Chapter 25
Leveraging Seaweeds as a Potential Biostimulant for Agriculture Sustainability

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25.1 Introduction

The pervasive inputs of synthetic chemical fertilizers and other chemicals such as pesticides and herbicides into the agricultural system have reduced productivity and nutritional quality of crops and also caused negative impacts on the environment (Kramer et al. 2006). In recent years, biostimulants are receiving much attention in sustainable agriculture as a means of boosting crop growth and productivity in eco-friendly and cost-effective ways and reducing the negative impacts of chemical synthetic fertilizers and displayed positive influence on plant growth and productivity, and soil sustainability (Craigie 2011; Singh et al. 2011a, b). Seaweeds are plant-like organisms with simple internal structures that largely inhabit coastal areas. Seaweeds include the members of red, brown, and green marine algae. The use of natural seaweed as fertilizers has allowed the partial replacement of synthetic chemical fertilizers and they have great potential in improving soil physiochemical properties and have substantial contribution in increasing crop growth and productivity (Li et al. 2017; Renuka et al. 2018; Thilagar et al. 2016; Zodape et al. 2010). They have the immense ability in the mobilization of inorganic and organic acids, nutrient mineralization, and production of biologically active compound which can be utilized for applications for plant improvement making them as a suitable option for biofertilizers (Gayathri et al. 2015; Hernández-Carlos and Gamboa-Angulo 2011; Jäger

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et al. 2010; Prasanna et al. 2016). Seaweed extracts are non-toxic, non-polluting, biodegradable, and non-hazardous to the environment, humans and animals, and have become popular agents as metabolic enhancers.

The products of seaweed extracts can be used as liquid extracts in the agricultural system and applied in the form of a soil drench, foliar spray, and powder or granular form (Thirumaran et al. 2009). A number of studies revealed that a wide range of seaweed extract derived from several species such as *Ascophyllum nodosum*, *Kappaphycus alvarezii, Sargassum muticum, Ecklonia maxima*, *Durvillaea pota-torum*, *Ulva lactuca*, *Caulerpa sertularioides*, *Padina gymnospora*, *Sargassum liebmannii*, *Sargassum johnstonii* are useful as biofertilizers (Hernández-Herrera et al. 2014). Among marine algae, the extracts of brown marine algae are mainly used in agriculture practices because of their growth-stimulating effects on plants and for their alleviating the negative impacts of abiotic and biotic stresses (Guinan et al. 2012; Sharma et al. 2014). The chemical constituents of seaweed extract include complex polysaccharide, fatty acids, vitamins, phytohormones, and mineral nutrients (Lafarga et al. 2020). Besides, they have a prominent role in maintaining the productivity of terrestrial and aquatic ecosystems through nitrogen fixation and photosynthesis thereby enhancing the accessibility of nutrients by cycling and transformations (Moroney and Ynalvez 2009). Seaweed can be regarded as a potential source of biofertilizers in fresh or dried form and it is a good source of macro and microelements for plant nutrition and it also enhances the biochemical constituents like lipids, proteins, carbohydrates ash, dietary fiber, phenol *etc* in the plant. This technology can be implemented for organic farming for sustainable agriculture which is a better solution for an eco-friendly approach.

25.2 Utilization of Seaweeds as Metabolic Enhancers in Agriculture Field

Seaweeds are valuable resource for plant development as they have higher contents of amino acids, mineral substances, vitamins, and phytohormones (Stirk and Van Staden 1997). The extracts of brown algae are widely used in agriculture and they have been shown to enhance the productivity of agricultural and horticultural plants including tomato, potato, beet, legumes, citrus, grasses, rice, wheat, maize, sugarcane, broccoli, spinach, cabbage, carrot, pepper, cucumber *etc* (Battacharyya et al. 2015; Renuka et al. 2018). The regulator of the plant growth may vary from the fertilizers in many ways such as they alter and manage the cell division, control of shoot and root elongation and initiation of flowering and other metabolic functions. Whereas, fertilizers supply the nutrients required for normal plant growth and development (Allen et al. 2001). Moreover, cytokinin is considered as the most important plant growth regulator in seaweed. The trace elements present in marine algae act as enzyme activators and play important roles in plant nutrition and physiology (Senn 1987). The application of seaweed extract in plants increased the antioxidant metabolites (for example α-tocopherol, carotene, and ascorbic acid) as well as antioxidant enzymes (superoxide dismutase, catalase, and peroxidase) activities

Table 25.1 Seaweeds extract as plant promoting agents and biofertilizers

Seaweed	Benefitted plant	Mechanism of enhanced plant growth	Reference
Ascophyllum nodosum, Sargassum muticum	Rice plants (*Oryza sativa*) and lettuce (*Lactuca sativa*)	Treatment had a positive effect on seed germination, plant development, and production	Silva et al. (2019)
Ascophyllum nodosum	Grapevine	Inoculation increased the physiological performance, and also improved the photosynthesis efficiency under water stress conditions	Frioni et al. (2021)
Ascophyllum nodosum (L.)	Soyabean	Bio-stimulants application provided higher photosynthetic rates, efficient mechanisms for dissipating excess energy and higher activities of antioxidant enzymes	do Rosário Rosa et al. (2021)
Kappaphycus alvarezii	Sugarcane	Increased sugar yield, lowering GHG's	Singh et al. (2018)
Ascophyllum nodosum	Tomato	Biostimulants application changes of chlorophyll, osmolytes levels, MDA production, dehydrin isoform pattern and dehydrin gene expression levels (expression of *tas14* dehydrin gene)	Goñi et al. (2018)
Ecklonia maxima	Bean (*Phaseolus vulgaris* L.)	Increased productivity and nutraceutical quality	Kocira et al. (2018)
Kappaphycus, Gracilaria	Rice	Increased grain yield	Sharma et al. (2017)
Gracilaria edulis, Sargassum wightii	*Withania somnifera*	Increased withanolides contents, enhanced expression of *SE, SS, HMGR and FPPS* genes	Sivanandhan et al. (2015)
Ascophyllum nodosum	Pepper	Enhanced yield, fruit diameter and chlorophyll content	Manna et al. (2012)
Enteromorpha intestinelis, Gelidium pectinutum, Ecklonia Maxima	Cucumber	Improved vegetative growth and yield	Ahmed and Shalaby (2012)
Ascophyllum nodosum	Mint and basil	Increased antibacterial activity, micro- and macronutrient and carbohydrates	Elansary et al. (2016)
Super fifty® and Ecoelicitor® (commercial extract from *Ascophyllum nodosum*)	Lettuce; oilseed rape	Enhanced plant growth and tolerance to biotic and abiotic stresses	Guinan et al. (2012)

(continued)

Table 25.1 (continued)

Seaweed	Benefitted plant	Mechanism of enhanced plant growth	Reference
Ascophyllum nodosum	*Hordeum vulgare*	Induced gibberellic acid independent amylase activity in Barley and promoted seed germination	Rayorath et al. (2008)
Ascophyllum nodosum	*Arabidopsis thaliana*	Improved plant growth by modulation of concentration and Localization of auxin	Rayorath et al. (2008)
AZAL5® (commercial extract from *A. nodosum*)	*Brassica napus*	Promotes plant growth and higher uptake of nitrate and sulfate	Jannin et al. (2013)
Ascophyllum nodosum	Cucumber	Improved plant defense against *Phytopthora melonis*	Abkhoo and Sabbagh (2016)
Ascophyllum nodosum	Tomato	Induced systemic resistance (ISR) against *Phytophthora capsica*	Panjehkeh and Abkhoo (2016)
Ascophyllum nodosum	*Arabidopsis thaliana*	Induced resistance against *pseudomonas syringae* pv. Tomato DC3000	Subramanian et al. (2011)
Ascophyllum nodosum	Carrot	Reduced the progression of disease caused by *Alternaria radicina* and *Botrytis cinerea*	Jayaraj et al. (2008)

(Allen et al. 2001). The impacts of seaweed extract on plant growth are summarized in Table 25.1.

25.3 Amelioration of Abiotic and Biotic Stresses Through Seaweeds

Abiotic and biotic stresses hamper growth and productivity of crops worldwide. In order to boost the agricultural production for the ever-increasing population chemical synthetic fertilizers are used. These synthetic chemical fertilizers posed a serious threat to the health of animals, plants, humans as well as for the entire biosphere (Damalas and Koutroubas 2016). The arable land is continuously shrinking due to the adverse effects of climate change and urbanization. The effects of climatic changes resulted into increased atmospheric $CO_{2,}$ temperature, nutrient imbalances (such as deficiency and toxicity of mineral) and soil salinization that affected the plant growth, productivity and quality of crops (Anderson et al. 2011; dos Reis et al. 2012; Matesanz et al. 2010). To meet the food demands for growing population, world food production must double by the year 2050 (Qin et al. 2011; Voss-Fels and Snowdon 2016). Therefore, an alternative approach is required to reduce the input of synthetic chemical fertilizers. In this context, plant biostimulant such as seaweeds are a new class of crop input into agricultural practices can reduce the application rate of synthetic chemical fertilizers and pesticides and thereby enhancing the quality and productivity of crops (Calvo et al. 2014; Van Oosten et al. 2017; Yakhin et al. 2017).

The pivotal role of seaweed extracts in enhancing plant growth as well as in increasing plant tolerance to abiotic (drought, salinity, nutrient deficiency, flooding, temperature stress) and biotic (diseases and insects) stresses has been reported (Jayaraman et al. 2011; Sangha et al. 2010). Among seaweeds, brown seaweeds (*Ascophyllum nodosum*, *Fucus vesiculosus*, *F. serratus*) are rich in phenolic compounds (Balboa et al. 2013; Keyrouz et al. 2011). Phenolic compounds are secondary metabolites which defend the cell and cellular components from the stressed induced damages and also chelate the metal ions (Wang et al. 2009). The phenolic compounds such as catechol (dihydroxy benzene) or galloyl (trihydroxy benzene), phloroglucinol, eckol and dieck showed strong chelating activities which make brown algae to effectively scavenge free radical (single oxygen, hydroxyl, superoxide, alkoxyl and peroxy radicals) and antioxidant activity (Andjelković et al. 2006). Study reported by Shibata et al. (2002). demonstrated that marine algae derived phlorotannis was highly efficient antioxidant as compared to the ascorbic acid, phlorofucofuroeckol, catechin, resveratrol, epigallocatechin eallate, α-tocopherol . The extracts of seaweed contain a number of plant hormone such as such as auxins, gibberellins, cytokinin, abscisic acid and brassinosteroids (Stirk et al. 2014). Osmolytes such as mannitol, an important protective compound in response to abiotic stresses are found in many brown algae such as *Laminaria digitata*, *L. hyperborea*, *L. saccharina*, *Halidrys siliquosa*, *Fucus serratus*, *F. spiralis*, *F. vesiculosus*, *Ascophyllum nodosum*, *Alaria esculenta*, *Pilayella littoralis* and *Ectocarpus siliculosus.* The chelating activity of mannitol revealed that seaweed can release the inaccessible elements to the soils (Reed et al. 1985).

Previous studies by several researchers revealed that seaweed extracts such as *Lessonia nigrescens, Grateloupia filicina, Kappaphycus alvarezii, Gracilaria dura* improved salinity and drought tolerance in several crops such as wheat, passion fruit, *Arabidopsis*, avocado and rice (Elansary et al. 2017; Di Stasio et al. 2018; Jithesh et al. 2018; Liu et al. 2019; Zou et al. 2019). Under salinity stress, both Rygex® and Super Fifty® the commercial extracts of *A. nodosum* triggered that accumulation of essential amino acids, antioxidant and minerals (Di Stasio et al. 2018). The extract of *A. nodosum* application mitigates the negative impacts of salinity stress in avocado and turfgrass by enhancing nutrient uptake (Elansary et al. 2017; Bonomelli et al. 2018).

Abiotic stress involves hyperosmotic and ionic imbalances leading to an oxidative stress generated from the overproduction of ROS (reactive oxygen species) and the antioxidant mechanisms (Debnath et al. 2011). ROS [includes the singlet oxygen ($^1O_2$), superoxide (O_2^-), hydroxyl (OH^-), hydrogen peroxide (H_2O_2)] are to known to impair biomolecule like proteins, DNA and lipids (Das and Roychoudhury 2014; Mittler 2002). To mitigate such damaging impacts, plant resort to several natural defensive mechanisms. ROS production controlled by the enzymatic and non-enzymatic antioxidants such as SOD (superoxide dismutase), GPX (guaiacol peroxidase), CAT (catalase), APX (ascorbate peroxidase), DHAR (dehydroascorbate reductase), GR (glutathione reductase), MDHAR (monodehydroascorbate reductase), AsA (ascorbic acid), tocopherol, glutathione and phenolic compounds (Gruszka et al. 2018; Yadav et al. 2019). The study of Zou et al. (Zou et al. 2019) demonstrated that potential of *Lessonia nigrescens* derived polysaccharides in the alleviation of salt stress on wheat and found that polysaccharides application significantly increased the root/shoot length and fresh/dry matters of wheat. They also noticed that polysaccharides application maintained osmotic status of salt stressed wheat seedlings by increasing the proline and sugar content as well as regulating the ratio of Na^+/K^+. A study of Liu et al. (Liu et al. 2019) observed that the impact of polysaccharides from *Grateloupia filicina* augmented rice seed development and mitigate the salinity-induced damage. A study by Jayaraman et al. (Jayaraman et al. 2011) examined the impacts of Stimplex™, a commercial extract from *A. nodosum* on some common cucumber fungal pathogen such as *Alternaria cucumerinum, Fusarium oxysporum, Didymella applanata.* They found that Stimplex™ application resulted in a significant increase in activities of various defense related enzymes including peroxidase, polyphenol oxidase, lipoxygenase, chitinase, phenylalanine ammonia lyase, glucanase and β-1,3-glucanase. In addition, treated plants also displayed a higher level of phenolics content and reduced the disease incidence of all tested pathogens. Similarly, the study of Guinan et al. (2012) revealed that extracts of Super Fifty® and Ecoelicitor® were found to be more effective in imparting tolerance to *Sclerotinia sclerotiorum* and *Alternaria brassicae.* The abiotic and biotic stress-responsive genes are elicited by seaweeds are enumerated in Table 25.2.

25.4 Nutritional and Bioactive Potential of Seaweed

A number of studies revealed that macroalgae have huge potential due to their bioactive compounds endowed with a wide range of activities such as antioxidant, anti-inflammatory, anti-tumor and antimicrobial (Rocha et al. 2018; Trifan et al. 2019). Among macroalgae, phaeophyceae members accumulate a variety of compounds including sterols, lipids, proteins, terpenoids, vitamins, phlorotannins with a range of biological activities (Balboa et al. 2013; Jiménez-Escrig et al. 2012). Seaweeds are the macroscopic, multicellular marine algae that form a vital part of the marine coastal ecosystem. Approximately, there are 9000 species of macrolage classified into three groups based on their pigmentation such as Chlorophyta (greem algae), Phaeophyta (brown algae), and Rhodophyta (red algae). Pheophyta is the second most abundant group comprising about 2000 species. This group of microalgae commonly used in agriculture (Blunden and Gordon 1986; Khan et al. 2009). Brown algae such as *Fucus* spp., *Ascophyllum nodosum*, *Sargassum* spp., *Turbinaria* spp., and *Laminaria* spp. are used as biofertilizers in agricultural practices (Hong et al. 2007). For centuries seaweeds are used as source of organic matter and fertilizer nutrients. Around 15 million metric tonnes of seaweed products are produced

Table 25.2 Effect of seaweed extracts on gene expression of plants under abiotic and biotic stress conditions

Seaweed	Plant	Abiotic stress responsive gene(s)	Reference
Lessonia nigrescens	Wheat	Down-regulation of *TaHKT2; 1*, and up-regulation of *TaSOS1* and *TaNHX2*	Zou et al. (2019)
Ascophyllum nodosum	Soybean	Enhanced expression of *GmRD22*, *GmDREB*, *GmFIB1a*, *GmERD1*, *GmBIPD GmPIP1b*	Shukla et al. (2018b)
Ascophyllum nodosum	*Arabidopsis thaliana*	Up-regulation of *SAUR33*, *SAUR59*, and *SAUR71*, down-regulation of *SAUR1* and *SAUR50*	Goñi et al. (2016)
AZAL5® (commercial extract from *A. nodosum*)	Oilseed rape (*Brassica napus*)	Enhanced expression of *BnNRT1.1*; *BnNRT2.1*, *BnSultr4.1*; *BnSultr4.2*	Jannin et al. (2013)
Ascophyllum nodosum	*Arabidopsis*	Up-regulation of CB73, RD29A, and COR15A.	Rayirath et al. (2009)
Ascophyllum nodosum	*Arabidopsis*	Enhanced expression *RAB18, RD29A, DFR, SOD,* APX_2	Santaniello et al. (2017)
Ascophyllum nodosum	Soybean	Induced the expression level of *CYP707A1a, CYP707A3b, GmDREB1B, GmRD22, fibrillin, ABA-response regulators (ABI1, ABI2), FIB1a*	Shukla et al. (2018b)
Ascophyllum nodosum	*Arabidopsis thaliana*	Up-regulation of *DREB1A/CBF3, COR15A, COR78/RD29A,* digalactosyldiacylglycerol synthaseencoding gene *DGD1,* salicylic acid *(SA) (At1g18870),* Spermine/spermidine biosynthesis *(At5g15950),* cytokinin conjugation *(UGT73B2, UGT76C1/2, At2g43820, At1g24100),* increased expression of the ABA responsive genes *RAB18* (At5g66400), RD29A (At5g52310), *PsbS (At1g44575)* and *VDE (At1g08550)* and lower expression of activating protein 2, betaine aldehyde dehydrogenase (*BADH*), glutathione S-transferase, and fucosyltransferase, reduced expression of *NCED3* (*At3g14440*)	De Saeger et al. (2019)
Ascophyllum nodosum	*Arabidopsis thaliana*	Increased expression of proline synthesis genes *P5CS1* and *P5CS2* and a marginal reduction in the expression of the proline dehydrogenase (*ProDH*) gene	Nair et al. (2012)
Ascophyllum nodosum	*Arabidopsis thaliana*	Elicit the expression of glutathione S transferase	Jithesh et al. (2018)
Ascophyllum nodosum	*Arabidopsis thaliana*	Higher transcript accumulation of *SnRK2*	Coello et al. (2011), Jithesh et al. (2018)
Ascophyllum nodosum	*Arabidopsis thaliana*	Induced expression of *IPT3*, *IPT4*, and *IPT5*	Wally et al. (2013)

(continued)

Table 25.2 (continued)

Seaweed	Plant	Abiotic stress responsive gene(s)	Reference
Ascophyllum nodosum	*Arabidopsis thaliana*	Down-regulate the expression of miR396a-5p, which resulted in a reduction in the expression of its target gene AtGRF7	Yang et al. (2009); Shukla et al. (2018a)
Ascophyllum nodosum	*Arabidopsis thaliana*	Treatment application induced the ath-miR398 targets superoxide dismutase 1 (AtCSD1), ath-miR168a targets ARGONAUTE 1 and ath-miR399a targets ubiquitin-conjugating E2 enzyme (AtUBC24) and wall-associated kinase 2 (AtWAK2)	Shukla et al. (2018a)
Ascophyllum nodosum	*Arabidopsis thaliana*	Induced the expression of JA-related genes such as PDF1.2,	Subramanian et al. (2011)
Ascophyllum nodosum derived extract (Stella Maris®)	*Arabidopsis thaliana*	Up-regulation of *WRKY30*, *CYP71A12*, and *PR-1*	Cook et al. (2018)
Ascophyllum nodosum	Carrot	Increased transcript accumulation of *PR-1, PR-5, NPR-1, LTP*	Jayaraj et al. (2008)

annually (FAO 2006), a substantial portion of which is used for nutrient supplements and as biostimulants to increased plant growth and productivity.

A number of products such as Agri-Gro Ultra, Tasco®, Acadian®, Alg-A-Mic, Bio-GenesisTM High TideTM, Biovita, Espoma, Soluble Seaweed Extract, Guarantee®, Kelp Meal, Synergy, Kelpro, Kelprosoil, Maxicrop, Nitrozime and Stimplex® are formulated from *Ascophyllum nodosum* seaweed and used in agriculture practices as a plant growth stimulant. Kelpak, Seasol®, Profert® and AgroKelp products are obtained from the *Ecklonia maxima*, *Durvillea potatorum, Durvillea antarctica* and *Macrocystis pyrifera* seaweed, respectively also these are used in agriculture as plant growth stimulant (Khan et al. 2009). In addition, application of seaweed extracts on plants promotes the seed germination and its establishment, imparts tolerance to abiotic and biotic stresses, enhanced crop performance and productivity, and also enhanced shelf-life of postharvest products (Norrie and Keathley 2006).

Seaweed extracts has been shown to have a positive impact on plant nutrient uptake (Table 25.3). Turan and Köse (Turan and Köse 2004) found that foliar application of commercial seaweed extract enhanced the micro- and macronutrient content of grapevine leaves. Study of Rathore et al. (Rathore et al. 2009) revealed that application of *Kappaphycus alvarezii* increased N, P, K, and S content of soybean under rainfed conditions. Seaweed extracts improve plant via improvement of soil structure and micronutrient solubility in the soil, as well as influencing the plant physiology through changes in root morphology and increased root colonization by AM fungi (Halpern et al. 2015). The polysaccharides such as fucoidans and alginates are found in brown seaweeds and these polysaccharides are bound with

Table 25.3 Effects of seaweed extracts on plant nutrient uptake

Benefitted plant	Seaweed	Impacts on plant	Reference
Maize	*Kappaphycus alvarezii, Gracilaria edulis*	Increased nitrogen, potassium and phosphorus uptake	Basavaraja et al. (2018)
Oilseed rape	*Ecklonia maxima*	Increased leaf phosphorus and potassium Content	Di Stasio et al. (2017)
Tomato	*Ecklonia maxima*	Enhanced fruit calcium concentration	Colla et al. (2017)
Tomato	*Ascophyllum nodosum*	Enhanced concentration of manganese, cooper, and zinc in root and leaf	Carrasco-Gil et al. (2018)
Oilseed rape	*Ascophyllum nodosum*	Increased relative manganese, cooper, and magnesium concentration in whole plant.	Billard et al. (2014)
Wheat	*Ascophyllum nodosum*	Enhanced grain potassium	Stamatiadis et al. (2015)
Oilseed rape	*Ascophyllum nodosum*	Stimulation of root and shoot nitrogen and sulfur	Jannin et al. (2013)
Soybean	*Kappaphycus alvarezii*	Increased nitrogen, phosphorus, potassium, sulfur grain uptake and nitrogen, phosphorus straw uptake	Rathore et al. (2009)
Tomato	Commercial extracts of *A. nodosum*, Rygex® and super fifty®	Macronutrient (N, P, K, ca, S) and micronutrient (mg, Zn, Mn, Fe) contents	Di Stasio et al. (2018)
Olive (*Olea europaea*)	*Ascophyllum nodosum*	Higher uptake of K, Fe, and cu	Chouliaras et al. (2009)
Brassica napus	AZAL5® (commercial extract from *A. nodosum*)	Higher uptake of nitrate and sulfate	Jannin et al. (2013)
Grapevines (*V. vinifera*)	Commercial Extracts Maxicrop®, proton®, and Algipower®	Increased cooper uptake	Turan and Köse (2004)
Ascophyllum nodosum	Avocado	Higher content of Ca^{2+} and K^{+}	Bonomelli et al. (2018)

metallic ions in soil to produce a gel that helps in the absorption of water and form an aggregate structure which assists the plant to grow a vigorous root architecture which in turn enhance the nutrient availability (Khan et al. 2009). Some of the studies also reported that the organic molecules in seaweed extracts can chelate the micronutrients and make them more accessible to plants. Spinelli et al. (Spinelli et al. 2010) showed that commercial extract of *A. nodosum* improved the solubility of micronutrients and that could be used to replace some of the standard iron chelates such as sequestrene.

25.5 Conclusion

Leveraging seaweeds as potential biostimulants have been shown to increase the plant growth, improved physiological and molecular machinery, and provides tolerance to abiotic and biotic stresses and better nutrient uptake in several crops and suggesting their usefulness in reducing chemical fertilizer application in agricultural practices without negatively affecting crop productivity. Although, commercial seaweeds extracts are readily available in the marketplace, they have not substantially reduced chemical fertilizers use in conventional agriculture. Before biostimulants can effectively use in agriculture system, it is important to find the most promising ones for those particular environmental conditions and the mechanism how they are best applied.

References

Abkhoo J, Sabbagh SK (2016) Control of Phytophthora melonis damping-off, induction of defense responses, and gene expression of cucumber treated with commercial extract from *Ascophyllum nodosum*. J Appl Phycol 28:1333–1342

Ahmed YM, Shalaby EA (2012) Effect of different seaweed extracts and composton vegetative growth, yield and fruit quality of cucumber. J Hortic Sci OrnamPlants 4:235–240

Allen VG, Pond KR, Saker KE, Fontenot JP, Bagley CP, Ivy RL, Evans RR, Schmidt RE, Fike JH, Zhang X, Ayad JY (2001) Tasco: influence of a brown seaweed on antioxidants in forages and livestock—A review. J Anim Sci 79:E21

Anderson JT, Willis JH, Mitchell-Olds T (2011) Evolutionary genetics of plant adaptation. Trends Genet 27:258–266

Andjelković M, Van Camp J, De Meulenaer B, Depaemelaere G, Socaciu C, Verloo M, Verhe R (2006) Iron-chelation properties of phenolic acids bearing catechol and galloyl groups. Food Chem 98:23–31

Balboa EM, Conde E, Moure A, Falqué E, Domínguez H (2013) In vitro antioxidant properties of crude extracts and compounds from brown algae. Food Chem 138:1764–1785

Basavaraja PK, Yogendra ND, Zodape ST, Prakash R, Ghosh A (2018) Effect of seaweed sap as foliar spray on growth and yield of hybrid maize. J Plant Nutr 41:1851–1861

Battacharyya D, Babgohari MZ, Rathor P, Prithiviraj B (2015) Seaweed extracts as biostimulants in horticulture. Sci Hortic 196:39–48

Billard V, Etienne P, Jannin L, Garnica M, Cruz F, Garcia-Mina JM, Yvin JC, Ourry A (2014) Two biostimulants derived from algae or humic acid induce similar responses in the mineral content and gene expression of winter oilseed rape (*Brassica napus* L.). J Plant Growth Regul 33:305–316

Blunden G, Gordon SM (1986) Betaines and their sulphono analogues in marine algae. In: Round FE, Chapman DJ (eds) Progress in phycological research, vol 4. Biopress Ltd, Bristol, pp 39–80

Bonomelli C, Celis V, Lombardi G, Mártiz J (2018) Salt stress effects on avocado (*Persea americana* mill). Plants with and without seaweed extract (*Ascophyllum nodosum*) application. Agronomy 8:64

Calvo P, Nelson L, Kloepper JW (2014) Agricultural uses of plant biostimulants. Plant Soil 383:3–41

Carrasco-Gil S, Hernandez-Apaolaza L, Lucena JJ (2018) Effect of several commercial seaweed extracts in the mitigation of iron chlorosis of tomato plants (*Solanum lycopersicum* L.). Plant Growth Regul 86:401–411

Chouliaras V, Tasioula M, Chatzissavvidis C, Therios I, Tsabolatidou E (2009) The effects of a seaweed extract in addition to nitrogen and boron fertilization on productivity, fruit maturation, leaf nutritional status and oil quality of the olive (*Olea europaea* L.). Cultivar Koroneiki. J Sci Food Agric 89:984–988

Coello P, Hey SJ, Halford NG (2011) The sucrose non-fermenting-1-related (SnRK) family of protein kinases: potential for manipulation to improve stress tolerance and increase yield. J Exp Bot 62:883–893

Colla G, Cardarelli M, Bonini P, Rouphael Y (2017) Foliar applications of protein hydrolysate, plant and seaweed extracts increase yield but dierentially modulate fruit quality of greenhouse tomato. HortScience 52:1214–1220

Cook J, Zhang J, Norrie J, Blal B, Cheng Z (2018) Seaweed extract (Stella Maris®) activates innate immune responses in *Arabidopsis thaliana* and protects host against bacterial pathogens. Mar Drugs 16:E221

Craigie JS (2011) Seaweed extract stimuli in plant science and agriculture. J Appl Phycol 23:371–393

Damalas C, Koutroubas S (2016) Farmers' exposure to pesticides: toxicity types and ways of prevention. Toxics 4:1

Das K, Roychoudhury A (2014) Reactive oxygen species (ROS) and response of antioxidants as ROS-scavengers during environmental stress in plants. Front Environ Sci 2:53

De Saeger J, Van Praet S, Vereecke D, Park J, Jacques S, Han T, Depuydt S (2019) Toward the molecular understanding of the action mechanism of *Ascophyllum nodosum* extracts on plants. J Appl Phycol:1–25

Debnath M, Pandey M, Bisen PS (2011) An omics approach to understand the plant abiotic stress. Omi J Integr Biol 15:739–762

Di Stasio E, Rouphael Y, Colla G, Raimondi G, Giordano M, Pannico A, El-Nakhel C, De Pascale S (2017) The influence of *Ecklonia maxima* seaweed extract on growth, photosynthetic activity and mineral composition of *Brassica rapa* L. subsp *sylvestris* under nutrient stress conditions. Eur J Hortic Sci 82:286–293

Di Stasio E, Van Oosten MJ, 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. J Appl Phycol 30:2675–2686

do Rosário Rosa V, Dos Santos ALF, da Silva AA, Sab MPV, Germino GH, Cardoso FB, de Almeida Silva M (2021) Increased soybean tolerance to water deficiency through biostimulant based on fulvic acids and *Ascophyllum nodosum* (L.) seaweed extract. Plant Physiol Biochem 158:228–243

dos Reis SP, Lima AM, de Souza CRB (2012) Recent molecular advances on downstream plant responses to abiotic stress. Int J Mol Sci 13:8628–8647

Elansary HO, Yessoufou K, Abdel-Hamid AME, El-Esawi MA, Ali HM, Elshikh MS (2016) Seaweed extracts enhance Salam turfgrass performance during prolonged irrigation intervals and saline shock. Front Plant Sci 8:830

Elansary HO, Yessoufou K, Abdel-Hamid AME, El-Esawi MA, Ali HM, Elshikh MS (2016) Seaweed extracts enhance Salam turfgrass performance during prolonged irrigation intervals and saline shock. Front Plant Sci 8. https://doi.org/10.3389/fpls.2017.00830

FAO (2006) Yearbook of fishery statistics, vol 98(1–2). Food and Agricultural Organisation of the United Nations, Rome

Frioni T, VanderWeide J, Palliotti A, Tombesi S, Poni S, Sabbatini P (2021) Foliar vs. soil application of *Ascophyllum nodosum* extracts to improve grapevine water stress tolerance. Sci Hortic 277:109807

Gayathri M, Kumar PS, Prabha AML, Muralitharan G (2015) In vitro regeneration of *Arachis hypogaea* L. and *Moringa oleifera* lam. Using extracellular phytohormones from *Aphanothece* sp. MBDU 515. Algal Res 7:100–105

Goñi O, Fort A, Quille P, McKeown PC, Spillane C, O'Connell S (2016) Comparative transcriptome analysis of two *Ascophyllum nodosum* extract biostimulants: same seaweed but different. J Agric Food Chem 64:2980–2989
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 Physiol Biochem 126:63–73
Gruszka D, Janeczko A, Dziurka M, Pociecha E, Fodor J (2018) Non-enzymatic antioxidant accumulations in BR-deficient and BR-insensitive barley mutants under control and drought conditions. Physiol Plant 163:155–169
Guinan KJ, Sujeeth N, Copeland RB, Jones PW, O'brien NM, Sharma HSS, Prouteau PFJ, O'sullivan JT (2012) Discrete roles for extracts of *Ascophyllum nodosum* in enhancing plant growth and tolerance to abiotic and biotic stresses. In: I World Congress on the Use of Biostimulants in Agriculture 1009, pp 127–135
Halpern M, Bar-Tal A, Ofek M, Minz D, Muller T, Yermiyahu U (2015) The use of biostimulants for enhancing nutrient uptake. Adv Agron 130:141–174
Hernández-Carlos B, Gamboa-Angulo MM (2011) Metabolites from freshwater aquatic microalgae and fungi as potential natural pesticides. Phytochem Rev 10:261–286
Hernández-Herrera RM, Santacruz-Ruvalcaba F, Ruiz-López MA, Norrie J, Hernández-Carmona G (2014) Effect of liquid seaweed extracts on growth of tomato seedlings (Solanum lycopersicum L.). J Appl Phycol 26(1):619–628. https://doi.org/10.1007/s10811-013-0078-4
Hong DD, Hien HM, Son PN (2007) Seaweeds from Vietnam used for functional food, medicine and biofertilizer. J Appl Phycol 19:817–826
Jäger K, Bartók T, Ördög V, Barnabás B (2010) Improvement of maize (*Zea mays* L.) anther culture responses by algae-derived natural substances. S Afr J Bot 76:511–516
Jannin L, Arkoun M, Etienne P, Laîné P, Goux D, Garnica M, Fuentes M, San Francisco S, Baigorri R, Cruz F, Houdusse F (2013) *Brassica napus* growth is promoted by *Ascophyllum nodosum* (L). Le Jol. Seaweed extract: microarray analysis and physiological characterization of N, C, and S metabolisms. J Plant Growth Regul 32:31–52
Jayaraj J, Wan A, Rahman M, Punja ZK (2008) Seaweed extract reduces foliar fungal diseases on carrot. Crop Prot 27:1360–1366
Jayaraman J, Norrie J, Punja ZK (2011) Commercial extract from the brown seaweed *Ascophyllum nodosum* reduces fungal diseases in greenhouse cucumber. J Appl Phycol 23:353–361
Jiménez-Escrig A, Gómez-Ordóñez E, Rupérez P (2012) Brown and red seaweeds as potential sources of antioxidant nutraceuticals. J Appl Phycol 24:1123–1132
Jithesh MN, Shukla PS, Kant P, Joshi J, Critchley AT, Prithiviraj B (2018) Physiological and transcriptomics analyses reveal that *Ascophyllum nodosum* extracts induce salinity tolerance in *Arabidopsis* by regulating the expression of stress responsive genes. Plant Growth Regul 38:463–478
Keyrouz R, Abasq ML, Le Bourvellec C, Blanc N, Audibert L, ArGall E, Hauchard D (2011) Total phenolic contents, radical scavenging and cyclic voltammetry of seaweeds from Brittany. Food Chem 126:831–836
Khan W, Rayirath UP, Subramanian S, Jithesh MN, Rayorath P, Hodges DM, Critchley AT, Craigie JS, Norrie J, Prithiviraj B (2009) Seaweed extracts as biostimulants of plant growth and development. Plant Growth Regul 28:386–399
Kocira A, Świeca M, Kocira S, Złotek U, Jakubczyk A (2018) Enhancement of yield, nutritional and nutraceutical properties of two common bean cultivars following the application of seaweed extract (*Ecklonia maxima*). Saudi J Biol Sci 25:563–571
Kramer SB, Reganold JP, Glover JD, Bohannan BJM, Mooney HA (2006) Reduced nitrate leaching and enhanced denitrifier activity and efficiency in organically fertilized soils. Proc Natl Acad Sci 103(12):4522–4527. https://doi.org/10.1073/pnas.0600359103
Lafarga T, Acién-Fernández FG, Garcia-Vaquero M (2020) Bioactive peptides and carbohydrates from seaweed for food applications: natural occurrence, isolation, purification, and identification. Algal Res 48:101909

Li R, Tao R, Ling N, Chu G (2017) Chemical, organic and bio-fertilizer management practices effect on soil physicochemical property and antagonistic bacteria abundance of a cotton field: implications for soil biological quality. Soil Tillage Res 167:30–38

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. Int J Biol Macromol 124:1197–1204

Manna D, Sarkar A, Maity TK (2012) Impact of biozyme on growth, yield andquality of chilli (*Capsicum annuum* L.). J Crop Weed 8:40–43

Matesanz S, Gianoli E, Valladares F (2010) Global change and the evolution of phenotypic plasticity in plants. Ann N Y Acad Sci 1206:35–55

Mittler R (2002) Oxidative stress, antioxidants and stress tolerance. Trends Plant Sci 7:405–410

Moroney JV, Ynalvez RA (2009) Algal photosynthesis. In: eLS, September 2009. John Wiley & Sons Ltd, Chichester. http://www.els.net

Nair P, Kandasamy S, Zhang J, Ji X, Kirby C, Benkel B, Hodges MD, Critchley AT, Hiltz D, Prithiviraj B (2012) Transcriptional and metabolomic analysis of *Ascophyllum nodosum* mediated freezing tolerance in *Arabidopsis thaliana*. BMC Genomics 13:1–23

Norrie J, Keathley JP (2006) Benefits of *Ascophyllum nodosum* marine-plant extract applications to 'Thompson seedless' grape production. (proceedings of the Xth international symposium on plant bioregulators in fruit production, 2005). Acta Hortic 727:243–247

Panjehkeh N, Abkhoo J (2016) Influence of marine brown alga extract (Dalgin) on damping-off tolerance of tomato. JMES 7:2369–2374

Prasanna R, Kanchan A, Kaur S, Ramakrishnan B, Ranjan K, Singh MC, Hasan M, Saxena AK, Shivay YS (2016) *Chrysanthemum* growth gains from beneficial microbial interactions and fertility improvements in soil under protected cultivation. Hortic Plant J 2:229–239

Qin F, Shinozaki K, Yamaguchi-Shinozaki K (2011) Achievements and challenges in understanding plant abiotic stress responses and tolerance. Plant Cell Physiol 52:1569–1582

Rathore SS, Chaudhary DR, Boricha GN, Ghosh A, Bhatt BP, Zodape ST, Patolia JS (2009) Effect of seaweed extract on the growth, yield and nutrient uptake of soybean (*Glycine max*) under rainfed conditions. S Afr J Bot 75:351–355

Rayirath P, Benkel B, Hodges DM, Allan-Wojtas P, MacKinnon S, Critchley AT, Prithiviraj B (2009) Lipophilic components of the brown seaweed, *Ascophyllum nodosum*, enhance freezing tolerance in *Arabidopsis thaliana*. Planta 230:135–147

Rayorath P, Jithesh MN, Farid A, Khan W, Palanisamy R, Hankins SD, Critchley AT, Prithiviraj B (2008) Rapid bioassays to evaluate the plant growth promoting activity of *Ascophyllum nodosum* (L.) Le Jol. Using a model plant, *Arabidopsis thaliana* (L.) Heynh. J Appl Phycol 20:423–429

Reed RH, Davison IR, Chudek JA, Foster R (1985) The osmotic role of mannitol in the Phaeophyta: an appraisal. Phycologia 24:35–47

Renuka N, Guldhe A, Prasanna R, Singh P, Bux F (2018) Microalgae as multi-functional options in modern agriculture: current trends, prospects and challenges. Biotechnol Adv 36:1255–1273

Rocha DHA, Seca AML, Pinto DCGA (2018) Seaweed secondary metabolites in vitro and in vivo anticancer activity. Mar Drugs 16:410

Sangha JS, Ravichandran S, Prithiviraj K, Critchley AT, Prithiviraj B (2010) Sulfated macroalgal polysaccharides l-carrageenan and i-carrageenan differentially alter *Arabidopsis thaliana* resistance to *Sclerotinia sclerotiorum*. Physiol Mol Plant Pathol 75:38–45

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. Front Plant Sci 8:1362

Senn LT (1987) Seaweed and plant growth. Clemson Univ., Clemson, SC. Seaweed and plant growth. Clemson Univ, Clemson, SC

Sharma HS, Fleming C, Selby C, Rao JR, 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. J Appl Phycol 26:465–490

Sharma L, Banerjee M, Malik GC, Gopalakrishnan VAK, Zodape ST, Ghosh A (2017) Sustainable agro-technology for enhancement of rice production in the red and lateritic soils using seaweed based biostimulants. J Clean Prod 149:968–975

Shibata T, Yamaguchi K, Nagayama K, Kawaguchi S, Nakamura T (2002) Inhibitory activity of brown algal phlorotannins against glycosidases from the viscera of the turban shell Turbo cornutus. Eur J Phycol 37:493–500

Shukla PS, Borza T, Critchley AT, Hiltz D, Norrie J, Prithiviraj B (2018a) *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:e0206221

Shukla PS, Shotton K, Norman E, Neily W, Critchley AT, Prithiviraj B (2018b) Seaweed extract improve drought tolerance of soybean by regulating stress-response genes. AoB Plants 10:plx051

Silva LD, Bahcevandziev K, Pereira L (2019) Production of bio-fertilizer from *Ascophyllum nodosum* and *Sargassum muticum* (Phaeophyceae). J Oceanol Limnol 37:918–927

Singh DP, Prabha R, Yandigeri MS, Arora DK (2011a) Cyanobacteria-mediated phenylpropanoids and phytohormones in rice (*Oryza sativa*) enhance plant growth and stress tolerance. Anton Leeuw 100:557–568

Singh I, Anand KV, Solomon S, Shukla SK, Rai R, Zodape ST, Ghosh A (2018) Can we not mitigate climate change using seaweed based biostimulant: A case study with sugarcane cultivation in India. J Clean Prod 204:992–1003

Singh JS, Pandey VC, Singh DP (2011b) Efficient soil microorganisms: a new dimension for sustainable agriculture and environmental development. Agric Ecosyst Environ 140:339–353

Sivanandhan G, Arunachalam C, Selvaraj N, Sulaiman AA, Lim YP, Ganapathi A (2015) Expression of important pathway genes involved in withanolides biosynthesis in hairy root culture of *Withania somnifera* upon treatment with *Gracilaria edulis* and *Sargassum wightii*. Plant Physiol Biochem 91:61–64

Spinelli F, Fiori G, Noferini M, Sprocatti M, andCosta, G. (2010) A novel type of seaweed extract as a natural alternative to the use of iron chelates in strawberry production. Sci Hortic 125:263–269

Stamatiadis S, Evangelou L, Yvin JC, Tsadilas C, Mina JMG, Cruz F (2015) Responses of winter wheat to Ascophyllum nodosum (L.) Le Jol. Extract application under the effect of N fertilization and water supply. J Appl Phycol 27:589–600

Stirk WA, Tarkowská D, Turečová V, Strnad M, van Staden J (2014) Abscisic acid, gibberellins and brassinosteroids in Kelpak®, a commercial seaweed extract made from *Ecklonia maxima*. J Appl Phycol 26:561–567

Stirk WA, Van Staden J (1997) Isolation and identification of cytokinins in a new commercial seaweed product made from *Fucus serratus* L. J Appl Phycol 9:327–330

Subramanian S, Sangha JS, Gray BA, Singh RP, Hiltz D, Critchley AT, Prithiviraj B (2011) Extracts of the marine brown macroalga, *Ascophyllum nodosum*, induce jasmonic acid dependent systemic resistance in *Arabidopsis thaliana* against *pseudomonas syringae* pv. Tomato DC3000 and *Sclerotinia sclerotiorum*. Eur J Plant Pathol 131:237–248

Thilagar G, Bagyaraja DJ, Rao MS (2016) Selected microbial consortia developed for chilly reduces application of chemical fertilizers by 50% under field conditions. Sci Hortic 198:27–35

Thirumaran G, Arumugam M, Arumugam R, Anantharaman P (2009) Effect of seaweed liquid fertilizer on growth and pigment concentration of *Cyamopsis tetrogonolaba* (L) Taub. Am Eurasian J Agric Environ Sci 2:50–56

Trifan A, Vasincu A, Luca SV, Neophytou C, Wolfram E, Opitz SE, Sava D, Bucur L, Cioroiu BI, Miron A, Constantinou AI (2019) Unravelling the potential of seaweeds from the Black Sea coast of Romania as bioactive compounds sources. Part I: *Cystoseira barbata* (Stackhouse) C. Agardh. Food Chem Toxicol 134:110820

Turan M, Köse C (2004) Seaweed extracts improve copper uptake of grapevine. Acta Agric Scand B Soil Plant Sci 54:213–220

Van Oosten MJ, Pepe O, De Pascale S, Silletti S, Maggio A (2017) The role of biostimulants and bioeffectors as alleviators of abiotic stress in crop plants. Chem Biol Technol Agric 4:5

Voss-Fels K, Snowdon RJ (2016) Understanding and utilizing crop genome diversity via high-resolution genotyping. Plant Biotechnol J 14:1086–1094

Wally OSD, Critchley AT, Hiltz D, Craigie JS, Han X, Zaharia LI, Abrams SR, Prithiviraj B (2013) Regulation of phytohormone biosynthesis and accumulation in *Arabidopsis* following treatment with commercial extract from the marine macroalga *Ascophyllum nodosum*. Plant Growth Regul 32:324–339

Wang T, Jonsdottir R, Ólafsdóttir G (2009) Total phenolic compounds, radical scavenging and metal chelation of extracts from Icelandic seaweeds. Food Chem 116:240–248

Yadav DS, Rai R, Mishra AK, Chaudhary N, Mukherjee A, Agrawal SB, Agrawal M (2019) ROS production and its detoxification in early and late sown cultivars of wheat under future O_3 concentration. Sci Total Environ 659:200–210

Yakhin OI, Lubyanov AA, Yakhin IA, Brown PH (2017) Biostimulants in plant science: a global perspective. Front Plant Sci 7:671

Yang F, Liang G, Liu D, Yu D (2009) *Arabidopsis* MiR396 mediates the development of leaves and flowers in transgenic tobacco. J Plant Biol 52:475–481

Zodape ST, Mukhopadhyay S, Eswaran K, Reddy MP, Chikara J (2010) Enhanced yield and nutritional quality in green gram (*Phaseolus radiata* L) treated with seaweed (*Kappaphycus alvarezii*) extract. J Sci Ind Res 69:468–471

Zou P, Lu X, Zhao H, Yuan Y, Meng L, Zhang C, Li Y (2019) Polysaccharides derived from the brown algae *Lessonia nigrescens* enhance salt stress tolerance to wheat seedlings by enhancing the antioxidant system and modulating intracellular ion concentration. Front Plant Sci 10:48