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REVIEW

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The power of seaweeds as plant biostimulants to boost crop production under abiotic stress

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Abstract

Abiotic stresses like drought and salinity are major factors resulting in crop yield losses and soil degradation worldwide. To meet increasing food demands, we must improve crop productivity, especially under increasing abiotic stresses due to climate change. Recent studies suggest that seaweed-based biostimulants could be a solution to this problem. Here, we summarize the current findings of using these biostimulants and highlight current knowledge gaps. Seaweed extracts were shown to enhance nutrient uptake and improve growth performance in crops under stressed and normal conditions. Seaweed extracts contain several active compounds, for example, polysaccharides, polyphenols and phytohormones. Although some of these compounds have growth-promoting properties on plants, the molecular mechanisms that underly seaweed extract action remain understudied. In this paper, we review the role of these extracts and their bioactive compounds as plant biostimulants. The targeted application of seaweed extract to improve crop performance and protein accumulation is also discussed.

KEYWORDS
crop productivity, mechanism of action, protein transition, seaweed biostimulants, sustainable agriculture

1 | INTRODUCTION

1.1 | Closing yield gaps

In the future, our world will face two major problems: climate change and a growing world population. The estimated global population is expected to reach 10 billion in 2050 (UN DESA, 2017), and with rising temperatures, more desiccation and salinization will be observed. This will likely have negative consequences on crop growth and productivity worldwide (Hassani et al., 2021; Mueller et al., 2012). Despite these challenging environmental conditions, substantial increases in food production must be met while decreasing the environmental footprint of agriculture.

The global shift to a more animal-based diet (Henchion et al., 2014) also puts extra demands on crop productivity. The global demand for animal-sourced food products is expected to increase by over 70% in 2050, necessitating a vast increase in high-protein fodder not only because of the growing world population but also due to increased welfare (Alexandratos & Bruinsma, 2012). With increasing welfare, the percentage of animal-based food products in the daily diets increases. For example, Western diets shifted from 40% of protein originating from animal sources in the 1960s to more than 60% today (Alexandratos & Bruinsma, 2012; Jalil et al., 2020). As a consequence of increasing animal-based food consumption, the demand for animal feed will increase even more. To produce 1 kg of animal protein, 3–6 kg of plant protein is needed (Alexandratos & Bruinsma, 2012). Therefore, as animal-based food consumption is increasing, the need for plant-based feed is soaring at a faster rate. It is predicted that the global protein demand only for feed will reach 1500 Mton in 2050, which will be a real challenge in view of the increasing food demand for the growing world population (Alexandratos & Bruinsma, 2012).

1.2 | Biostimulants as alternatives to enhance crop productivity

One approach to increase food production while dealing with less favourable conditions is to cultivate crops that are more resilient to environmental stresses. Traditionally, crop resilience has been increased through breeding programs. The success rate and time required for breeding new varieties have, however, been a major challenge due to the high genetic complexity of abiotic stress resilience in crops. Therefore, breeding new cultivars takes between 10 and 15 years. Recent alternatives to enhance crop growth, such as the use of plant biostimulants, have attracted researchers' attention due to their diverse applications that can enhance plant fitness. Biostimulants are 'materials other than fertilizers and pesticides' that stimulate nutritional processes independent of the crop's nutrient content with the specific aim of enhancing nutrient use efficiency, resilience to abiotic stress, quality traits, or availability of confined nutrients in the soil or rhizosphere (EU, 2019; Rouphael & Colla, 2020). These materials can be substances and/or microorganisms that enhance plant growth, increase tolerance to unfavourable environmental conditions, and promote efficient use of plant resources (Campobenedetto et al., 2021; Yakhin et al., 2017). Biostimulants are obtained from, for example, microorganisms, plant- or animal-based by-products recycled from the food industry, or seaweed extracts.

1.3 | Seaweed extracts as plant biostimulants

One of the most promising classes of biostimulants is seaweed extract. Seaweed extracts represent the fastest-growing biostimulant industry (Carmody et al., 2020; Markets & Markets, 2019). Seaweeds or macroalgae are multicellular marine algae that form an essential part of marine coastal ecosystems. Seaweeds are divided into three main classes based on their pigmentation, namely, *Phaeophyta* (brown), *Rhodophyta* (red) and *Chlorophyta* (green). The extracts derived from seaweeds contain a plethora of bioactive compounds. Some of these compounds are polysaccharides, pigments, phenolic compounds, proteins and (bioactive) peptides, phytohormones and micro- and macronutrients (El Boukhari et al., 2020; Craigie, 2011; Khan et al., 2009; Stirk & Van Staden, 2014). This complex chemical composition could explain the wide range of biofunctionality of these extracts. Several papers have shown the potential and advantages of using seaweed extracts as biostimulants in both normal (nonstressed) and stress conditions (Khan et al., 2009; Shukla et al., 2019). Seaweed-derived biostimulants have great potential because: (a) seaweed extracts function in very low concentrations; (b) off-shore seaweed cultivation does not compete with land use for producing food; (c) seaweed extracts are able to increase abiotic stress resilience in many crops; and (d) the application of seaweed biostimulants can enhance protein production in protein-rich crops.

In our paper, we discuss the current status on (a) how seaweed extracts increase crop productivity under abiotic stresses, (b) the metabolite composition of seaweed-based biostimulants, (c) mechanism of action in response to biostimulant application, and (d) effect of seaweed extracts on protein production in crops. More knowledge of seaweed extracts' composition and the mode of action will likely optimize their use in agriculture. For example, the production process (e.g., quality of seaweed starting materials and extraction method) can be adapted according to the desired chemical composition of the resulting extract. More insight into the mode of action of specific seaweed compounds in relation to the effect on different crops will lead to the targeted use of seaweed extracts and improved growth-promoting effects.

2 | SEAWEED EXTRACTS INCREASE CROP PRODUCTIVITY UNDER ABIOTIC STRESSES

Biostimulants derived from seaweed have been commercialized in recent years as substances that improve plant productivity. Under normal environmental conditions, the use of seaweed extracts may result in higher crop productivity (Rouphael & Colla, 2020; Yakhin et al., 2017). Field-grown crops (and even sometimes, crops grown in greenhouses) are typically exposed to various stresses during their life cycle. Abiotic stresses such as drought and salinity are responsible for large crop losses, causing up to a 50% reduction in crop yield as well as reducing the productivity potential of arable land (Food and Agriculture Organization of the United Nations and Intergovernmental Technical Panel on Soils [FAO & ITPS], 2015; Gull et al., 2019). It is estimated that at least 10% of total arable land experiences salinity, drought or a combination of the two (FAO & ITPS, 2015; Rojas, 2020; Shahid et al., 2018). It is therefore important to mitigate the disastrous effects of abiotic stress on crops while improving crop productivity under these stress conditions. Most of these abiotic stress experiments were performed in controlled greenhouses, but positive results of seaweed extracts have also been replicated on farm fields (Arioli et al., 2021; Sharma et al., 2019). The results obtained in field experiments highlight the applicability and potential benefits of using seaweed extracts under more realistic farming conditions.

Crops treated with seaweed extracts recovered from the damaging effects of heat and frost and showed improved growth and survival under drought and saline conditions (Shukla et al., 2019).

The application of seaweed extracts reduced relative water loss and encouraged plant recovery from short-term (4–10 days) drought stress in *Arabidopsis*, tomato, soybean and wheat (Goñi et al., 2018; Santaniello et al., 2017; Sharma et al., 2019; Shukla et al., 2018). A reduction in leaf wilting and a significant increase in plant growth were also observed in these studies. Chickpea plants treated with seaweed extracts before salinity stress exposure showed a significant increase in vegetative growth compared to their control, and are saline-stressed plants when not treated with seaweed extracts (Abdel Latef et al., 2017). Seaweed extracts also enhanced the growth of rice and wheat grown under saline conditions (Liu et al., 2019; Zou et al., 2018).

Application of seaweed extracts in promoting vegetative growth under drought and salinization is important; in addition, indicating the impact seaweed extracts have on subsequent harvestable crop yield and product quality under such stress conditions is even more essential to encourage adoption by farmers. Pretreatment of cherry tomato seeds with an *Ascophyllum nodosum*-based biostimulant resulted in enhanced fruit quality (measured as total soluble solids, lycopene and flavonoids) and up to 65% increase in crop fruit yield, even in the presence of drought stress (Murtic et al., 2018). Similar positive results were observed in two studies of wheat grown under drought conditions. Here, foliar treatment with extracts from either *Gracilaria dura* or *Kappaphycus* spp. improved crop seed yield by 70% and 200% (double the initial yield), respectively (Sharma et al., 2019; Trivedi et al., 2018). Rapeseed plants treated with any of the extracts from *Ulva lactuca*, *Cystoseira* spp. or *Gelidium crinale* and grown either under mild (75 mM NaCl) or severe (150 mM NaCl) salinity also showed improvements (Hashem et al., 2019). In this case, crop seed yield was up by 50% and 65% under mild and severe salt stress, respectively, and a significant increase in seed oil percentage compared to the untreated plants was also recorded (Hashem et al., 2019). Tomato plants treated with two commercial *Ascophyllum*-derived extracts showed improved fruit quality under salinity stress, denoted as a significant increase in vitamin C (ascorbate) content (Di Stasio et al., 2018).

Results obtained from experiments where seaweed extracts were applied are not always positive and biostimulants should therefore not be sold as 'miracle' inputs. In a few published cases, crops treated with seaweed extracts and grown under abiotic stress conditions showed no significant differences in crop yield (Di Stasio et al., 2018) or even inhibitory germination responses (Masondo et al., 2018). In most cases, crop productivity was still reduced under severe stress conditions even with seaweed extract treatment, albeit to a lesser extent than in nontreated plants (Hashem et al., 2019; Murtic et al., 2018; Trivedi et al., 2018). For example, salinity stress decreased crop productivity of cherry tomatoes by ~50%. The use of the *Ascophyllum nodosum*-based biostimulant increased productivity by 85% of the initial crop yield under normal conditions; therefore, the yield gap was not fully closed (Murtic et al., 2018). Thus, seaweed extracts are not always able to completely reverse or eliminate stress-induced damage, especially under severe abiotic stress. They do, however, result in an improved resilience to abiotic stress in these crops.

The number of applications, application rate (dosage) and timing (in the life cycle of the crop) of extract application must be optimized by manufacturers of biostimulants to provide the best results for farmers. Insights into the metabolite composition of seaweed-based biostimulants and deciphering the underlying plant mechanisms associated with the application of the biostimulants may give leads for optimization of seaweed extracts and confer efficient use of the biostimulants for maximum crop performance.

3 | METABOLITE COMPOSITION OF SEAWEED-BASED BIOSTIMULANTS

Based on the source of raw materials (seaweed) and the extraction method used for the production of biostimulants, seaweed extracts contain many different bioactive compounds (Nanda et al., 2021; Shukla et al., 2019). Seaweed extracts are enriched in phytohormones, sterols, carbohydrates, polysaccharides, sugars, polyphenols, macro- and micronutrients, vitamins, lipids, amino acids, peptides and proteins (Khan et al., 2009; Shukla et al., 2019). Furthermore, the concentration of several components in seaweeds can vary greatly over growing seasons or due to certain environmental conditions. Seasonal variation in polysaccharides, polyamines, lipids and proteins was observed in multiple seaweed species (Fletcher et al., 2017; Khairy & El-Shafay, 2013; Papenfus et al., 2012). However, the variability in source material is mostly associated with extraction from wild seaweeds since these are grown in nature. Commercially available seaweed extracts often contain more than one species of seaweed since nonspecific selection may occur during wild harvesting (Mac Monagail et al., 2017). Interestingly, over the last decade, there has been great progress in the field of seaweed cultivation, which nowadays accounts for more than 90% of the global seaweed harvest (Little et al., 2016). Cultivation may allow for controlled production of seaweeds with less influence from environmental factors, resulting in a more constant chemical composition of the source material. However, the cultivation of many different seaweed species has not yet been successful, including species important for the seaweed extracts industry such as the brown seaweed *Ascophyllum nodosum* (Shukla et al., 2019).

Bioactive polysaccharides identified in seaweed extracts are galactans (carrageenans and agarans) and floridean starch, ulvans, starch, lignin and cellulose, laminarin, fucoidan and alginic acid (Shukla et al., 2019). Most seaweed extraction methods result in a (partial) depolymerization of the polysaccharide pool, resulting in a dominant presence of oligo- and monosaccharides in seaweed extracts (Gullón et al., 2020). Fucoidan oligosaccharides function as elicitors of the local defence response and as priming agents in the systemic defence of plants (Klarzynski et al., 2003). Seaweed-derived alginates and their oligo-derivatives are reported to act in the stimulation of plant growth, development and resistance (Mukherjee & Patel, 2020; Shukla et al., 2019). For example, foliar application of an alginate oligosaccharide (AOS) solution in a short-term hydroponic experiment ameliorated the stress caused by polyethylene glycol-induced drought in wheat (Liu et al., 2013). This study also reported that upon application of AOS, there was an upregulation of abscisic acid (ABA)-responsive genes that are often related to drought resistance (Liu et al., 2013). These results suggest that AOS stimulate drought resilience via the ABA-signalling pathway (Liu et al., 2013). The fact that alginate comprises up to 45% of the dry weight of brown seaweed implies an important role for this (depolymerized) polysaccharide in seaweed extract bioactivity (Vera et al., 2011).

Another polysaccharide, laminarin, has been well described as a bio-elicitor in plant defence responses against various pathogens (Garde-Cerdán et al., 2017; Pugliese et al., 2018; Romanazzi et al., 2016). Additionally, laminarin oligosaccharides increased transient Ca^{2+} influx in the cytosol of tobacco (*Nicotiana plumbaginifolia*) cells (Lecourieux et al., 2002). Free cytosolic Ca^{2+} is known to mediate many cellular processes involved in plant growth, development and resistance (Lecourieux et al., 2002). Carrageenans and oligo-carrageenans (polysaccharides abundant in red seaweeds) also enhance the growth of various plants by altering key physiological and/or biochemical processes. Stimulating effects on growth and development after polysaccharide κ-carrageenan treatment were observed in maize and chickpea (Bi et al., 2011). However, in most cases, depolymerization of carrageenans was shown to be necessary to elicit a response in plants (Gonzalez et al., 2013a). In tobacco plants, κ-, λ- and ι-oligo-carrageenan treatment resulted in stimulation of growth, photosynthesis and basal metabolism (Castro et al., 2012). These observations were accompanied by an increase in the activity of several key enzymes involved in carbon and nitrogen assimilation (Castro et al., 2012). Similarly, the accumulation of several essential nutrients and enhanced activity of basal metabolism-related enzymes, as well as improved growth rate, was observed in pine trees after κ-oligo-carrageenan treatment (Saucedo et al., 2015). Interestingly, plant growth after the application of both poly- and oligo-saccharides of carrageenan was associated with increased cell number. Together with the fact that transcript levels of cell regulatory proteins were increased after treatment, it was suggested that oligo-carrageenans affect the cell division mechanism (Castro et al., 2012; Gonzalez et al., 2013a). Furthermore, extensive research in eucalyptus trees showed the stimulating effect of κ-oligo-carrageenan treatment on photosynthesis, basal metabolism and growth (Gonzalez et al., 2013a; Gonzalez et al., 2013b). Another potential mode of action in which oligo-carrageenans, if still present in the seaweed extracts that are used as biostimulant, affect the plants is via the direct or indirect upregulation of phytohormone synthesis. Increased levels of the bioactive auxin indole-3-acetic acid (IAA), gibberellic acid (GA3) and *trans*-zeatin were reported after purified κ-oligo-carrageenan treatment in pine and eucalyptus trees (Gonzalez et al., 2013b; Saucedo et al., 2015). It must be clear that these results discussed above were obtained by directly applying purified seaweed polysaccharides. Thus, the same effects observed in the plants may not occur when using seaweed biostimulants (extracts).

Compounds present in seaweed have been shown to have positive effects not only on plant growth and resilience but also on soil health. For example, soluble alginates from seaweeds and protein hydrolysates have been reported to facilitate the aggregation of soil particles, which improves the nutrient availability, aeration and water holding capacity in the soil (Colla et al., 2017; Khan et al., 2009). Apart from the direct benefits for the plant, seaweed extracts positively affect the soil microbiome, promoting an increased activity of beneficial organisms. Microbes are reported to absorb free amino acids to a higher extent than plants. In various crops, it was observed that only 6%–25% of the flagged amino acids were absorbed by the roots, while the rest was taken up by the soil microbiome (Moe, 2013). However, another study indicated that microbes excrete a substantial part of the amino acid-derived nitrogen back into the soil as ammonium, where it can be captured by the plant (Jones et al., 2005, 2009). Interestingly, Rouphael et al. (2017) showed a synergistic effect in lettuce between a microbe-based biostimulant and a plant-based protein hydrolysate-rich extract. Crop performance was improved in the combined treatment, compared to the treatment with solely the microbe-based product. This performance was characterized by a higher total root length and surface, enhanced chlorophyll levels and an increase in nitrogen assimilation. Together, this represents a strategy to ameliorate salt stress (Rouphael et al., 2017), suggesting that general crop performance can be enhanced by supplementing the plant's microbiome with protein hydrolysates derived from seaweed extracts.

Many other complex organic compounds have been classified as bioactive components of seaweed extracts in various fields of application. For example, polyamines have emerged as an interesting bioactive group in seaweed extracts. These compounds are present in most plants and have plant growth-regulating properties (Chen et al., 2019). Additionally, betaines are known constituents of seaweed extracts that function as cytoplasmic antioxidants or elicitors of physiological responses in the plant (Blunden et al., 2010; MacKinnon et al., 2010). In seaweeds, many different types of phenolic compounds have been identified and described as well. In general, brown seaweeds contain mostly phlorotannins, whereas red and green species are abundant in bromophenols, flavonoids and phenolic acid (Cotas et al., 2020). Compared to other phenolic compounds, phlorotannins contain a higher amount of phenol rings, a property that is associated with higher antioxidant bioactivity (Venkatesana et al., 2020). Additionally, a group of three phenolic compounds, catechol, resorcinol and tannic acid, were reported to have an antioxidant effect in wheat when exogenously applied to the leaves (Zhao & Zou, 2002). To further optimize the production and application of these biostimulants, it is important to understand which compounds are responsible for the observed effects, as well as their mode of action in plants. However, it is poorly understood how these different compounds are recognized and perceived by the plant. The depolymerization and degree of sulfation of polysaccharides are associated with their bioactivity, thus both processes may be important for the perception of these compounds (Battacharyya et al., 2015; Shukla et al., 2016).

Other bioactive compounds in seaweed extracts are pigments. Seaweed pigments are classified into three main groups: chlorophylls, carotenoids and phycobiliproteins that possess a variety of bioactive functions (Aryee et al., 2018). Micronutrients are also present in seaweed products, existing in the fresh, dried or extract form (Sharma et al., 2014). Another group of bioactive molecules identified in seaweed extracts are plant hormones. The hormonal profile of seaweeds largely resembles that of terrestrial plants. Although their activity in seaweeds remains poorly understood, many different phytohormones have been detected including the bioactive forms of auxins, cytokinins (CKs), ABA and gibberellins (Lu & Xu, 2015). Ethylene, brassinosteroids, salicylic acid, jasmonates and strigolactones were identified in seaweed extracts as well (Stirk & Van Staden, 2014). Importantly, the presence of phytohormones in seaweed extract is not only determined by the seaweed source. Extraction and purification of phytohormones are dependent on the versatility in chemical structure and properties like water solubility and alkalinity or acidity levels. Therefore, the presence of these bioactive compounds in the seaweed extracts depends not only on the species used, or on the extraction methods, but also on geographical location and the season in which the seaweeds were harvested (Shukla et al., 2019).

4 | MECHANISM OF ACTION IN RESPONSE TO BIOSTIMULANT APPLICATION

Seaweed extract efficacy and their mode of action in crops have not yet been fully characterized. Seaweed extracts are thought to have specific modes of action because of the presence of phycocolloids, for example, alginate, carrageenan, laminarin and fucoidan, which are absent in land plants. Propositions on how seaweed extracts may increase crop productivity and stress resilience have been suggested (Ali et al., 2021; Shukla et al., 2019; Yakhin et al., 2017), but linking and validating specific underlying mechanisms stimulated by the seaweed extracts to beneficial crop responses remains mostly unanswered. Chemical analyses of seaweed extracts depicted bioactive components that can be linked to plant metabolic and hormone pathways. These are the first indicators, providing some perception into (possible) underlying mechanisms used by seaweed extracts. There is no direct correlation yet between the presence of a specific seaweed compound or protein/peptide and the biostimulant activity that can be found in (specific) crops.

Compounds in seaweed extracts may act as signalling molecules regulating key pathways at the transcriptional and/or post-translational levels (microRNAs), causing differential expression of essential genes in crops (Figure 1 and Table 1) that contribute to increased plant growth and abiotic stress resilience. Transcriptome analysis indicated modulation of several genes due to exposure of *Arabidopsis* plants to seaweed extracts in nonstress conditions (Goñi et al., 2016). Genes involved in cell metabolism, including lipid, amino acid and nucleotide metabolism, glycolysis and transport, photosynthesis, and cell and cell wall development, all showed changes in transcript levels. The highest induction was recorded for ion transporters, *CAX3*, a vacuolar cation exchanger and *COPT2*, a copper transporter, while fatty acid and phospholipid synthesis genes were mostly downregulated (Goñi et al., 2016).

Application of seaweed extracts to crops under abiotic stress caused upregulation of stress-responsive genes such as Na^+/K^+ transporters, late embryogenesis abundant (LEA) proteins including dehydrins, and aquaporins (Goñi et al., 2018; Rasul et al., 2021; Zou et al., 2018). Several aquaporins that are involved in transmembrane transport of water and other solutes, for example, *PIP1;2* (plasma membrane intrinsic protein 1;2), *PIP2;2* and *PIP2;3* were stimulated in response to seaweed extracts' treatment (Rasul et al., 2021; Santaniello et al., 2017). Treatment with an *Ascophyllum*-based biostimulant also caused strong upregulation of drought-responsive genes *LEA4-5*, *LEA7* and *LEA46* (Rasul et al., 2021). In another study, dehydrins, especially *TAS14* that was previously linked to long-term improvement of crops to drought and salinity, were also strongly induced (Goñi et al., 2018; Muñoz-Mayor et al., 2012). Further upregulation of Na^+/K^+ transporters *NHX2* (Na^+/H^+ exchanger 2) and *SOS1* (salt overly sensitive1) especially in the leaves, and simultaneous inhibition of *HKT2;1* (high-affinity K^+ transporter 2;1) in wheat plants exposed to another seaweed extract, led to increased K^+ levels and lower Na^+ content in the plants (Zou et al., 2018). Application of an *Ascophyllum*-derived seaweed extract in the presence of salinization stimulated expression of the microRNAs (miR) miR169g-5p, miR399, miR827 and miR2111b, which resulted in altered expression of target genes, herewith inducing phosphate uptake and salinity resilience of *Arabidopsis* plants (Shukla et al., 2018). These data suggest that seaweed extracts can promote the maintenance of protein integrity, water availability, ion homeostasis and nutrient uptake in crops by regulating the underlying genes associated with these processes, thereby reducing the deleterious effects caused by plant exposure to abiotic stress.

Growth stimulation and improved crop quality due to the application of seaweed extracts may also be linked to several other mechanisms (Figure 1 and Table 1). A higher photosynthetic rate and corresponding increased levels of chlorophyll pigments (chlorophyll a, b and carotenoids) relative to their nontreated and abiotic stressed counterparts have been reported in cowpea, chickpea and maize plants (Abdel Latef et al., 2017; Hussein et al., 2021; Trivedi et al., 2018). Mediating the activity of enzymes and genes involved in efficient nutrient assimilation is another proposed mode of action (Table 1), resulting in higher macro- and micronutrient concentrations in crops (Trivedi et al., 2018; Zodape et al., 2011). Crops treated with seaweed extracts also accumulate more carbohydrates, amino acids, proteins and vitamins independent of the presence or absence of stress (Hussein et al., 2021; Trivedi et al., 2018; Di Stasio et al., 2018). Furthermore, higher production of phenolic acids such as flavonoids, for example, naringenin and rutin in tomato, are stimulated by seaweed extract treatment (Figure 1b,d), leading to enhanced fruit colouring and flavour profile of the crops (Murtic et al., 2018). The positive effect seaweed extracts have on photosynthetic activities,

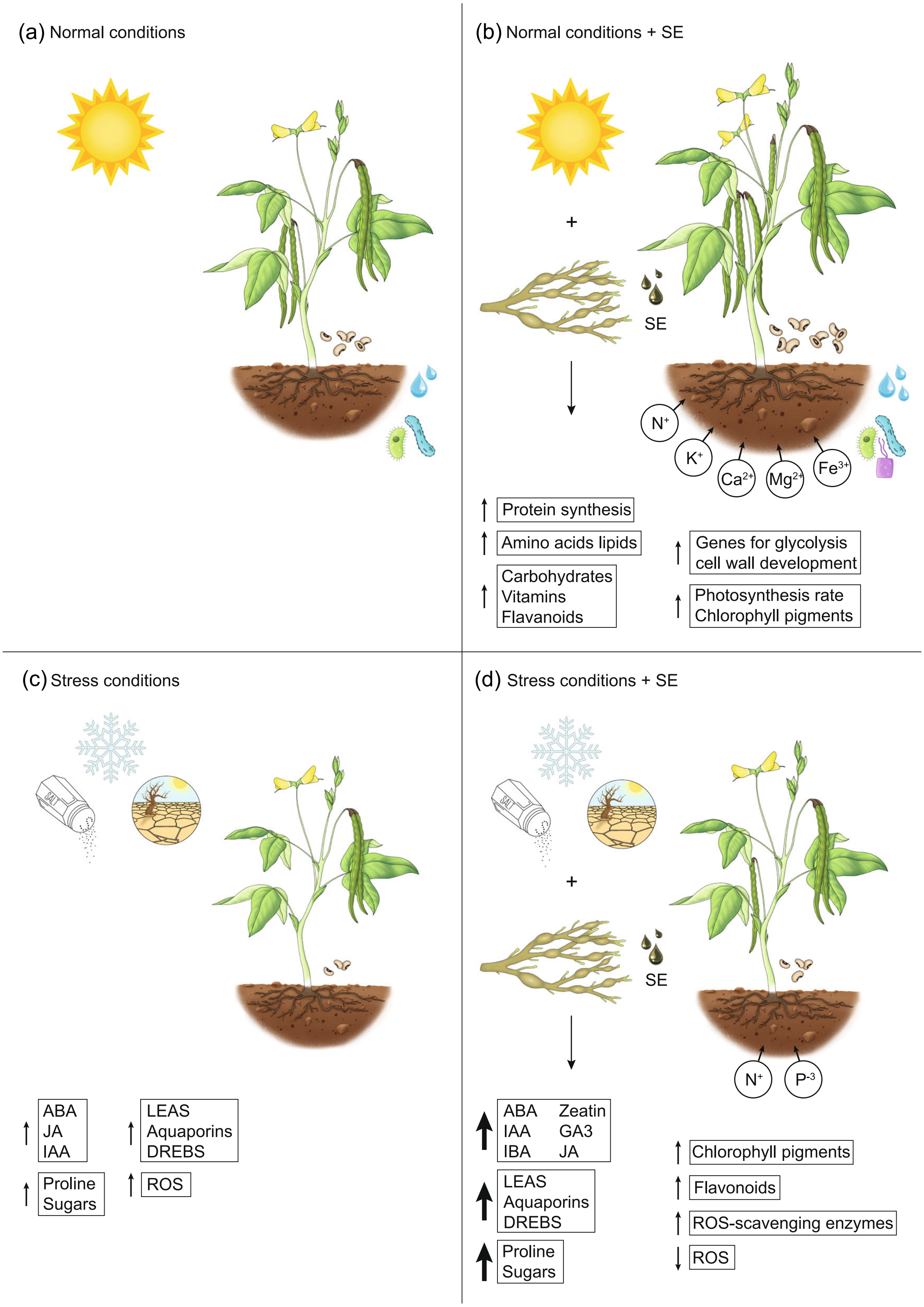

FIGURE 1 (See caption on next page)

nutrient uptake and polyphenol accumulation all simultaneously boost crop growth and quality, thus indicating that seaweed extracts have biostimulant activity on these pathways (Table 1). For example, its effect on plant photosynthesis may be due to the induction of several enzymes involved in plant photosynthetic processes, previously reported by Castro et al. (2012) and Saucedo et al. (2015), while it may enhance nutrient accumulation by upregulating calcium, nitrate, phosphate and sulphate transport and assimilation genes (Castro et al., 2012; Goñi et al., 2016; Saucedo et al., 2015; Zou et al., 2018).

Additionally, seaweed extracts alleviate abiotic stresses by increasing the antioxidant activity of reactive oxygen species (ROS) scavenging enzymes, for example, superoxide dismutase, peroxidases, catalases and phenolic antioxidants (Abdel Latef et al., 2017; Hussein et al., 2021). This leads to a reduction in ROS accumulation (Figure 1d), observed as decreased H_2O_2 levels and reduced accumulation of lipid peroxidation, measured as the malondialdehyde content (Abdel Latef et al., 2017; Goñi et al., 2018; Trivedi et al., 2018). The accumulation of osmoprotectants such as proline, sugars and organic acids also occurs on application of seaweed extracts (Figure 1d). Drought and salt-exposed plants treated with seaweed extracts show increased proline and sugar (glucose, fructose and sucrose) levels (Goñi et al., 2018) that serve as osmolytes essential for maintaining osmotic balance during the stress (Singh et al., 2015). Alginate oligosaccharides derived from brown seaweed and a *Gracilaria*-based seaweed extract both induced P5CS (pyrroline-5-carboxylate synthetase), an enzyme involved in proline biosynthesis (Liu et al., 2013; Sharma et al., 2019), which may explain the observed proline increase in such crops (Abdel Latef et al., 2017; Di Stasio et al., 2018). Thus, further induction of osmolytes and a reduction of ROS levels are two other activities prompted in crops after their exposure to seaweed extracts.

Modulation of hormone pathways due to seaweed extract application also promotes plant growth and development under stress conditions (Figure 1d and Table 1). Derivatives of the phytohormones ABA, auxin (e.g., IAA and indole-3-butyric acid [IBA]), CK (e.g., benzyl adenine and zeatin), gibberellin (e.g., GA3) and jasmonic acid were further induced in rapeseed plants treated with certain seaweed extracts and exposed to salinity stress (Hashem et al., 2019). The hormone pathways regulate plant growth and development by modulating several plant activities including nutrient assimilation and both physiological (tropisms) and molecular responses to abiotic stress (Ryu & Cho, 2015). Therefore, the extracts' biostimulant activity on the availability of the aforementioned phytohormones can be used to further unravel the associated underlying mechanism.

Exposure of *Arabidopsis* plants to *Ascophyllum*-based seaweed extracts modulated several ABA biosynthesis and signalling genes that support the observed increased ABA levels in the plants (Rasul et al., 2021; Santaniello et al., 2017). Although not all crop responses are ABA-dependent, deciphering exactly how ABA signalling can be linked to some of the identified molecular pathways induced during biostimulant treatment (as direct targets, or even downstream targets of ABA signalling) is of interest. Wheat plants under drought stress and exposed to seaweed extracts showed an increment of ABA biosynthesis enzyme *NCED3* (9-*cis*-epoxycarotenoid dioxygenase) that resulted in ABA accumulation in the crop (Sharma et al., 2019). ABA accumulation in the crop accelerated stomatal closure, which led to reduced water loss in such plants (Sharma et al., 2019). Increased ABA levels furthermore induced LEA and dehydrin expression, thereby promoting salinity and drought resilience in the crops (Muñoz-Mayor et al., 2012; Sharma et al., 2019; Zamora-Briseño & de Jiménez, 2016). Other stress-responsive genes needed for maintaining ionic balance, for example, *SOS2* a regulator in the SOS pathway, *NHX1* and *NHX2*, may also be regulated in an ABA-dependent manner (Ohta et al., 2003; Yokoi et al., 2002). Therefore, regulation of the ABA pathway is a possible key mechanism used by seaweed extract to promote crop survival under abiotic stress.

Principal component analysis showed strong correlations between the levels of laminarin, fucoidan and mannitol present in seaweed extracts and differential expression of specific genes, for example, transcription factor (TF) *WRKY40* and lipid

FIGURE 1 Underlying mechanism of action under (a) normal conditions and (b) normal conditions with the application of seaweed extracts (SE). Under normal (nonstressed) conditions, seaweed extracts may stimulate a number of processes resulting in improved crop growth and productivity. Seaweed extracts facilitate the assimilation of both macro- and micronutrients, for example, N (nitrogen), K (potassium), Ca (calcium), Mg (magnesium) and Fe (iron). Alginates present in seaweed extracts improve soil quality and structure by boosting water retention, air circularity and promoting microbial activity. Seaweed extracts induce genes/enzymes involved in cell wall biosynthesis and photosynthesis. Induction of other genes/enzymes of important metabolic pathways by seaweed extracts results in higher crop protein, amino acid, carbohydrate, vitamin, flavonoid, chlorophyll and carotene content. Proposed mechanism of action in response to (c) abiotic stress conditions and (d) abiotic stress conditions with seaweed extract application. Under abiotic stresses like salinity and drought, seaweed extracts may mediate certain metabolic processes, resulting in improved crop resilience and growth under the stress. Seaweed extracts cause upregulation of microRNAs involved in maintaining N and P (phosphorus) homeostasis. The application of seaweed extracts to crops increases the levels of the phytohormone ABA and hormonal derivatives IAA, IBA, zeatin, GA3 and JA. Stress-responsive DREB transcription factors, LEA proteins and aquaporins are further induced in the presence of seaweed extracts. Osmotic balance is maintained by a further accumulation of osmoprotectants like proline and sugars, by the seaweed extracts. The extracts have a positive effect on chlorophyll pigment and flavonoid accumulation. ROS production is inhibited upon treatment with seaweed extracts. ABA, abscisic acid

TABLE 1 Underlying mechanism of action under normal and stress conditions with the application of seaweed extracts

Seaweed extract source	Bioactive compounds in the extract	Plant Species	Biological process modulated	Genes/molecular pathway affected	Source
Unspecified red seaweed species	Carrageenan	*Nicotiana tabacum*; *Pinus* spp.	Nitrogen and sulphur uptake	Induction of nitrogen assimilation enzyme GDH (glutamate dehydrogenase); and sulphur assimilation enzyme OASTL (O-acetylserine thiol-lyase)	Castro et al. (2012) and Saucedo et al. (2015)
Ascophyllum nodosum	Unspecified compound in seaweed extract	*Arabidopsis thaliana*	Phosphorus and sulphur uptake	Stimulation of microRNAs (miRNA), for example, miR2111b and miR395 that modulate phosphate and sulphur assimilation, respectively	Shukla et al. (2018)
Ascophyllum nodosum; *Pyropia yezoensis*	Unspecified compound in seaweed extract	*Arabidopsis thaliana*; *Triticum aestivum*	Maintenance of ion homeostasis, and increasing endogenous levels of K^+ and Ca^{2+}	Modulation of Na^+/K^+ transporters, for example, *NHX2* (Na^+/H^+ exchanger 2), *SOS1* (salt overly sensitive1) and *HKT2;1* (high-affinity K^+ transporter 2;1); and upregulation of H^+/Ca^{2+} transporters, for example, *CAX3* (cation exchanger 3)	Goñi et al. (2016) and Zou et al. (2018)
Ascophyllum nodosum	Unspecified compound in seaweed extract	*Arabidopsis thaliana*	Copper uptake	Upregulation of *COPT2* (copper transporter 2)	Goñi et al. (2016)
Kappaphycus alvarezii	Unspecified compound in seaweed extract	*Zea mays*	Uptake of other nutrients (Mg and Fe)	Unspecified mechanism	Trivedi et al. (2018)
Unspecified brown seaweed species	Alginate	*Lycopersicum esculentum*; ornamental plants, for example, *Angelonia angustifolia*, *Dodecatheon pulchellum*, *Achillea* spp.	Improving soil properties, that is, promoting water retention, air circularity and microbial activity	Unspecified mechanism	Reviewed in Khan et al. (2009)
Unspecified red seaweed species	Carrageenan	*Nicotiana tabacum*	Amino acid synthesis	GDH enzyme activity	Castro et al. (2012)
Kappaphycus alvarezii; mixture of *Ulva fasciata*, *Cystoseira compressa* and *Laurencia obtusa*	Unspecified compound in seaweed extract	*Vigna sinensis*; *Zea mays*	Protein and carbohydrate accumulation	Unspecified mechanism	Trivedi et al. (2018) and Hussein et al. (2021)
Ascophyllum nodosum	Unspecified compound in seaweed extract	*Solanum lycopersicum*	Improved fruit quality is determined as vitamin C (ascorbate) content; and flavonoids, for example, naringenin and rutin accumulation	Unspecified mechanism	Di Stasio et al. (2018) and Murtic et al. (2018)

TABLE 1 (Continued)

Seaweed extract source	Bioactive compounds in the extract	Plant Species	Biological process modulated	Genes/molecular pathway affected	Source
Ascophyllum nodosum	Unspecified compound in seaweed extract	*Arabidopsis thaliana*	Fortifying cell wall	Upregulation of cell wall development genes, for example, *CSLE1* (cellulose synthase-like E1), *UGE1* (UDP-glucose 4-epimerase 1) and *PAE8* (pectin acetylesterase 8)	Goñi et al. (2016)
Unspecified red seaweed species	Carrageenan	*Eucalyptus globulus*	Fortifying cell wall structure by increasing α-cellulose and holocellulose content	Unspecified mechanism	Gonzalez et al. (2013a)
Unspecified red seaweed species	Carrageenan	*Nicotiana tabacum*; *Pinus* spp.	Photosynthetic process observed as increased levels of total chlorophyll content	Induction of Rubisco (ribulose 1,5 biphosphate carboxylase-oxygenase) enzyme activity; and NAD(P)H synthesizing enzymes, for example, G6PDH (glucose 6-phosphate dehydrogenase), IMPDH (inosine monophosphate dehydrogenase), and DHODH (dehydroorotate dehydrogenase)	Castro et al. (2012) and Saucedo et al. (2015)
Kappaphycus alvarezii; *Jania rubens*; *Sargassum muticum*; mixture of *Ulva fasciata*, *Cystoseira compressa* and *Laurencia obtusa*	Unspecified compound in seaweed extract	*Cicer arietinum*; *Vigna sinensis*; *Zea mays*	Photosynthetic process observed as higher photosynthetic rate and increased levels of chlorophyll pigments such as chlorophyll a, b and carotenoids	Unspecified mechanism	Abdel Latef et al. (2017), Trivedi et al. (2018) and Hussein et al. (2021)
Cystoseira spp.; *Gelidium crinale*; *Ulva lactuca*	Unspecified compound in seaweed extract	*Brassica napus*	Accumulation of abscisic acid (ABA), auxin, cytokinin, gibberellin and jasmonate derivatives	Unspecified mechanism	Hashem et al. (2019)
Unspecified red seaweed species	Carrageenan	*Pinus* spp.	Accumulation of auxin and gibberellin derivatives	Unspecified mechanism	Saucedo et al. (2015)
Ascophyllum nodosum	Unspecified compound in seaweed extract	*Arabidopsis thaliana*	Accumulation of ABA and modulation of downstream ABA responses	Modulation of ABA biosynthesis and signalling genes, for example, *NCED3* (9-*cis*-epoxycarotenoid dioxygenase), *PP2CA* (protein phosphatase 2CA), *PP2C52*, *PYL8* (regulatory component of ABA receptor 8), *ABI1* (ABA insensitive 1), *ABI2*, *SnRK2.8* (sucrose non-fermenting 1-related protein kinase 2.8), *DREB1A* (dehydration	Santaniello et al. (2017) and Rasul et al. (2021)

(Continues)

TABLE 1 (Continued)

Seaweed extract source	Bioactive compounds in the extract	Plant Species	Biological process modulated	Genes/molecular pathway affected	Source
				response element binding B1A) and *DREB3*.	
Unspecified brown seaweed species	Alginate	*Triticum aestivum*		ABA signalling gene *SnRK2*	Liu et al. (2013)
Ascophyllum nodosum	Unspecified compound in seaweed extract	*Arabidopsis thaliana*	Modulating stress-responsive genes	Induction of LEA (late embryogenesis abundant) proteins, for example, *LEA4-5*, *LEA7* and *LEA46*; and *TAS14* dehydrin gene	Goñi et al. (2018) and Rasul et al. (2021)
Ascophyllum nodosum	Unspecified compound in seaweed extract	*Arabidopsis thaliana*	Improving water transport and availability	Induction of Aquaporins, for example, *PIP1;2* (plasma membrane intrinsic protein 1;2), *PIP2;2* and *PIP2;3*	Santaniello et al. (2017) and Rasul et al. (2021)
Gracilaria dura	Unspecified compound in seaweed extract	*Triticum aestivum*	Maintenance of osmotic balance due to increased proline levels	Induction of proline biosynthesis enzyme, for example, P5CS (pyrroline-5-carboxylate synthetase)	Sharma et al. (2019)
Unspecified brown seaweed species	Alginate				Liu et al. (2013)
Ascophyllum nodosum	Unspecified compound in seaweed extract	*Arabidopsis thaliana*; *Solanum lycopersicum*	Maintenance of osmotic homeostasis by increasing proline and sugar, for example, fructose, glucose and sucrose levels,	Unspecified mechanism	Di Stasio et al. (2018) and Goñi et al. (2018)
Jania rubens; *Sargassum muticum*	Unspecified compound in seaweed extract	*Cicer arietinum*	Inhibition of ROS production	Induction of ROS-scavenging enzymes, for example, SOD (superoxide dismutase), POD (peroxidase), CAT (catalase) and APX (ascorbate peroxidase)	Abdel Latef et al. (2017)

TABLE 2 Seaweed extracts increase protein content in crops

Seaweed species	Crop	Concentration of seaweed extract (%)	Increased protein concentration (%)	Note	Source
Ascophyllum nodosum	*Allium cepa*	0.55	40.00		Hidangmayum and Sharma (2017)
Ascophyllum nodosum	*Glycine max* (Annushka)	0.70	6.00	Single application: extract sprayed only after 3–5 leaves emergence	Kocira et al. (2018)
Ascophyllum nodosum	*Glycine max (Atlanta)*	0.70	9.00	Extract sprayed only after 3–5 leaves emergence	Kocira et al. (2018)
Ascophyllum nodosum	*Glycine max* (Mavka)	1.00	6.00	Double application: 2nd spraying at beginning of flower blooming	Kocira et al. (2018)
Ecklonia maxima	*Spinacea oleracea*	0.40	16.30	Fertilizer applied. Extract application started after 3 weeks of growth	Kulkarni et al. (2019)
Ecklonia maxima	*Brassica oleracea*	0.40	14.29	Fertilizer applied in addition to extract	Rengasamy et al. (2016)
Caulerpa chemnitzia	*Vigna sinensis*	20.00	195.48	Seeds soaked in extract before germination	Sivasankari et al. (2006)
Sargassum wightii	*Vigna sinensis*	20.00	124.38	Seeds soaked in extract before germination	Sivasankari et al. (2006)
Sargassum wightii	*Abelmoschus esculentus*	20.00	25.00	Seeds soaked in extract before germination	Jothinayagi and Anbazhagan (2009)
Kapaphycus alvarezii	*Triticum aestivum*	7.50	3.07	Fertilizer applied in addition to extract	Shah et al. (2013)
Gracilaria edulis	*Triticum aestivum*	7.50	26.33	Fertilizer applied in addition to extract	Shah et al. (2013)
Gracilaria edulis	*Oryza sativa*	15.00	7.20	Fertilizer applied in addition to extract	Layek et al. (2018)
Kapaphycus alvarezii	*Oryza sativa*	15.00	6.36	Fertilizer applied in addition to extract	Layek et al. (2018)
Kapaphycus alvarezii	*Musa* spp. (Robusta)	5.00	45.83	Fertilizer applied in addition to extract	Karthikeyan and Shanmugam (2016)
Kapaphycus alvarezii	*Musa* spp. (Njali poovan)	5.00	34.26	Fertilizer applied in addition to extract	Karthikeyan and Shanmugam (2016)
Kapaphycus alvarezii	*Musa* spp. (Red banana)	5.00	6.19	Fertilizer applied in addition to extract	Karthikeyan and Shanmugam (2016)
Kapaphycus alvarezii	*Musa* spp. (Nendran)	5.00	8.82	Fertilizer applied in addition to extract	Karthikeyan and Shanmugam (2016)
Kapaphycus alvarezii	*Vigna radiata*	10.00	6.64	Fertilizer applied. Application of seaweed extract only started at flowering stage	Zodape et al. (2011)

degradation enzyme *GGL22*, but this association was not determined for many other genes similarly modulated during exposure of the plants to the seaweed extracts (Goñi et al., 2016), indicating that changes in gene transcript levels cannot always be directly connected to components present in seaweed extracts. Identification of the TF *WRKY40* as one of the genes correlating with levels of phycocolloids in a seaweed extract presents another key for unravelling this complicated story, since WRKYs typically regulate several other TFs and genes (Eulgem et al., 2000; Goñi et al., 2016). This TF forms a heterocomplex with *WRKY60* and *WRKY18* to mediate ABA responses during germination and root growth, as well as plant sensitivity to salinity and osmotic stress (Chen et al., 2010; Phukan et al., 2016), thus highlighting again the involvement of ABA signalling, which we have previously proposed as a key mechanism. Identifying other direct targets of *WRKY40* (or other regulatory TFs and miRs) that are also modulated upon crop exposure to seaweed extracts may give new insights into the seaweed biostimulant activity. The relationship between the composition of seaweed extract and the resulting activities caused by the seaweed extracts remains complex and therefore concrete inferences cannot yet be surmised from current studies.

It is important to note that small differences in the level of components in extracts derived from the same seaweed species may still lead to a much bigger variation at the molecular or cellular level along with differences in underlying mechanisms activated and overall crop responses where these seaweed extracts are applied (Ertani et al., 2018; Goñi et al., 2016). Thus, generalizations on the mode of action (and resulting benefits) of the seaweed extracts should not be made, rather independent experiments per seaweed extract and per crop must be performed to confirm hypotheses.

Most of the strategies discussed in the paragraphs above are typically used by plants during their life cycle, including the activation of specific pathways to cope with abiotic stress (Zhu, 2016; Figure 1c). Furthermore, cross-talk occurs between molecular pathways where induction of one phytohormone pathway leads to the modulation of another (Rowe et al., 2016; Wang et al., 2007). The application of a single seaweed extract also induces and/or represses multiple pathways or metabolic processes simultaneously. This presents the major difficulty in deciphering and characterizing specific underlying mechanisms used by seaweed extracts. Although the presence of phycocolloids (seaweed-specific polysaccharides) supports the argument that these extracts have a unique mode of action, this may not be the case, especially because the application of phycocolloids, for example, carrageenan, simultaneously induced several molecular pathways (Castro et al., 2012; Saucedo et al., 2015), while multiple phycocolloids, for example, alginate and carrageenan, may still stimulate the same pathway in the plants (Liu et al., 2013; Sharma et al., 2019). It is likely that the application of a single seaweed-based extract has broad-spectrum additive impact on crops, modulating several molecular pathways to stimulate the growth and survival of plants in both normal and stressed conditions.

5 | EFFECT OF SEAWEED EXTRACTS ON PROTEIN PRODUCTION IN CROPS

Global seaweed production has risen exponentially in recent decades to 30 Mton annually. Moreover, apart from their potential as a direct food source for humans and animals, seaweed extracts were not only shown to boost abiotic stress resistance in crops but also to increase their nutritional value (Shukla et al., 2019). Overall crop yield could be increased by the application of seaweed extracts as biostimulants under normal and stress conditions. Here, we summarize (Table 2) that seaweed extracts can also increase protein productivity in crops. Several reports showed that seaweed extracts increased the crude protein content in plant families like Fabaceae and Poaceae. The highest increase in protein content by twofold (~200%) was reported in *Vigna sinensis* (Table 2). Considerable protein increase was shown as well in *Triticum aestivum*, *Musa* spp. and *Allium cepa* (Table 2). An explanation for the increased protein content is the amplified plant uptake of more essential nutrients for protein production that may be due to enhanced root systems because of the seaweed extract application as reported by Sivasankari et al. (2006). Alteration of the root system and increased nutrient assimilation in crops has also been reported during abiotic stress (El Boukhari et al., 2020; Campobenedetto et al., 2021; Shukla et al., 2019), so there is a potential for increased protein productivity during abiotic stress. However, whether seaweed extracts improve root system and therefore crop protein productivity under adverse conditions remains unanswered, since all the experiments (Table 2) were only performed under normal conditions.

These findings suggest that for future agricultural practices, we can use seaweed biostimulants to increase crop yield by increasing per hectare the nutritional value and protein content in crops.

6 | PERSPECTIVE

Currently, there are many commercial seaweed biostimulants available for agricultural use, which can allow for a broad use of seaweed extracts in agriculture (Khan et al., 2009; Shukla et al., 2019). Although the effectiveness of many of these extracts has been proven, especially under experimentally controlled conditions, not all mechanisms of action have been identified. Moreover, the specific bioactive compounds present in the seaweed biostimulant extracts responsible for the positive effects are not yet fully known. In addition, more field trials testing the optimal concentration of extracts for different crops and under varied soil conditions should be carried out. Future field experiments should also address the business case, that is, how many seaweed extract applications are needed and what is the return on investment. Furthermore, these experiments may, in combination with seaweed extract factory production data, give insight into which direction large-scale commercial seaweed production should evolve. Further elaboration on the question ‘whether seaweeds should be cultivated to stimulate productivity of arable crops under normal and stressed conditions, or are they more beneficial as a direct food source for humans?' remains of interest. We advocate that less seaweed cultivation surface area is needed to produce similar or more protein productivity in arable crops after seaweed extract application, compared to direct seaweed (protein) consumption.

Crops grown in the field are often exposed to different stresses at the same time. Application of several extracts together, or at specific timepoints, may moderate the impact of multiple stresses on crops. Furthermore, the multifunctionality of seaweed extracts should be explored since a single extract often induces several plant stress signalling pathways. More research is needed to investigate if the beneficial effects of the seaweed extracts will increase when combined with other nonseaweed-derived biostimulants, for example, microbial biostimulants, or even with fertilizers and manures. Insight into the mode of action and which seaweed extract compounds are essential for these interactions will enable product improvement of seaweed extracts.

Overall, seaweed biostimulants have numerous positive effects on plant growth and thus have the potential to solve some of the problems agriculture will face in the future. However, not all researchers share this optimistic view since seaweeds accumulate harmful contaminants (Rodríguez-Martínez et al., 2020). Seaweed cultivated in an area (on sea) containing heavy metals and other undesirable components can accumulate such compounds to high concentrations. When used as biostimulants, the highly concentrated minerals (e.g., heavy metals) from the seaweed extracts will remain in the soil or will be taken up by the plants. With the routine application of the seaweed extracts, concentrations of the heavy metals will increase over time, rendering the land unsuitable for crop cultivation. In contrast, other research shows that seaweed biostimulants can help recover polluted soil via biosorption processes. It was found that seaweed species *Gracilaria corticata* and *Grateloupia lithophila* remove heavy metals such as chromium, mercury, lead, cobalt and cadmium (Nabti et al., 2017). The application of seaweed extracts to improve soil quality (Shukla et al., 2019) may be further explored as a potential solution for soil recovery or to facilitate bioremediation. In the future, standard tests should be established to measure the quality of the seaweed extracts (and the presence of undesirable compounds) before their use in agriculture.

Our findings suggest that future agricultural practices can make use of seaweed-based biostimulants to increase crop yield, nutritional value and protein content per hectare, including crops grown on marginal lands currently subject to severe drought and salinity. Thus, seaweed extracts can contribute to an increased annual global protein productivity, without increasing arable land use at the cost of precious natural habitat and biodiversity.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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REFERENCES

Abdel Latef, A.A.H., Srivastava, A.K., Saber, H., Alwaleed, E.A. & Tran, L.S.P. (2017) *Sargassum muticum*and *Jania rubens* regulate amino acid metabolism to improve growth and alleviate salinity in chickpea. *Scientific Reports*, 7, 10537. Available from: https://doi.org/10.1038/s41598-017-07692-w

Alexandratos, N. & Bruinsma, J. (2012) *World agriculture towards 2030/2050. The 2012 revision, ESA Working Paper No. 12-03*. Rome, Springer Nature. https://doi.org/10.1002/jso.2930300113

Ali, O., Ramsubhag, A. & Jayaraman, J. (2021) Biostimulant properties of seaweed extracts in plants: implications towards sustainable crop production. *Plants*, 10, 531. Available from: https://doi.org/10.3390/plants10030531

Arioli, T., Mattner, S.W., Hepworth, G., McClintock, D. & McClinock, R. (2021) Effect of seaweed extract application on wine grape yield in Australia. *Journal of Applied Phycology. Journal of Applied Phycology*, 33, 1883–1891. Available from: https://doi.org/10.1007/s10811-021-02423-1

Aryee, A.N., Agyei, D. & Akanbi, T.O. (2018) Recovery and utilization of seaweed pigments in food processing. *Current Opinion in Food Science*, 19, 113–119. Available from: https://doi.org/10.1016/j.cofs.2018.03.013

Battacharyya, D., Babgohari, M.Z., Rathor, P. & Prithiviraj, B. (2015) Seaweed extracts as biostimulants in horticulture. *Scientia Horticulturae*, 196, 39–48. Available from: https://doi.org/10.1016/j.scienta.2015.09.012

Bi, F., Iqbal, S., Arman, M., Ali, A. & Hassan, M. (2011) Carrageenan as an elicitor of induced secondary metabolites and its effects on various growth characters of chickpea and maize plants. *Journal of Saudi Chemical Society*, 15, 269–273. Available from: https://doi.org/10.1016/j.jscs.2010.10.003

Blunden, G., Morse, P.F., Mathe, I., Hohmann, J., Critchley, A.T. & Morrell, S. (2010) Betaine yields from marine algal species utilized in the preparation of seaweed extracts used in agriculture. *Natural Product Communications*, 5(4), 581–585. Available from: https://doi.org/10.1177/1934578x1000500418

El Boukhari, M.E.M., Barakate, M., Bouhia, Y. & Lyamlouli, K. (2020) Trends in seaweed extract based biostimulants: manufacturing process and beneficial effect on soil–plant systems. *Plants*, 9, 359.

Campobenedetto, C., Mannino, G., Beekwilder, J., Contartese, V., Karlova, R. & Bertea, C.M. (2021) The application of a biostimulant based on tannins affects root architecture and improves tolerance to salinity in tomato plants. *Scientific Reports*, 11, 354. Available from: https://doi.org/10.1038/s41598-020-79770-5

Carmody, N., Goñi, O., Łangowski, Ł. & O'Connell, S. (2020) *Ascophyllum nodosum*extract biostimulant processing and its impact on enhancing heat stress tolerance during tomato fruit set. *Frontiers in Plant Science*, 11, 807. Available from: https://doi.org/10.3389/fpls.2020.00807

Castro, J., Vera, J., Gonzalez, A. & Moenne, A. (2012) Oligo-carrageenans stimulate growth by enhancing photosynthesis, basal metabolism, and cell cycle in tobacco plants (var. burley). *Journal of Plant Growth*

Regulation, 31, 173–185. Available from: https://doi.org/10.1007/s00344-011-9229-5

Chen, D., Shao, Q., Yin, L., Younis, A. & Zheng, B. (2019) Polyamine function in plants: metabolism, regulation on development, and roles in abiotic stress responses. *Frontiers in Plant Science*, 9, 1945. Available from: https://doi.org/10.3389/fpls.2018.01945

Chen, H., Lai, Z., Shi, J., Xiao, Y., Chen, Z. & Xu, X. (2010) Roles of arabidopsis WRKY18WRKY40 and WRKY60 transcription factors in plant responses to abscisic acid and abiotic stress. *BMC Plant Biology*, 10, 281. Available from: https://doi.org/10.1186/1471-2229-10-281

Colla, G., Hoagland, L., Ruzzi, M., Cardarelli, M., Bonini, P., Canaguier, R. et al. (2017) Biostimulant action of protein hydrolysates: unraveling their effects on plant physiology and microbiome. *Frontiers in Plant Science*, 8, 2202. Available from: https://doi.org/10.3389/fpls.2017.02202

Cotas, J., Leandro, A., Monteiro, P., Pacheco, D., Figueirinha, A., Gonçalves, A.M.M. et al. (2020) Seaweed phenolics: from extraction to applications. *Marine Drugs*, 18, 384.

Craigie, J.S. (2011) Seaweed extract stimuli in plant science and agriculture. *Journal of Applied Phycology*, 23, 371–393. Available from: https://doi.org/10.1007/s10811-010-9560-4

Ertani, A., Francioso, O., Tinti, A., Schiavon, M., Pizzeghello, D. & Nardi, S. (2018) Evaluation of seaweed extracts from laminaria and *Ascophyllum nodosum* spp. as biostimulants in *Zea mays* L. using a combination of chemical, biochemical and morphological approaches. *Frontiers in Plant Science*, 9, 428. Available from: https://doi.org/10.3389/fpls.2018.00428

EU. (2019) Regulation of the European parliament and of the council laying down rules on the making available on the market of EU fertilising products and amending regulations (EC) no. 1069/2009 and (EC) no. 1107/2009 and repealing regulation (EC) no. 2003/2003. *Official Journal of the European Union*. Available from: https://eur-lex.europa.eu/legal-content/EN/TXT/PDF/?uri=CELEX:32019R1009%26from=EN

Eulgem, T., Rushton, P.J., Robatzek, S. & Somssich, I.E. (2000) The WRKY superfamily of plant transcription factors. *Trends in Plant Science*, 5(5), 199–206. Available from: https://doi.org/10.1016/S1360-1385(00)01600-9

Food and Agriculture Organization of the United Nations and Intergovernmental Technical Panel on Soils (FAO & ITPS). (2015) *Status of the World's Soil Resources (SWSR)—main report*. Rome, Italy. Available at: http://www.fao.org/3/a-i5199e.pdf

Fletcher, H.R., Biller, P., Ross, A.B. & Adams, J.M.M. (2017) The seasonal variation of fucoidan within three species of brown macroalgae. *Algal Research*, 22, 79–86. Available from: https://doi.org/10.1016/j.algal.2016.10.015

Garde-Cerdán, T., Mancini, V., Carrasco-Quiroz, M., Servili, A., Gutiérrez-Gamboa, G., Foglia, R. et al. (2017) Chitosan and laminarin as alternatives to copper for *Plasmopara viticola* control: effect on grape amino acid. *Journal of Agricultural and Food Chemistry*, 65(34), 7379–7386. Available from: https://doi.org/10.1021/acs.jafc.7b02352

Goñi, O., Fort, A., Quille, P., McKeown, P.C., Spillane, C. & O′Connell, S. (2016) Comparative transcriptome analysis of two *Ascophyllum nodosum* extract biostimulants: same seaweed but different. *Journal of Agricultural and Food Chemistry*, 64, 2980–2989. Available from: https://doi.org/10.1021/acs.jafc.6b00621

Goñi, O., Quille, P. & O′Connell, S. (2018) *Ascophyllum nodosum*extract biostimulants and their role in enhancing tolerance to drought stress in tomato plants. *Plant Physiology and Biochemistry*, 126, 63–73. Available from: https://doi.org/10.1016/j.plaphy.2018.02.024

Gonzalez, A., Castro, J., Vera, J. & Moenne, A. (2013a) Seaweed oligosaccharides stimulate plant growth by enhancing carbon and nitrogen assimilation, basal metabolism, and cell division. *Journal of Plant Growth Regulation*, 32, 443–448. Available from: https://doi.org/10.1007/s00344-012-9309-1

Gonzalez, A., Contreras, R.A. & Moenne, A. (2013b) Oligo-carrageenans enhance growth and contents of cellulose, essential oils and polyphenolic compounds in *Eucalyptus globulus* trees. *Molecules*, 18, 8740–8751. Available from: https://doi.org/10.3390/molecules18088740

Gull, A., Lone, A.A. & Wani, N.U.I. (2019) Biotic and abiotic stresses in plants. *IntechOpen*, 85832. Available from: https://doi.org/10.5772/intechopen.85832

Gullón, B., Gagaoua, M., Barba, F.J., Gullón, P., Zhang, W. & Lorenzo, J.M. (2020) Seaweeds as promising resource of bioactive compounds: overview of novel extraction strategies and design of tailored meat products. *Trends in Food Science and Technology*, 100, 1–18. Available from: https://doi.org/10.1016/j.tifs.2020.03.039

Hashem, H.A., Mansour, H.A., El-Khawas, S.A. & Hassanein, R.A. (2019) The potentiality of marine macro-algae as bio-fertilizers to improve the productivity and salt stress tolerance of canola (*Brassica napus* L.) plants. *Agronomy*, 9, 146. Available from: https://doi.org/10.3390/agronomy9030146

Hassani, A., Azapagic, A. & Shokri, N. (2021) Global predictions of primary soil salinization under changing climate in the 21st century. *Nature Communications*, 12, 6663. Available from: https://doi.org/10.1038/s41467-021-26907-3

Henchion, M., McCarthy, M., Resconi, V.C. & Troy, D. (2014) Meat consumption: trends and quality matters. *Meat Science*, 98, 561–568. Available from: https://doi.org/10.1016/j.meatsci.2014.06.007

Hidangmayum, A. & Sharma, R. (2017) Effect of different concentrations of commercial seaweed liquid extract of *Ascophyllum nodosum* as a plant bio stimulant on growth, yield and biochemical constituents of onion (*Allium cepa* L.). *Journal of Pharmacognosy and Phytochemistry*, 6(4), 658–663.

Hussein, M.H., Eltanahy, E., Al Bakry, A.F., Elsafty, N. & Elshamy, M.M. (2021) Seaweed extracts as prospective plant growth bio-stimulant and salinity stress alleviator for *Vigna sinensis* and *Zea mays*. *Journal of Applied Phycology. Journal of Applied Phycology*, 33, 1273–1291. Available from: https://doi.org/10.1007/s10811-020-02330-x

Jalil, A.J., Tasoff, J. & Bustamante, A.V. (2020) Eating to save the planet: evidence from a randomized controlled trial using individual-level food purchase data. *Food Policy*, 95, 101950. Available from: https://doi.org/10.1016/j.foodpol.2020.101950

Jones, D.L., Healey, J.R., Willett, V.B., Farrar, J.F. & Hodge, A. (2005) Dissolved organic nitrogen uptake by plants—an important N uptake pathway?*Soil Biology and Biochemistry*, 37, 413–423. Available from: https://doi.org/10.1016/j.soilbio.2004.08.008

Jones, D.L., Nguyen, C. & Finlay, R.D. (2009) Carbon flow in the rhizosphere: carbon trading at the soil–root interface. *Plant and Soil*, 321, 5–33. Available from: https://doi.org/10.1007/s11104-009-9925-0

Jothinayagi, N. & Anbazhagan, C. (2009) Effect of seaweed liquid fertilizer of *Sargassum wightii* on the growth and biochemical characteristics of *Abelmoschus esculentus* (L.) medikus. *Recent Research in Science and Technology*, 1(4), 155–158.

Karthikeyan, K. & Shanmugam, M. (2016) Grain yield and functional properties of red gram applied with seaweed extract powder manufactured from *Kappaphycus alvarezii*. *International Journal of Recent Advances in Multidisciplinary Research*, 3(3), 1353–1359.

Khairy, H.M. & El-Shafay, S.M. (2013) Seasonal variations in the biochemical composition of some common seaweed species from the coast of Abu Qir Bay, Alexandria, Egypt. *Oceanologia*, 55(2), 435–452. Available from: https://doi.org/10.5697/oc.55-2.435

Khan, W., Rayirath, U.P., Subramanian, S., Jithesh, M.N., Rayorath, P., Hodges, D.M., Critchley, A.T., Craigie, J.S., Norrie, J. & Prithiviraj, B. (2009) Seaweed extracts as biostimulants of plant growth and development. *Journal of Plant Growth Regulation*, 28, 386–399. Available from: https://doi.org/10.1007/s00344-009-9103-x

Klarzynski, O., Descamps, V., Plesse, B., Yvin, J.C., Kloareg, B. & Fritig, B. (2003) Sulfated fucan oligosaccharides elicit defense responses in tobacco and local and systemic resistance against tobacco mosaic virus. *Molecular Plant-Microbe Interactions*, 16(2), 115–122. Available from: https://doi.org/10.1094/MPMI.2003.16.2.115

Kocira, S., Szparaga, A., Kocira, A., Czerwińska, E., Wójtowicz, A., Bronowicka-Mielniczuk, U., Koszel, M. & Findura, P. (2018) Modeling biometric traits, yield and nutritional and antioxidant properties of seeds of three soybean cultivars through the application of biostimulant containing seaweed and amino acids. *Frontiers in Plant Science*, 9, 388. Available from: https://doi.org/10.3389/fpls.2018.00388

Kulkarni, M.G., Rengasamy, K.R.R., Pendota, S.C., Gruz, J., Plačková, L., Novák, O., Doležal, K. & Van Staden, J. (2019) Bioactive molecules derived from smoke and seaweed *Ecklonia maxima* showing phytohormone-like activity in *Spinacia oleracea* L.*New Biotechnology*, 48, 83–89. Available from: https://doi.org/10.1016/j.nbt.2018.08.004

Layek, J., Das, A., Idapuganti, R.G., Sarkar, D., Ghosh, A., Zodape, S.T., Lal, R., Yadav, G.S., Panwar, A.S., Ngachan, S. & Meena, R.S. (2018) Seaweed extract as organic bio-stimulant improves productivity and quality of rice in eastern Himalayas. *Journal of Applied Phycology*, 30, 547–558. Available from: https://doi.org/10.1007/s10811-017-1225-0

Lecourieux, D., Mazars, C., Pauly, N., Ranjeva, R. & Pugin, A. (2002) Analysis and effects of cytosolic free calcium increases in response to elicitors in *Nicotiana plumbaginifolia* cells. *Plant Cell*, 14, 1–15. Available from: https://doi.org/10.1105/tpc.005579

Little, D.C., Newton, R.W. & Beveridge, M.C.M. (2016) Aquaculture: a rapidly growing and significant source of sustainable food? Status, transitions and potential. *Proceedings of the Nutrition Society*, 75, 274–286. Available from: https://doi.org/10.1017/S0029665116000665

Liu, H., Chen, X., Song, L., Li, K., Zhang, X., Liu, S., Qin, Y. & Li, P. (2019) Polysaccharides from *Grateloupia filicina* enhance tolerance of rice seeds (*Oryza sativa* L.) under salt stress, *International Journal of Biological Macromolecules*, 124, pp. 1197–1204. Available from: https://doi.org/10.1016/j.ijbiomac.2018.11.270

Liu, H., Zhang, Y.H., Yin, H., Wang, W.X., Zhao, X.M. & Du, Y.G. (2013) Alginate oligosaccharides enhanced *Triticum aestivum* L. tolerance to drought stress. *Plant Physiology and Biochemistry. Elsevier Masson SAS*, 62, 33–40. Available from: https://doi.org/10.1016/j.plaphy.2012.10.012

Lu, Y. & Xu, J. (2015) Phytohormones in microalgae: a new opportunity for microalgal biotechnology? *Trends in Plant Science*, 20(5), 273–282. Available from: https://doi.org/10.1016/j.tplants.2015.01.006

MacKinnon, S.L., Hiltz, D., Ugarte, R. & Craft, C.A. (2010) Improved methods of analysis for betaines in *Ascophyllum nodosum* and its commercial seaweed extracts. *Journal of Applied Phycology*, 22, 489–494. Available from: https://doi.org/10.1007/s10811-009-9483-0

Markets and Markets. (2019) *Biostimulants market by active ingredient (humic substances, amino acids, seaweed extracts, microbial amendments), crop type (fruits & vegetables, cereals, turf & ornamentals), application method, form, and region—global forecast to 2025*. Available at: https://www.marketsandmarkets.com/Market-Reports/biostimulant-market-1081.html. [Accessed 21st May 2021].

Masondo, N.A., Kulkarni, M.G., Finnie, J.F. & Van Staden, J. (2018) Influence of biostimulants-seed-priming on *Ceratotheca triloba* germination and seedling growth under low temperatures, low osmotic potential and salinity stress. *Ecotoxicology and Environmental Safety*, 147, 43–48. Available from: https://doi.org/10.1016/j.ecoenv.2017.08.017

Moe, L.A. (2013) Amino acids in the rhizosphere: from plants to microbes. *American Journal of Botany*, 100(9), 1–14. Available from: https://doi.org/10.3732/ajb.1300033

Mac Monagail, M., Cornish, L., Morrison, L., Araújo, R. & Critchley, A.T. (2017) Sustainable harvesting of wild seaweed resources. *European Journal of Phycology*, 52(4), 371–390. Available from: https://doi.org/10.1080/09670262.2017.1365273

Mueller, N.D., Gerber, J.S., Johnston, M., Ray, D.K., Ramankutty, N. & Foley, J.A. (2012) Closing yield gaps through nutrient and water management. *Nature. Nature Publishing Group*, 490, 254–257. Available from: https://doi.org/10.1038/nature11420

Mukherjee, A. & Patel, J.S. (2020) Seaweed extract: biostimulator of plant defense and plant productivity. *International Journal of Environmental Science and Technology*, 17, 553–558. Available from: https://doi.org/10.1007/s13762-019-02442-z

Muñoz-Mayor, A., Pineda, B., Garcia-Abellán, J.O., Antón, T., Garcia-Sogo, B., Sanchez-Bel, P., Flores, F.B., Atarés, A., Angosto, T., Pintor-Toro, J.A., Moreno, V. & Bolarin, M.C. (2012) Over-expression of dehydrin tas14 gene improves the osmotic stress imposed by drought and salinity in tomato. *Journal of Plant Physiology*, 169, 459–468. Available from: https://doi.org/10.1016/j.jplph.2011.11.018

Murtic, S., Oljaca, R., Murtic, M.S., Vranac, A., Koleska, I. & Karic, L. (2018) Effects of seaweed extract on the growth, yield and quality of cherry tomato under different growth conditions. *Acta Agriculturae Slovenica*, 111(2), 315–325. Available from: https://doi.org/10.14720/aas.2018.111.2.07

Nabti, E., Jha, B. & Hartmann, A. (2017) Impact of seaweeds on agricultural crop production as biofertilizer. *International Journal of Environmental Science and Technology. Springer Berlin Heidelberg*, 14, 1119–1134. Available from: https://doi.org/10.1007/s13762-016-1202-1

Nanda, S., Kumar, G. & Hussain, S. (2021) Utilization of seaweed-based biostimulants in improving plant and soil health: current updates and future prospective. *International Journal of Environmental Science and Technology*. Available from: https://doi.org/10.1007/s13762-021-03568-9

Ohta, M., Guo, Y., Halfter, U. & Zhu, J.K. (2003) A novel domain in the protein kinase SOS2 mediates interaction with the protein phosphatase 2C ABI2. *Proceedings of the National Academy of Sciences of the United States of America*, 100(20), 11771–11776. Available from:https://doi.org/10.1073/pnas.2034853100

Papenfus, H.B., Stirk, W.A., Finnie, J.F. & Van Staden, J. (2012) Seasonal variation in the polyamines of *Ecklonia maxima*. *Botanica Marina*, 55(5), 539–546. Available from: https://doi.org/10.1515/bot-2012-0150

Phukan, U.J., Jeena, G.S. & Shukla, R.K. (2016) WRKY transcription factors: molecular regulation and stress responses in plants. *Frontiers in Plant Science*, 7, 760. Available from: https://doi.org/10.3389/fpls.2016.00760

Pugliese, M., Monchiero, M., Gullino, M.L. & Garibaldi, A. (2018) Application of laminarin and calcium oxide for the control of grape powdery mildew on *Vitis vinifera* cv. moscato. *Journal of Plant Diseases and Protection*, 125, 477–482. Available from: https://doi.org/10.1007/s41348-018-0162-8

Rasul, F., Gupta, S., Olas, J.J., Gechev, T., Sujeeth, N. & Mueller-Roeber, B. (2021) Priming with a seaweed extract strongly improves drought tolerance in arabidopsis. *International Journal of Molecular Sciences*, 22, 1469. Available from: https://doi.org/10.3390/ijms22031469

Rengasamy, K.R.R., Kulkarni, M.G., Pendota, S.C. & Van Staden, J. (2016) Enhancing growth, phytochemical constituents and aphid resistance capacity in cabbage with foliar application of eckol—a biologically active phenolic molecule from brown seaweed, *New Biotechnology*, 33, pp. 273–279. Available from: https://doi.org/10.1016/j.nbt.2015.11.002

Rodríguez-Martínez, R.E., Roy, P.D., Torrescano-Valle, N., Cabanillas-Terán, N., Carrillo-Domínguez, S., Collado-Vides, L., García-Sánchez, M. & vanTussenbroek, B.I. (2020) Element concentrations in pelagic Sargassum along the Mexican Caribbean coast in 2018–2019. *PeerJ*, 8, e8667. Available from: https://doi.org/10.7717/peerj.8667

Rojas, O. (2020) Agricultural extreme drought assessment at global level using the FAO-Agricultural Stress Index System (ASIS). *Weather and Climate Extremes*, 27, 100184. Available from: https://doi.org/10.1016/j.wace.2018.09.001

Romanazzi, G., Mancini, V., Feliziani, E., Servili, A., Endeshaw, S. & Neri, D. (2016) Impact of alternative fungicides on grape downy mildew control and vine growth and development. *Plant Disease*, 100(4), 739–748. Available from: https://doi.org/10.1094/PDIS-05-15-0564-RE

Rouphael, Y., Cardarelli, M., Bonini, P. & Colla, G. (2017) Synergistic action of a microbial-based biostimulant and a plant derived-protein hydrolysate enhances lettuce tolerance to alkalinity and salinity. *Frontiers in Plant Science*, 8, 131. Available from: https://doi.org/10.3389/fpls.2017.00131

Rouphael, Y. & Colla, G. (2020) Editorial: biostimulants in agriculture. *Frontiers in Plant Science*, 11, 40. Available from: https://doi.org/10.3389/fpls.2020.00040

Rowe, J.H., Topping, J.F., Liu, J. & Lindsey, K. (2016) Abscisic acid regulates root growth under osmotic stress conditions via an interacting hormonal network with cytokinin, ethylene and auxin. *New Phytologist*, 211, 225–239. Available from: https://doi.org/10.1111/nph.13882

Ryu, H. & Cho, Y.G. (2015) Plant hormones in salt stress tolerance. *Journal of Plant Biology*, 58, 147–155. Available from: https://doi.org/10.1007/s12374-015-0103-z

Santaniello, A., Scartazza, A., Gresta, F., Loreti, E., Biasone, A., Di Tommaso, D., Piaggesi, A. & Perata, P. (2017) *Ascophyllum nodosum*seaweed extract alleviates drought stress in *Arabidopsis* by affecting photosynthetic performance and related gene expression. *Frontiers in Plant Science*, 8, 1362. Available from: https://doi.org/10.3389/fpls.2017.01362

Saucedo, S., Contreras, R.A. & Moenne, A. (2015) Oligo-carrageenan kappa increases C, N and S assimilation, auxin and gibberellin contents, and growth in *Pinus radiata* trees. *Journal of Forestry Research*, 26(3), 635–640. Available from: https://doi.org/10.1007/s11676-015-0061-9

Shah, M.T., Zodape, S.T., Chaudhary, D.R., Eswaran, K. & Chikara, J. (2013) Seaweed sap as an alternative liquid fertilizer for yield and quality improvement of wheat. *Journal of Plant Nutrition*, 36, 192–200. Available from: https://doi.org/10.1080/01904167.2012.737886

Shahid, S.A., Zaman, M. & Heng, L. (2018) Soil salinity: historical perspectives and a world overview of the problem. In: Zaman, M., Shahid, S.A. & Heng, L. (Eds.) *Guideline for salinity assessment, mitigation and adaptation using nuclear and related techniques*. Switzerland: Springer Nature, pp. 43–54.

Sharma, H.S.S., Fleming, C., Selby, C., Rao, J.R. & Martin, T. (2014) Plant biostimulants: a review on the processing of macroalgae and use of extracts for crop management to reduce abiotic and biotic stresses. *Journal of Applied Phycology*, 26, 465–490. Available from: https://doi.org/10.1007/s10811-013-0101-9

Sharma, S., Chen, C., Khatri, K., Rathore, M.S. & Pandey, S.P. (2019) Gracilaria dura extract confers drought tolerance in wheat by modulating abscisic acid homeostasis. *Plant Physiology and Biochemistry*, 136, 143–154. Available from: https://doi.org/10.1016/j.plaphy.2019.01.015

Shukla, P.S., Borza, T., Critchley, A.T., Hiltz, D., Norrie, J. & Prithiviraj, B. (2018) *Ascophyllum nodosum*extract mitigates salinity stress in *Arabidopsis thaliana* by modulating the expression of miRNA involved in stress tolerance and nutrient acquisition. *PLoS ONE*, 13(10), e0206221. Available from: https://doi.org/10.1371/journal.pone.0206221

Shukla, P.S., Borza, T., Critchley, A.T. & Prithiviraj, B. (2016) Carrageenans from red seaweeds as promoters of growth and elicitors of defense response in plants. *Frontiers in Marine Science*, 3, 81. Available from: https://doi.org/10.3389/fmars.2016.00081

Shukla, P.S., Mantin, E.G., Adil, M., Bajpai, S., Critchley, A.T. & Prithiviraj, B. (2019) *Ascophyllum nodosum*-based biostimulants: sustainable applications in agriculture for the stimulation of plant growth, stress tolerance, and disease management. *Frontiers in Plant Science*, 10, 655. Available from: https://doi.org/10.3389/fpls.2019.00655

Shukla, P.S., Shotton, K., Norman, E., Neily, W., Critchley, A.T. & Prithiviraj, B. (2018) Seaweed extract improve drought tolerance of soybean by regulating stress-response genes. *AoB PLANTS*, 10, plx051. Available from: https://doi.org/10.1093/aobpla/plx051

Singh, M., Kumar, J., Singh, S., Singh, V.P. & Prasad, S.M. (2015) Roles of osmoprotectants in improving salinity and drought tolerance in plants: a review. *Reviews in Environmental Science and Biotechnology*, 14, 407–426. Available from: https://doi.org/10.1007/s11157-015-9372-8

Sivasankari, S., Venkatesalu, V., Anantharaj, M. & Chandrasekaran, M. (2006) Effect of seaweed extracts on the growth and biochemical constituents of *Vigna sinensis*. *Bioresource Technology*, 97, 1745–1751. Available from: https://doi.org/10.1016/j.biortech.2005.06.016

Di Stasio, E., Van Oosten, M.J., Silletti, S., Raimondi, G., Dell′Aversana, E., Carillo, P. & Maggio, A. (2018) *Ascophyllum nodosum*-based algal extracts act as enhancers of growth, fruit quality, and adaptation to stress in salinized tomato plants. *Journal of Applied Phycology*, 30, 2675–2686. Available from: https://doi.org/10.1007/s10811-018-1439-9

Stirk, W.A. & Van Staden, J. (2014) Plant growth regulators in seaweeds: occurrence, regulation and functions. In: Bourgougnon, N. (Ed.) *Advances in botanical research: sea plants*. London, UK: Elsevier. Available at: https://doi.org/10.1016/B978-0-12-408062-1.00005-6

Trivedi, K., Vijay Anand, K.G., Kubavat, D., Patidar, R. & Ghosh, A. (2018) Drought alleviatory potential of Kappaphycus seaweed extract and the role of the quaternary ammonium compounds as its constituents towards imparting drought tolerance in *Zea mays* L. *Journal of Applied Phycology*, 30, 2001–2015. Available from: https://doi.org/10.1007/s10811-017-1375-0

UN DESA. (2017) *World population projected to reach 9.8 billion in 2050, and 11.2 billion in 2100*. Available at: https://www.un.org/development/desa/en/news/population/world-population-prospects-2017.html [Accessed 15th May 2020].

Venkatesana, J., Keekana, K.K., Anilb, S., Bhatnagarc, I. & Kim, S.-K. (2020) ‘Phlorotannins’. *Encyclopedia of Food Chemistry*, 3, 515–527.

Vera, J., Castro, J., Gonzalez, A. & Moenne, A. (2011) Seaweed polysaccharides and derived oligosaccharides stimulate defense responses and protection against pathogens in plants. *Marine Drugs*, 9, 2514–2525. Available from: https://doi.org/10.3390/md9122514

Wang, Y., Liu, C., Li, K., Sun, F., Hu, H., Li, X., Zhao, Y., Han, C., Zhang, W., Duan, Y., Liu, M. & Li, X. (2007) Arabidopsis EIN2 modulates stress response through abscisic acid response pathway. *Plant Molecular Biology*, 64, 633–644. Available from: https://doi.org/10.1007/s11103-007-9182-7

Yakhin, O.I., Lubyanov, A.A., Yakhin, I.A. & Brown, P.H. (2017) Biostimulants in plant science: a global perspective. *Frontiers in Plant Science*, 7, 2049. Available from: https://doi.org/10.3389/fpls.2016.02049

Yokoi, S., Quintero, F.J., Cubero, B., Ruiz, M.T., Bressan, R.A., Hasegawa, P.M. & Pardo, J.M. (2002) Differential expression and function of *Arabidopsis thaliana* NHX Na^+/H^+ antiporters in the salt stress response. *The Plant Journal*, 30(5), 529–539.

Zamora-Briseño, J.A. & deJiménez, E.S. (2016) A LEA 4 protein up-regulated by ABA is involved in drought response in maize roots. *Molecular Biology Reports*, 43, 221–228. Available from: https://doi.org/10.1007/s11033-016-3963-5

Zhao, H.J. & Zou, Q. (2002) Protective effects of exogenous antioxidants and phenolic compounds on photosynthesis of wheat leaves under irradiance and oxidative stress. *Photosynthetica*, 40(4), 523–527.

Zhu, J.-K. (2016) Abiotic stress signaling and responses in plants. *Cell*, 167, 313–324. Available from: https://doi.org/10.1016/j.cell.2016.08.029

Zodape, S.T., Gupta, A., Bhandari, S.C., Rawat, U.S., Chaudhary, D.R., Eswaran, K. & Chikara, J. (2011) Foliar application of seaweed sap as biostimulant for enhancement of yield and quality of tomato (*Lycopersicon esculentum* Mill.). *Journal of Scientific & Industrial Research*, 70, 215–219. Available from: https://doi.org/10.1115/DETC2010-29226

Zou, P., Lu, X., Jing, C., Yuan, Y., Lu, Y., Zhang, C., Meng, L., Zhao, H. & Li, Y. (2018) Low-molecular-weight polysaccharides from *Pyropia yezoensis* enhance tolerance of wheat seedlings (*Triticum aestivum* L.) to salt stress. *Frontiers in Plant Science*, 9, 427. Available from: https://doi.org/10.3389/fpls.2018.00427

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