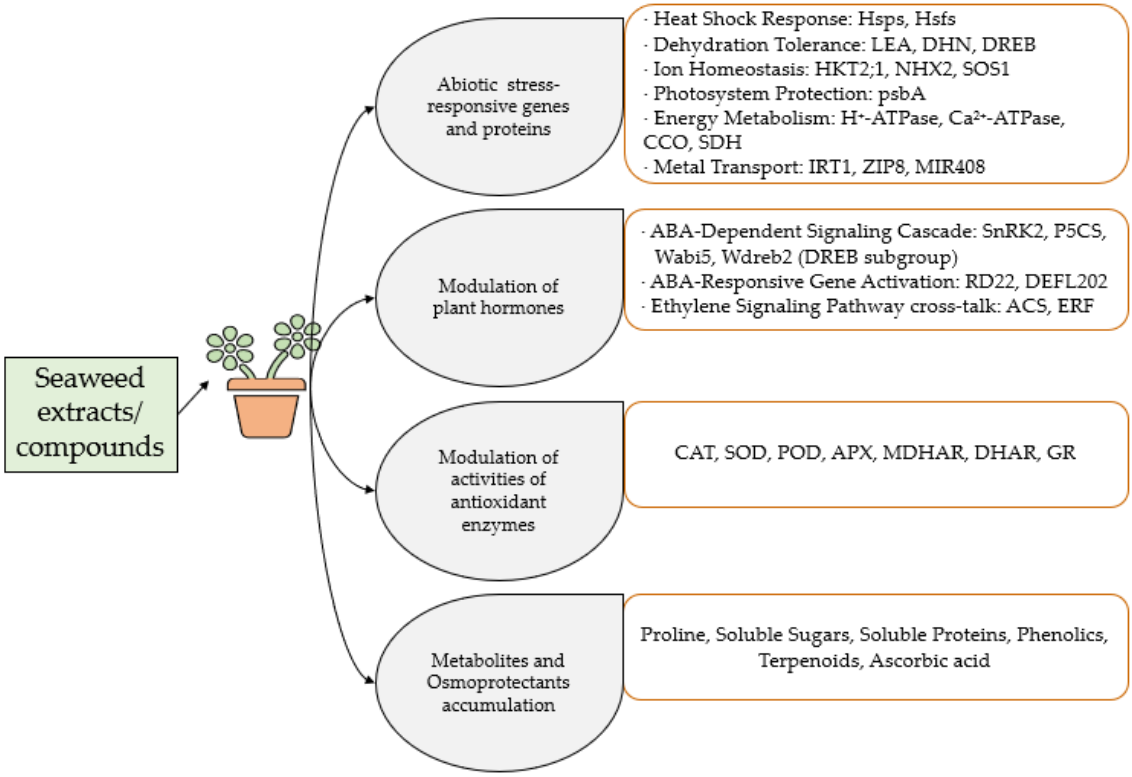

Figure 2. Schematic illustration highlighting the interaction of seaweed extract (SE) or -derived compounds with plants under abiotic stress

Hsps – heat shock proteins; Hsfs – heat shock factors; LEA – late embryogenesis abundant proteins; DHN – dehydrins; DREB – dehydration-responsive element-binding proteins; HKT2;1 – high-affinity K^+ transporter 2;1; NHX2 – Na^+/H^+ exchanger 2; SOS1 – salt overly sensitive 1; PsbA – photosystem II D1 protein; H^+-ATPase – proton ATPase; Ca^{2+}-ATPase – calcium ATPase; CCO – cytochrome c oxidase; SDH – succinate dehydrogenase; IRT1 – iron-regulated transporter 1; ZIP8 – zinc-iron permease 8; SnRK2 – SNF1-related protein kinase 2; P5CS – Δ^1-pyrroline-5-carboxylate synthetase; ABI5 – abscisic acid insensitive 5; RD22 – responsive to dehydration 22; DEFL202 – defensin-like protein 202; ACS – 1-aminocyclopropane-1-carboxylate synthase; ERF – ethylene response factor; CAT – catalase; SOD – superoxide dismutase; POD – peroxidase; APX – ascorbate peroxidase; MDHAR – monodehydroascorbate reductase; DHAR –dehydroascorbate reductase; GR – glutathione reductase

era enhanced wheat seedling tolerance under 120 mM NaCl stress when applied as foliar treatment at 0.5–1 mg/mL concentrations (Zou et al. 2021). This intervention resulted in substantial growth improvements, including 46.1% increases in fresh weight and 12.5% enhancement in shoot length, while simultaneously reducing oxidative damage through 43.4% malondialdehyde (MDA) reduction and enhancing osmotic adjustment via 77.1% proline accumulation. Moreover, fucoidan treatment effectively maintained ion homeostasis by reducing sodium accumulation by 55.6%. Similarly, polysaccharides from *L. nigrescens* (LNP-2, MW 40.2 kDa, sulfate content 40.5%) exhibited comprehensive stress alleviation in wheat under more severe 150 mM NaCl conditions through 10-day nutrient solution supplementation (Zou et al. 2019). This treatment enhanced photosynthetic capacity through dramatic chlorophyll increases (chlorophyll *a* by 75.9%, chlorophyll *b* by 141.1%). It also facilitated substantial sodium exclusion, reducing sodium levels by 25.6% in roots and 59.1% in leaves, while promoting a significant rise in proline accumulation (87.1%) to support osmotic balance. Similarly, oligo-alginate (MW 32 000 g/mol) applied as bulb coating treatment to *Eucomis autumnalis* resulted in comprehensive morphological improvements, including plant height increasing by 30.8%, leaf length by 33.2%, and fresh weight gains of 46.5% in above-ground biomass under 100 mM NaCl stress (Salachna et al. 2018). Enhanced photosynthetic function was also observed by 13.8%

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Table 5. Summary of seaweed-derived compounds against various abiotic stress

Seaweed extract/ compound	Seaweed (Phylum)	Abiotic stress type	Crop	Effective concentration	Application mode	Experimental condition	Efficacy results	Mechanism / mode of action	References
Methanolic fraction (MEA)	*A. nodosum* (Phaeophyceae)	Salinity (NaCl 100/150 mM)	*Arabidopsis thaliana* (3-week-old at treatment)	1 g/L	Root irrigation after 24h NaCl stress; *in vitro*: MS agar, root-bending assay	Greenhouse	↑Biomass (FW) 46–57%, ↑ leaf area 37%, ↑ plant height 29–33%, ↑ number of leaves 26–33%, ↑ root growth under NaCl (vs NaCl control)	Upregulation of LEA, DREB/CBF, galactinol/ raffinose synthase, partial transcriptome reprogramming	Jithesh et al. 2018
Ethyl acetate fraction (EAA)	*A. nodosum* (Phaeophyceae)	Salinity (NaCl 150 mM)	*A. thaliana* (3-week-old at treatment)	1 g/L (most effective; 0.5–1 g/L effective, 2 g/L inhibitory)	*In vivo*: root irrigation after 24h NaCl stress; *in vitro*: MS agar, root-bending assay	Greenhouse	↑ Biomass (FW) 52%, ↑ plant height 48%, ↑ leaf area 62%, ↑ leaf number, ↑root growth (50% reversal of NaCl inhibition) (vs NaCl control)	Transcriptomic activation (> 400 genes): ↑ LEA, RAB18, DREB/CBF, ABA/JA pathway, osmoprotectant/flavonoid synthesis, ↓ WAK1/PME	Jithesh et al. 2018
Chloroform fraction (CFA)	*A. nodosum* (Phaeophyceae)	Salinity (NaCl 150 mM)	*A. thaliana* (3-week-old at treatment)	1 g/L	*In vivo*: root irrigation after 24h NaCl stress; *in vitro*: MS agar, root-bending assay	Greenhouse	↑ Biomass (FW) 36%, ↑ plant height 58%, ↑ leaf area 33%, ↑ leaf number, slight ↑ root growth under NaCl (vs NaCl control)	Partial upregulation of stress genes, less extensive transcriptome response than EAA, moderate improvement of salt tolerance	Jithesh et al. 2018
Fucoidan (sulfated polysaccharide, Mw 11.1 kDa, sulfate content 28.6%)	*Macrocystis pyrifera* (Phaeophyceae)	Salt stress (NaCl 120 mM)	*Triticum aestivum* (2nd leaf fully expanded at treatment)	0.5–1 mg/mL	Foliar spray (15 mL/group, 3 applications every other day)	Growth chamber	↑ Growth parameters (fresh weight +46.1%, shoot length +12.5%), ↓ MDA (43.4%), ↓ REL (29.2%), ↓ H_2O_2 (29.2%), ↓ Proline (77.1%), ↑ Na↓ accumulation (55.6% in sheaths), ↑ K^+ content (vs NaCl control)	↑ Antioxidant enzymes (SOD↑ 58.5-60.7%, POD↑ 117-130%, CAT ↑), osmoregulation (proline↑), ion homeostasis (Na^+↓/ K^+↑, lower Na^+/K^+ ratio)	Zou et al. 2021

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Table 5. To be continued...

Seaweed extract/ compound	Seaweed (Phylum)	Abiotic stress type	Crop	Effective concentration	Application mode	Experimental condition	Efficacy results	Mechanism / mode of action	References
Aqueous extract (main compounds: phenolics, flavonoids, reducing sugars, polysaccharides)	*Padina gymnospora* (Phaeophyceae)	Salt stress (NaCl 300 mM)	*Solanum lycopersicum* (5–6 leaves at treatment start)	2 g/L (applied as 100 mL per plant, 3 times at 20, 25, 30 DAG)	Soil drench (*in vivo*)	Growth chamber	↑ Photosynthetic efficiency (Fv/Fm), ↑ chlorophyll content, ↑ total phenolics (1.9×), ↑ reducing sugars, ↑ antioxidant capacity (DPPH, ABTS), ↑ APX activity, proline maintained, ↓ NPQ (vs NaCl control)	↑ Antioxidant enzymes (APX↑, CAT↑), ↑ stress-responsive genes (SlHB7↑ 10×, SlRD29↑ 3×, SlDR1A↑ 3×, SlHKT1;2↑, SlSOD1↑ 3×, SlAOX↑)	Hernández-Herrera et al. 2024
Polysaccharides (LNP-2: MW 40.2 kDa, sulfate 40.5%)	*Lessonia nigrescens* (Phaeophyceae)	Salt stress (150 mM NaCl)	*T. aestivum* (2nd leaf fully expanded at treatment)	Purified fractions applied equally (not specified)	Nutrient solution supplementation (10-day treatment)	Growth incubator	↑ Shoot length (12.0%), ↑root length (37.3%), ↑ FW (17.7%),↑ DW (30.9%), ↓MDA (52.4%), ↓ REL (47.7%), ↑ Chl-*a* (75.9%), ↑ Chl-*b* (141.1%), ↑ soluble sugars (35.3%), ↑ proline (87.1%), ↑ SOD (96.0%), ↑ POD (43.9%), ↓Na^+ accumulation (roots: 25.6%, leaves: 59.1%),↑ K^+ retention (vs NaCl control)	↑ Antioxidant enzymes (SOD↑ 96.0%, POD↑ 43.9%, CAT↑), osmotic adjustment (proline↑ 87.1%, sugars↑ 35.3%), ion homeostasis (TaHKT2;1↓, TaNHX2↑, TaSOS1↑), membrane stabilization	Zou et al. 2019
Low-MW polysaccharides (DPP1: 3.2 kDa)	*Pyropia yezoensis* (Rhodophyta)	Salt stress (100 mM NaCl)	*T. aestivum* (2nd leaf fully expanded at treatment)	0.01% (*w/v*)	Nutrient solution supplementation (10-day treatment)	Growth incubator	↑ Shoot length (6.1%), ↑ root length (9.5%), ↑ FW (40.6%), ↑ DW (52.5%), ↓ MDA (47.6%), ↓ REL (52.2%), ↑ Chl-a (48.3%), ↑ soluble sugars, ↑ proline (61.9%), ↑ SOD (62.9%), ↑ POD (45.3%), ↑ Na^+ accumulation, ↓ K^+ retention (vs NaCl control)	↑ Antioxidant enzymes (SOD↑ 62.9%, POD↑ 45.3%, CAT ↑), osmotic adjustment (proline↑ 61.9%, sugars↑), ion homeostasis (TaHKT2;1↓, TaNHX2↑, TaSOS1↑)	Zou et al. 2018

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Table 5. To be continued...

Seaweed extract/ compound	Seaweed (Phylum)	Abiotic stress type	Crop	Effective concentration	Application mode	Experimental condition	Efficacy results	Mechanism / mode of action	References
Oligo-alginate (depolymerised sodium alginate, MW 32 000 g/mol)	Commercial sodium alginate (Phaeophyceae)	Salt stress (NaCl 100 mM)	*Eucomis autumnalis* (bulbs, 14–16 cm perimeter)	1% solution for bulb coating (32 000 g/mol fraction)	Bulb coating (*ex vivo*, 30 s immersion), then pot cultivation under greenhouse conditions	Greenhouse (plastic tunnel)	↑ Plant height (30.8%), ↑ plant width (28.6%), ↑ leaf length (33.2%), ↑ inflorescence length (33.6%), ↑ number of florets (29.3%), ↑ chlorophyll a (13.8%), ↑ chlorophyll *a* + *b* (13.8%), ↑ carotenoids, ↑ total polyphenols, ↑ L-ascorbic acid, ↑ DPPH antioxidant activity, ↑ stomatal conductance (39.6%), ↑ SPAD index (21.8%), ↓ Na^+ and Cl^- accumulation under salt stress, ↑ fresh weight (above-ground: 46.5%, bulb: 26.0%) (vs salt control)	↑ Antioxidant system (ascorbic acid↑, DPPH↑), ↑ phenolic biosynthesis (polyphenols ↑), ↑ photosynthetic pigments (Chl a↑, Chl *a* + *b* ↑), Na^+/Cl^- uptake, enhanced stress adaptation mechanisms	Salachna et al. 2018
Alkaline extract (pH 10, highest protein content)	*F. spiralis* (Phaeophyceae)	Drought stress (10 days of water withholding)	*Vicia faba* L. (cv. Super Aguadulce)	5% (*v/v*)	Soil drench (22 DAS) + foliar spray 40 DAS, 51 DAS)	Field	↑ Dry weight (significantly), ↑ proline accumulation (68.25%), ↑ soluble sugars (14.22%), ↓ total phenols, ↓ MDA concentration, ↓ PIabs during drought (vs stressed control)	Osmotic adjustment via proline accumulation (68.25% increase), enhanced carbohydrate metabolism, phenolic compound regulation, lipid peroxidation reduction, stress-induced metabolic reprogramming	El Boukhari et al. 2023

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Table 5. To be continued...

Seaweed extract/ compound	Seaweed (Phylum)	Abiotic stress type	Crop	Effective concentration	Application mode	Experimental condition	Efficacy results	Mechanism / mode of action	References
Acid extract (pH 3, highest soluble sugars, 7× higher proline content)	*U. lactuca* (Chlorophyta)	Drought stress (10 days of water withholding)	*V. faba* L. (cv. Super Aguadulce)	5% (*v/v*)	Soil drench (22 DAS) + foliar spray (40 DAS, 51 DAS)	Field	↑ Soluble sugars (16.16%), ↓ total phenols, ↓ H_2O_2 (2.2%), ↓ MDA concentration, and the highest H_2O_2 at the recovery phase (vs stressed control)	Carbohydrate metabolism enhancement (16.16% increase), ROS scavenging (H_2O_2 reduction), phenolic compound modulation, and membrane protection through MDA reduction	El Boukhari et al. 2023
Acid extract (pH 3, low soluble sugar content)	*L. ochroleuca* (Phaeophyceae)	Drought stress (10 days of water withholding)	*V. faba* L. (cv. Super Aguadulce)	5% (*v/v*)	Soil drench (22 DAS) + foliar spray (40 DAS, 51 DAS)	Field	↓ Total phenols, ↓ H_2O_2 (6.3%), ↓ MDA concentration (significantly at recovery phase), enhanced recovery response (vs stressed control)	ROS scavenging (6.3% H_2O_2 reduction), enhanced membrane stability (significant MDA reduction), and phenolic compound regulation	El Boukhari et al. 2023
Alginate oligosaccharides (AOS) (degraded alginate oligomers)	Commercial alginate (Phaeophyceae)	Drought stress (PEG-6000-induced, 150 g/L)	*T. aestivum* L. cv. Xinong 979 (3-day-old seedlings at treatment)	1 000 mg/L	Foliar spray (applied 1h post-stress induction) *in vivo* hydroponic culture (Hoagland's solution, controlled environment)	Growth incubator	↑ Seedling length (18%), ↑ root length (26%), fresh weight (43%), ↑ RWC (33%), ↑ chlorophyll content (2×), ↑ proline (53%), ↓ MDA (37.9%), ↑ SOD activity (4%), ↑ POD activity (13.2%) (vs PEG control)	↑ ABA-dependent signalling (LEA1↑ peak at 24h, SnRK2↑ peak at 3h, P5CS↑ peak at 24h), ↑ photosystem protection (psbA↑ at 6h), ↑ antioxidant enzymes (SOD↑, POD↑), osmotic adjustment (proline↑)	Liu et al. 2013

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Table 5. To be continued...

Seaweed extract/ compound	Seaweed (Phylum)	Abiotic stress type	Crop	Effective concentration	Application mode	Experimental condition	Efficacy results	Mechanism / mode of action	References
Alkaline extract (Commercial, Super Fifty (SF))	*A. nodosum* (Phaeophyceae)	Drought stress (11 days without irrigation)	*A. thaliana* (25 DAG at first treatment)	0.2% (*v/v*)	Foliar spray (2 applications at 25 and 27 DAG)	Greenhouse	↑ Rosette diameter and leaf number, ↓ electrolyte leakage ($p < 0.05$), ↑ RWC maintenance, ↓ H_2O_2 accumulation, ↑ rosette growth maintenance, ↑ leaf initiation rate (LIR), ↓ RD26 expression (almost completely inhibited), ↑ HIS4 expression (highly expressed vs undetectable), ↑ CYCP2;1 expression (downregulation reversed), ↑ CYCA3;2 expression, ↑ APX activity, ↓ PRX34 expression (7.6-fold vs 118-fold), ↓ ARR2 expression (induction mitigated), ↓ guard cell H_2O_2 (vs H2O+Dr control)	↑ Antioxidant enzyme system (APX4, TAPX 3.6-7.7×, DHAR3, GPX1, GSTL2), ↑ ABA-dependent signaling (PP2C52 maintenance, SnRK2.8 8.5× higher, ABF3 2×, DREB1A, DREB3 activation), ↓ oxidative stress genes (72 genes downregulated), ↑ ROS detoxification, ↑ shoot apical meristem (SAM) function maintenance, ↑ cell cycle progression (HIS4, CYCP2;1, CYCA3;2), ↓ cytokinin-mediated stomatal closure (ARR2, PRX34 modulation), stress-responsive transcriptome reprogramming	Rasul et al. 2021
A. nodosum extract (ANE) (carbohydrates, amino acids)	*A. nodosum* (Phaeophyceae)	Drought stress (dehydration)	*A. thaliana* (20-day-old at treatment)	3 g/L	Hydroponic pretreatment (5 days), followed by controlled dehydration (4 days on filter paper)	Growth chamber	↑ Survival rate (90% mortality in untreated vs. marginal in ANE-treated), ↑ plot water content, ↑ WUE (105% intrinsic, 93% instantaneous), ↑ NPQ, maintained Fv/Fm (0.8), ↑ stomatal conductance (55%), ↓ transpiration (53%) (vs untreated control)	↑ ABA-responsive genes (RAB18↑, RD29A↑), ↓ MYB60 expression, ↑ antioxidant genes (SOD↑, DFR↑), ↑ photoprotection (PsbS↑, VDE↑), ↑ mesophyll conductance maintenance (PIP1;2↑, βCA1↑)	Santaniello et al. 2017

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Table 5. To be continued...

Seaweed extract/ compound	Seaweed (Phylum)	Abiotic stress type	Crop	Effective concentration	Application mode	Experimental condition	Efficacy results	Mechanism / mode of action	References
A. nodosum extract (ASE) (44% organic matter, >13% alginic acid, amino acids, vitamins, minerals, NPK)	*A. nodosum* (Phaeophyceae)	Drought stress (soil water content at 50%, 75%, 100% FC)	*S. lycopersicum* (20-day-old two-leaf stage at transplanting)	5 mL/L ASE + 100 kg K_2O/ha	Soil drench (weekly for 6 weeks starting 2 weeks post-transplanting, 100 mL/pot)	Greenhouse (polyhouse)	↑ Plant height (55%), ↑ leaf area (178%), ↑ shoot DM (71%), ↑ root DM (82%), ↑ fruit yield (193%), ↑ fruit number (204%), ↑ water productivity (178%), ↑ LRWC (60%), ↑ membrane stability index (125%), ↑ net photosynthetic rate (189%), ↑ stomatal conductance (500%), ↑ transpiration rate (186%), ↑ proline (70%), ↓ electrolyte leakage (48%) (vs control)	↑ Water relations (LRWC↑), ↑ photosynthesis (Pn↑ 189%, gs↑ 500%), ↑ osmotic adjustment (proline↑ 70%), ↑ membrane stability (MSI↑ 125%), ↓ cell damage (electrolyte leakage ↓ 48%), synergistic K interaction	Ahmed et al. 2024
Low molecular weight polysaccharides (LPU, 14.2 kDa, sulfate content 18.97%)	*U. prolifera* (Chlorophyta)	Osmotic stress (20% *w/v* PEG-6000-induced)	*T. aestivum* cv. Jimai-22 (7-day-old seedlings at treatment)	0.05% (0.01%, 0.03%, 0.05% tested)	Polysaccharide-PEG mixture treatment in hydroponic culture (Hoagland's solution, controlled environment, 120 h treatment)	Growth incubator	↑ Shoot/root length, ↑ root fresh weight (15.57–17.80%), ↑ shoot fresh weight (14.47%), ↑ soluble protein (1.86–2.13×), ↑ proline, ↑ RWC maintenance, ↓ MDA (19.82-23.13%), ↑ antioxidant enzymes (CAT↑ 25.37–34.69%, APX↑, SOD ↑, POD↑, GPX↑), ↑ AsA (20.41–42.52%), ↑ GSH, ↑ ABA content (26.51–43.74%) (vs PEG control)	↑ ABA-dependent signalling pathway (P5CS↑ 2.85–6.64×, SnRK2↑, Wabi5↑, Wdreb2↑), ↑ LEA/Cor genes (Wdhn13↑, Wrab17↑, Wrab18↑ 1.67–2.81×, Wrab19↑), ↑ antioxidant defence system, osmotic adjustment (proline↑, soluble protein↑), membrane protection	Zuo et al. 2021

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Table 5. To be continued...

Seaweed extract/ compound	Seaweed (Phylum)	Abiotic stress type	Crop	Effective concentration	Application mode	Experimental condition	Efficacy results	Mechanism / mode of action	References
Commercial biostimulant (1.2% mannitol, 2% alginic acid, 99% *A. nodosum* extract, 15% dry matter, cold extraction by Gentle Extraction® method)	*A. nodosum* (Phaeophyceae)	Heat stress (40 °C vs 26.35 °C control)	*Glycine max* (cv. 95R95-IPRO)	1 L/ha	Foliar application at R1 stage (43 DAS)	Greenhouse covered with transparent LDPE film (150 µm) (*in vivo*)	↑ CO_2 assimilation (56.56%), ↑ stomatal conductance (94.97%), ↑ transpiration (71.59%), ↑ carboxylation efficiency (67.47%), ↓ internal CO_2 concentration (6.47%), ↓ leaf temperature (10.46%), ↑ SOD activity (837% at 0.75 L/ha), ↑ CAT activity (171.81% at 0.75 L/ha), ↑ plant height (23.93%), ↑ leaf area (5.41%), ↑ shoot dry weight (14.84%), ↑ root dry weight (19.93%), ↑ number of nodules (43%, 73 vs 51), ↑ pods per plant (75.72%), ↑ pods with 3 grains (131.78%), ↑ productivity (19.21%) (vs heat stress control)	Enhanced photosynthetic performance, improved gas exchange, antioxidant enzyme activation (SOD, CAT), reduced leaf temperature, improved growth and nodulation, enhanced reproductive success under heat stress	Repke et al. 2022

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Table 5. To be continued...

Seaweed extract/ compound	Seaweed (Phylum)	Abiotic stress type	Crop	Effective concentration	Application mode	Experimental condition	Efficacy results	Mechanism / mode of action	References
Fucoidan (medium MW, ≥ 95% purity)	– (Phaeophyceae)	Chilling stress (4 °C, 90% RH, 12 days cold storage)	*Cucumis sativus* cv. Sunstar (10 days post-flowering)	15 g/L (0, 5, 10, 15 g/L tested)	Fruit coating (dipping treatment, 300 fruits/ replicate, 3 replicates, polyethylene bag storage)	–	↓ Chilling injury index (from 0.65), ↓ weight loss, ↓ electrolyte leakage, ↓ MDA, ↓ DPPH & -OH scavenging rates, ↓ O_2^- production rate, ↓ H_2O_2 content, ↑ SOD, CAT, POD activities, ↑ APX, MDHAR (63% higher day 6), DHAR, GR activities, ↑AsA content (12% higher day 12), ↑ GSH content, ↑ AsA/DHA ratio, ↑ GSH/GSSG ratio, ↑ ATP (14% higher day 12), ↑ ADP (35% higher day 12), ↓ AMP (25% lower day 12), ↑ energy charge, ↑ H^+-ATPase (33% higher day 12), ↑ Ca^{2+}-ATPase, ↑ CCO (50% higher day 12), ↑ SDH (37% higher day 3) activities (vs control)	↑ Antioxidant enzyme system (SOD↑, CAT↑, POD↑, APX↑, MDHAR ↑, DHAR↑, GR↑), ↑ ROS scavenging capacity, ↑ AsA-GSH cycle maintenance, ↑ energy metabolism (H^+-ATPase↑, Ca^{2+}-ATPase↑, CCO↑, SDH↑), ↑ gene expression (CsPOD↑, CsCAT2↑, CsSOD↑, CsAPX↑, CsMDHAR↑, CsDHAR↑, CsGR↑, CsH↑-ATPase↑, $CsCa^{2+}$-ATPase↑, CsCCO↑, CsSDH↑), membrane stability enhancement, cellular energy homeostasis maintenance	Lin et al. 2022

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Table 5. To be continued...

Seaweed extract/ compound	Seaweed (Phylum)	Abiotic stress type	Crop	Effective concentration	Application mode	Experimental condition	Efficacy results	Mechanism / mode of action	References
Laminarin (β-1,3-glucan)	*L. digitata* (Phaeophyceae)	Heat stress (42 °C for 3h), Salt stress (75–125 mM NaCl)	*A. thaliana* (Col-0, 3-6 day-old seedlings at treatment)	25 mg/L	Root application via 1/2 MS culture medium (*in vitro* controlled conditions, 23 °C)	Growth incubator	↑ Fresh weight, ↑ survival under heat stress, ↑ green cotyledon ratio under salt/heat stress, ↑ root length under salt stress, ↓ salt-induced chloroplast degradation, enhanced recovery after heat treatment (vs untreated control)	↑ Transcriptome reprogramming (112 genes > 2×), ↑ heat shock response (Hsps↑, Hsfs↑), metal transporters (IRT1↑ highest, ZIP8↑, Cu transporters↑, MIR408↑), ↑ terpenoid synthesis, ↑ ET signaling pathway (ACS4↑, ERFs↑), ↑ DEFL202 expression → ↑ antioxidant enzymes (SOD↑, APX↑), ↑ photosystem stability (PsbA-D1↑), ↑ ABA response (RD22↑), chloroplast antioxidant system enhancement	Wu et al. 2016
Aqueous extract (ultrasonication + hot water extraction)	*C. ericoides* (Phaeophyceae)	Heavy metal stress (Pb, 100 µmol)	Tomato (*S. lycopersicum*)	4% (*v/v*)	Hydroponic medium supplementation (2 weeks of treatment)	Growth chamber (hydroponic culture)	↑ Aboveground biomass (73.3%), ↑ root biomass (53.0%), ↓chlorophyll *a* + *b* under Pb stress, ↓ anthocyanin (85%), ↓ proline, ↓ Pb accumulation in roots (81% vs Pb control), no effect on shoot Pb (vs Pb-stressed control)	Enhanced growth under Pb stress, reduced oxidative stress markers (anthocyanin↓), osmotic adjustment (proline regulation), root Pb sequestration (↓ root Pb retention), and membrane stabilisation	El Khattabi et al. 2023
Aqueous extract (ultrasonication + hot water extraction)	*F. spiralis* (Phaeophyceae)	Heavy metal stress (Pb, 100 µmol)	Tomato (*S. lycopersicum*)	4% (*v/v*)	Hydroponic medium supplementation (2 weeks of treatment)	Growth chamber (hydroponic culture)	↑ Aboveground biomass (59.9%), ↑ root biomass (56.7%), ↓ chlorophyll *a* + *b* (20% in Pb-free), ↓ anthocyanin (90%), ↓ proline, ↑ Pb accumulation in shoots (37% vs Pb control), ↓ Pb in roots (285% decrease vs Pb control) (vs Pb-stressed control)	Enhanced growth under Pb stress, reduced oxidative stress markers (anthocyanin↓), osmotic adjustment (proline regulation), altered Pb translocation (↑ shoot accumulation, ↓ root retention), phytoextraction enhancement	El Khattabi et al. 2023

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Table 5. To be continued...

Seaweed extract/ compound	Seaweed (Phylum)	Abiotic stress type	Crop	Effective concentration	Application mode	Experimental condition	Efficacy results	Mechanism / mode of action	References
Aqueous extract (ultrasonication + hot water extraction)	*U. lactuca* (Chlorophyta)	Heavy metal stress (Pb, 100 µmol)	Tomato (*S. lycopersicum*)	4% (*v/v*)	Hydroponic medium supplementation (2 weeks of treatment)	Growth chamber (hydroponic culture)	No significant effect on biomass under Pb stress, ↓ chlorophyll *a* + *b* under Pb stress, no significant effect on anthocyanin, ↓ proline, ↓ Pb accumulation in roots (104% vs Pb control), no effect on shoot Pb (vs Pb-stressed control)	Limited protective effects, minimal growth enhancement, reduced root Pb retention, osmotic adjustment (proline regulation), low antioxidant capacity (low DPPH activity)	El Khattabi et al. 2023

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increases in chlorophyll content and 39.6% improvement in stomatal conductance, alongside reduced Na^+ and Cl^- accumulation (Salachna et al. 2018). In another study, low molecular weight polysaccharides from *P. yezoensis* (DPP1, 3.2 kDa) exhibited enhanced salt tolerance in wheat following 0.01% (*w/v*) applications under 100 mM NaCl stress (Zou et al. 2018). This treatment resulted in substantial physiological improvements, including fresh weight gains (40.6%) and reduced oxidative damage as evidenced by decreased MDA levels (47.6%). Additionally, these protective effects were accompanied by enhanced photosynthetic capacity through 48.3% chlorophyll increase, strengthened antioxidant defence via SOD (62.9%) and POD (45.3%) activation, and improved osmotic adjustment through 61.9% proline accumulation. Further investigations examining the efficacy of crude seaweed extracts in mitigating abiotic stresses, including salt stress, across diverse plant species and experimental conditions are detailed in Table 5.

Drought and osmotic stress. Drought is a significant global challenge that can reduce crop growth and yield by 30% to 90%, depending on the crop species, developmental stage, and severity of stress (Hussain et al. 2019). Under this stress condition, ROS-induced oxidative damage leads to lipid peroxidation and increased MDA content, indicating cellular membrane damage (Hasanuzzaman et al. 2020). In addition, the ABA-dependent signalling pathway activates genes encoding osmotic protection proteins, including late embryogenesis abundant (LEA) proteins and regulatory kinases, which facilitate cellular osmoregulation and drought tolerance in plants (Hasanuzzaman et al. 2020). Liu and coworkers reported that AOS derived from commercial alginate sources exhibited substantial ameliorative effects against PEG-6000-induced osmotic stress when administered as foliar applications at 1 000 mg/L concentrations to wheat seedlings (Liu et al. 2013). Additionally, this treatment resulted in comprehensive physiological improvements, such as fresh weight gains of 43%, elevated relative water content (33%), and doubled chlorophyll accumulation. Likewise, low molecular weight polysaccharide (MW 14.2 kDa and sulfate content of 18.97%) from *U. prolifera* (LPU) was found to exhibit comprehensive osmotic tolerance enhancement when applied at 0.05% concentrations during 120 h PEG-6000 treatments (Zuo et al. 2021). This LPU treatment led to soluble protein content increases up to 2.13 fold and biomass gains in roots and shoots by 17.80% and 14.47%, respectively. Notably, reduced oxidative damage was evidenced by the decreased MDA levels (by 23.13%) and enhanced antioxidant enzyme activities, particularly CAT (increased by 23.13%).

Temperature stress. Temperature stress is considered one of the critical threats to maintaining crop productivity, and frost damage is a significant factor leading to substantial economic losses in global crop yields (Hua et al. 2025). Beyond cold stress, the yield losses in staple grains, such as wheat, rice, and maize, are expected to increase by 10–25% for every one-degree rise in global surface temperature (Deutsch et al. 2018). Lin and coworkers demonstrated that fucoidan showed remarkable efficacy in mitigating chilling injury when applied as a fruit coating treatment to cucumber under prolonged cold storage conditions (4 °C, 90% RH, 12 days) (Lin et al. 2022). The optimal 15 g/L concentration significantly reduced the chilling injury index and minimised weight loss, while substantially elevating antioxidant enzyme activities, including monodehydroascorbate reductase (MDHAR) activity (63% increase on day 6) and ascorbate content (12% increase on day 12). Conversely, laminarin was found to exert a protective effect on Arabidopsis seedlings from heat stress (42 °C for 3 h) when administered at 25 mg/L concentrations through root application (Wu et al. 2016). This treatment also significantly increased survival rates under heat stress and improved the green cotyledon ratio when plants were exposed to combined salt and heat stress conditions. Heat stress applications primarily target photosynthetic efficiency and cellular redox homeostasis, while chilling stress treatments focus on membrane fluidity maintenance and antioxidant enzyme activation.

Heavy metal stress. Heavy metal contamination affects 14–17% of global cropland and gives rise to significant public health issues and ecological risks (Hou et al. 2025). In this context, research on the role of seaweed-derived metabolites in enhancing plant tolerance to heavy metal stress remains remarkably limited. El Khattabi and coworkers screened the efficacy of aqueous extracts from three different types of seaweeds, *Cystoseira ericoides*, *Fucus spiralis*, and *U. lactuca*, on tomato plants against heavy metal stress (Pb, 100 µmol) via a hydroponic system (El Khattabi et al. 2023). Initially, *C. ericoides* demonstrated significant protective effects in tomato plants, which resulted in substantial

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growth improvements with aboveground biomass increasing by 73.3% and root biomass by 53.0% compared to Pb-stressed controls, alongside a remarkable reduction in oxidative stress markers, evidenced by an 85% decrease in anthocyanin content. The protective mechanism involved enhanced root Pb sequestration with 81% reduction in root Pb accumulation compared to untreated Pb-stressed plants, while maintaining shoot Pb levels unchanged, suggesting effective compartmentalisation strategies for metal tolerance. In the case of *F. spiralis* treatment, unique phytoextraction capabilities were observed under identical experimental conditions, enhancing aboveground biomass by 59.9% and root biomass by 56.7% while demonstrating the most pronounced reduction in anthocyanin content (90% decrease) among tested species. Notably, *F. spiralis* treatment significantly altered Pb translocation patterns by increasing Pb accumulation in shoots up to 37% while dramatically reducing root Pb content by 285% compared to Pb-stressed controls. This unique translocation enhancement suggests utility for phytoextraction applications where metal removal from contaminated soils is the primary objective. In contrast, *U. lactuca* extract did not significantly affect biomass parameters or anthocyanin content, though it achieved a 104% reduction in root Pb accumulation under Pb stress conditions. These findings demonstrate that systemic approaches are essential for elucidating the complex interactions among compound structure, processing conditions, and application protocols that govern the efficacy of seaweed-based agricultural interventions.

Mechanisms of seaweed metabolites in plant abiotic stress tolerance

Seaweed metabolites confer plant abiotic stress tolerance through multiple interconnected mechanisms, including induction of stress-responsive genes and signaling pathways (ABA-dependent SnRK2, LEA1, P5CS activation, and LEA/Cor genes Wdhn13, Wrab17, Wrab18, Wrab19 upregulation, plus ethylene signaling via ACS4 and ERF genes) (Wu et al. 2016; Zuo et al. 2021), comprehensive modulation of antioxidant defense systems (SOD enhancement by 60.7%, POD and CAT increases of 130%, plus APX, MDHAR, DHAR, GR activation) (Liu et al. 2013; Zou et al. 2018; Zou et al. 2019; Zou et al. 2021; Lin et al. 2022), and physiological homeostasis maintenance through ion transport regulation (TaHKT2;1 downregulation, TaNHX2 and TaSOS1 upregulation), energy metabolism enhancement (H^+-ATPase, Ca^{2+}-ATPase, CCO, SDH activation), photosynthetic protection (psbA and PsbA-D1 upregulation), and metal transport optimization (IRT1, ZIP8, MIR408 enhancement) (Liu et al. 2013; Wu et al. 2016; Zou et al. 2018; Zou et al. 2019; Lin et al. 2022) (Figure 2).

Induction of stress-responsive genes and signalling pathways

The molecular basis for seaweed metabolite-induced abiotic stress tolerance relies on the activation of sophisticated stress-responsive gene networks and hormonal signalling cascades, primarily involving ABA-dependent signalling pathways, late embryogenesis abundant (LEA) and cold-responsive (Cor) activation, heat shock responses, and ethylene signalling crosstalk. The comprehensive transcriptomic reprogramming observed across multiple seaweed metabolites demonstrates their capacity to function as complex signal molecules capable of triggering systemic stress preparation responses (Figure 2). ABA-dependent signalling is the central mechanism by which seaweed-derived polysaccharides mediate plant adaptation to abiotic stress. For instance, a foliar application of AOS in wheat plants resulted in a temporally specific modulation of key ABA signalling components under drought stress. Notably, SnRK2 kinase activity peaked at 3 h, while the expression levels of LEA1 and P5CS reached their maximum at 24 h post-treatment. The temporal dynamics of these responses indicate that plants modulate immediate and prolonged mechanisms to cope with stress. Similarly, the treatment of low molecular weight polysaccharides from *U. prolifera* in wheat plants enhanced ABA-dependent signalling through substantial upregulation of P5CS, SnRK2, Wabi5, and Wdreb2 genes under osmotic stress conditions (Zuo et al. 2021). Furthermore, this application led to the coordinated upregulation of key ABA pathway downstream targets, such as several LEA/Cor genes (Wdhn13, Wrab17, Wrab18, Wrab19). This proves that seaweed-derived metabolites induce a comprehensive activation of dehydration stress response networks. Root application of laminarin to Arabidopsis induced extensive transcriptomic reprogramming, evidenced by over 2-fold expression changes in 112 genes under heat stress (Wu et al. 2016). This was accompanied by the concur-

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rent activation of the ethylene signalling pathway by upregulating ACS4 and ERF genes. Furthermore, enhanced ABA-responsive gene expression, particularly of RD22 and DEFL202 (known to activate downstream antioxidant enzymes), suggests the integration of multiple stress-sensing and response mechanisms.

Modulation of antioxidant defence systems and cellular protection

Seaweed-derived metabolites also confer abiotic stress tolerance through comprehensive modulation of antioxidant enzyme systems, ROS scavenging mechanisms, membrane stabilisation, and cellular antioxidant networks. The antioxidant enzyme defence system represents the primary cellular protection mechanism activated by seaweed metabolites across diverse stress conditions, providing multilayered protection against oxidative damage induced by environmental stressors. Fucoidan-treated wheat under salt stress conditions (120 mM NaCl) demonstrated comprehensive antioxidant enzyme activation, including SOD activity enhancement by 60.7%, the most dramatic POD and CAT increases of 130% activation (Zou et al. 2021). In another study, wheat treated with polysaccharides from *L. nigrescens* exhibited significantly increased SOD (96.0%) and POD (43.9%) activation, alongside moderately enhanced CAT activity, in response to salt stress (150 mM NaCl). Additionally, this treatment promoted the accumulation of soluble sugars (35.3%), contributing to both osmotic adjustment and antioxidant capacity through complementary protective mechanisms (Zou et al. 2019). Consistent with these findings, polysaccharides and their derivatives enhanced the activity of antioxidant enzymes under the tested stress conditions. Specifically, low molecular weight DPP1 from *P. yezoensis* enhanced SOD and POD under salt stress, AOS promoted SOD and POD activation under drought stress, fucoidan stimulated SOD, CAT, POD, APX, MDHAR, dehydroascorbate reductase (DHAR), and glutathione reductase (GR) under chilling stress, and laminarin led to increased SOD and APX activity under heat stress conditions (Liu et al. 2013; Wu et al. 2016; Zou et al. 2018; Lin et al. 2022).

Physiological homeostasis and metabolic adaptation

Seaweed-derived metabolites maintain cellular function under abiotic stress through sophisticated regulation of osmotic adjustment, ion homeostasis, energy metabolism, photosynthetic protection, secondary metabolism, and metal transport systems. Proline accumulation emerged as a universal osmotic adjustment strategy across multiple seaweed metabolites and stress types, representing a fundamental mechanism for maintaining cellular water balance and turgor pressure under stress conditions (Alvarez et al. 2022). Polysaccharides (MW 40.2 kDa) from *L. nigrescens* achieved the most remarkable proline elevation of 87.1%, while low molecular weight polysaccharides (DPP1: 3.2 kDa) from *P. yezoensis* enhanced proline content by 61.9% (Zou et al. 2018; Zou et al. 2019). Fucoidan treatment induced substantial proline increases under salt stress conditions (Zou et al. 2021), with additional proline accumulation documented for AOS and *U. prolifera* polysaccharides under drought and osmotic stress conditions (Liu et al. 2013; Zuo et al. 2021). Ion homeostasis regulation represents a critical adaptation mechanism for maintaining cellular ionic balance under salt stress conditions through multiple coordinated strategies (Amin et al. 2021). At the physiological level, fucoidan treatment from *Macrocystis pyrifera* achieved effective Na^+/K^+ ratio regulation, establishing a lower and more favorable ionic environment essential for cellular function under saline conditions (Zou et al. 2021). Oligo-alginate treatment provided additional ionic protection through reduced Na^+ and Cl^- uptake under salt stress, demonstrating direct ion exclusion mechanisms (Salachna et al. 2018). At the molecular level, both *L. nigrescens* and *P. yezoensis* polysaccharides modulated key ion transport genes, including downregulation of TaHKT2;1 and upregulation of TaNHX2 and TaSOS1 (Zou et al. 2018; Zou et al. 2019), collectively enhancing sodium exclusion and compartmentalisation mechanisms. Energy metabolism maintenance proved essential for sustaining cellular processes under stress conditions. Fucoidan treatment under chilling stress enhanced multiple energy-related enzymes, including H^+-ATPase, Ca^{2+}-ATPase, cytochrome c oxidase (CCO), and succinate dehydrogenase (SDH), collectively maintaining cellular energy homeostasis during low-temperature stress (Lin et al. 2022). This comprehensive energy system enhancement ensures continued ATP production and cellular energy charge maintenance under adverse conditions (Lin et al. 2022). Photosynthetic protection mechanisms demonstrated both immediate and long-term

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adaptive responses to stress conditions. Alginate oligosaccharides provided acute photosystem protection through psbA upregulation 6 hours post-treatment (Liu et al. 2013), indicating rapid photosystem II repair mechanisms. Laminarin treatment enhanced photosystem stability through PsbA-D1 upregulation under heat stress (Wu et al. 2016), ensuring continued photosynthetic function under elevated temperatures. Oligo-alginate treatment enhanced photosynthetic pigment content, including chlorophyll and total chlorophyll levels (Salachna et al. 2018), supporting sustained light-harvesting capacity and photosynthetic efficiency under stress conditions. Metabolite accumulation contributed to stress adaptation through enhanced biosynthetic capacity for protective compounds. Oligo-alginate treatment stimulated phenolic biosynthesis, increasing polyphenol content (Salachna et al. 2018). Laminarin treatment specifically enhanced terpenoid synthesis under heat stress (Wu et al. 2016). Ascorbic acid content increased significantly following oligo-alginate treatment, contributing to enhanced antioxidant capacity (Salachna et al. 2018). Soluble sugar accumulation reached a 35.3% increase with *L. nigrescens* polysaccharides (Zou et al. 2019), with additional sugar elevation observed for *P. yezoensis* polysaccharides (Zou et al. 2018). Soluble protein content was dramatically enhanced 1.86–2.13 fold with *U. prolifera* polysaccharides, indicating comprehensive metabolic reprogramming for osmotic protection (Zuo et al. 2021). These findings suggest that accumulation of metabolites and osmoprotectants provides additional cellular protection through stress-protective properties. Metal transport regulation showed particular importance under combined stress conditions, with laminarin treatment enhancing multiple metal transporters, including IRT1 (showing the highest upregulation), ZIP8, and copper transporters, alongside MIR408 upregulation, suggesting improved metal homeostasis and micronutrient availability (Wu et al. 2016). These transport systems will likely contribute to maintaining essential metal cofactor availability for stress-responsive enzymes.

Integrative cross-tolerance mechanisms: Laminarin as an elicitor bridging biotic and abiotic stress

As comprehensively detailed in the preceding analysis, laminarin was found to be a potent universal elicitor through its remarkable capacity to simultaneously activate plant defence responses against both biotic (*F. oleagineum* and *E. onukii*) and abiotic stressors (heat and salt stresses) (Wu et al. 2016; Xin et al. 2019; Tziros et al. 2021). An earlier structure-activity study also demonstrated that the structural basis for laminarin's efficacy lies in its specific linear β-1,3-glucan linkages, which uniquely distinguish it from fungal cell wall glucans (Klarzynski et al. 2000). Unlike conventional elicitors that typically target specific stress categories (Rani et al. 2023), laminarin may contribute to priming a multi-layered defense system through PRR-mediated pattern recognition (Tziros et al. 2021), MAPK-WRKY signaling cascade activation (Xin et al. 2019), and comprehensive transcriptome reprogramming, involving over 112 genes (Wu et al. 2016). This coordinated response subsequently triggers extensive defence enzyme activation, including phenylpropanoid pathway enzymes (PAL), antimicrobial proteins (chitinase, β-glucanase), and copper-dependent oxidases (CuAO) that provide both structural reinforcement and direct pathogen suppression (Xin et al. 2019; Tziros et al. 2021).

Moreover, laminarin treatment strengthens cellular protection mechanisms through enhanced antioxidant systems comprising enzymatic antioxidants (SOD and APX) and non-enzymatic antioxidants (phenolics) for ROS detoxification. This synergistic antioxidant response creates a comprehensive oxidative stress management system that protects against biotic and abiotic challenges (Wu et al. 2016; Xin et al. 2019). In addition, laminarin shows context-dependent hormonal selectivity, activating SA pathways for biotic stress defence and ABA pathways for abiotic stress tolerance while maintaining JA-independent signalling patterns (Xin et al. 2019). This strategic approach enables laminarin to circumvent the typical growth-defence trade-off, providing comprehensive stress protection without compromising plant development and productivity. Notably, laminarin has gained attention as an eco-friendly copper alternative to chemical fungicides to avoid accumulating heavy metals in the soil. For example, the endogenous copper oxidase (CuAO) was activated within plants to achieve equivalent antimicrobial efficacy through dual mechanisms, including generating H_2O_2 via polyamine oxidation and synthesising phenolic antimicrobial compounds (Tziros et al. 2021). Wu and coworkers demonstrated that this molecule also confers heat stress tolerance indirectly by upregulating copper transporter gene expression, thus ensuring adequate copper cofactor supply to chlo-

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roplast antioxidant enzymes (Wu et al. 2016). This approach provides dual benefits by enhancing biotic and abiotic stress tolerance, representing a sustainable agricultural strategy that maintains crop protection without compromising soil health or long-term productivity.

Beyond laminarin's versatile properties, other marine polysaccharides, including fucoidan and alginate derivatives, demonstrate protective effects against both biotic and abiotic stressors (Liu et al. 2013; Salachna et al. 2018; Zhang et al. 2019; Zou et al. 2021; Lin et al. 2022; Wang et al. 2023b). Previous studies indicate that low molecular weight polysaccharides show enhanced bioactivity compared to their high molecular weight counterparts (Jiao et al. 2011; Zuo et al. 2021). To optimise these beneficial properties, extensive experimental investigation is necessary to understand structure-activity relationships, particularly how molecular size, sulfation patterns, and glycosidic linkages influence polysaccharide bioactivity.

CONCLUSION

Interest in utilising seaweed extracts and their bioactive metabolites has increased to enhance crop yield and resilience against biotic and abiotic stressors. Several studies have highlighted the potential of seaweed extracts and isolated compounds to enhance plant growth and tolerance to various stress factors. This review has presented the potential applications of seaweed extracts and their metabolites, including polysaccharides, phenolic acids, and fatty acids, along with their underlying mechanism of action for mitigating diverse types of stressors. Seaweed extracts or their derived bioactive compounds act as elicitors, recognised by plant transmembrane PRRs, triggering defence signalling pathways akin to PAMP recognition. This leads to the activation of key signalling molecules like SA and JA. These pathways produce PR proteins, ROS-scavenging enzymes, and defensive secondary metabolites. Ultimately, this enhances plant resistance against various pathogens and insect pests such as bacteria, viruses, oomycetes, fungi (ascomycetes and basidiomycetes), nematodes, and herbivorous insect pests. Similarly, under abiotic stresses (such as salinity, drought, extreme temperatures, and heavy metals), seaweed extracts or metabolites mitigated abiotic stresses through the induction of stress-responsive genes and signalling pathways, modulating plant hormones, and activities of antioxidant enzymes, including inducing the accumulation of osmoprotectants. However, current research on seaweed-derived metabolites remains predominantly limited to controlled environments (laboratory, growth chamber, greenhouse), and further field validation studies are warranted. Moreover, various crops' dosage, application method, and treatment duration must be optimised to achieve long-term benefits. In addition, identifying and characterising novel bioactive metabolites in different chemical classes from various seaweed species that enhance plant stress resilience should be prioritised to unlock the full potential of marine-derived agricultural solutions.

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