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REVIEW

Impact of seaweeds on agricultural crop production as biofertilizer

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Abstract Seaweeds or marine macroalgae are rich in diverse compounds like lipids, proteins, carbohydrates, phytohormones, amino acids, osmoprotectants, antimicrobial compounds and minerals. Their potential for agricultural applications is used since antiquity, but recent demands of organic farming and organic food stimulated much the application of organic treatments like seaweed extracts in agriculture. The benefits of seaweeds application in agricultural field are numerous and diverse such as stimulation of seed germination, enhancement of health and growth of plants namely shoot and root elongation, improved water and nutrient uptake, frost and saline resistance, biocontrol and resistance toward phytopathogenic organisms, remediation of pollutants of contaminated soil and fertilization. In this review, scientific progress in this field was collected and critically assessed to lay grounds for further investigations and applications.

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Introduction

Seaweeds or macroalgae are aquatic plants belonging to the plant kingdom *Thallophyta* (Silva 1992; Dhargalkar et al. 2001; Kerswell 2006; Jothinayagi and Anbazhagan 2009; Arioli et al. 2015). These organisms are often regarded as an under-utilized bioresource, although many species have been used as sources of food, industrial gums, and in therapeutic and botanical applications for centuries (Khan et al. 2009). Many studies concerning plant growth stimulating effects of marine algae have been performed (Challen and Heminway 1965; Russo and Berlyn 1990). Seaweeds have been proven as a source of antioxidants, plant growth hormones, osmoprotectants, mineral nutrients and many other organic compounds including novel bioactive molecules (Akila and Jeyadoss 2010; Ramarajan et al. 2013; Ismail and El-Shafay 2015; Pacholczak et al. 2016a). The utilization of seaweeds as biofertilizer was considered to compensate for the lack and deficiency of N, P and K in soils (Sangeetha and Thevanathan 2010; Srijaya et al. 2010; Sunarpi et al. 2010; Tuhy et al. 2015; Singh et al. 2016; Vyomendra and kumar 2016). The importance of seaweeds as manure has been recognized in many countries. The possibility of seaweeds' exploitation in modern agriculture has been widely explored, and different varieties of preparations of these marine algae as liquid fertilizer and either whole or finally chopped powdered algal manures are being used.

Recently, attention of scientists has been paid to novel extraction methods, such as enzyme-assisted extraction, microwave-assisted extraction, pressurized liquid

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extraction, supercritical fluid extraction, and ultrasound-assisted extraction, enabling improved extraction of biologically active compounds without their degradation (Michalak and Chojnacka 2015).

Seaweed extracts are known to contain a wide range of bioactive compounds. Their extraction methods are purpose dependent. Unfortunately, there is a remarkable lack of detailed data about processes of algal extraction technologies for agricultural purposes, mostly because the manufacture methods are rarely published and held as proprietary information (Craigie 2011). In fact, several extraction procedures have been adopted for agricultural biostimulant production from marine macroalgae. In most cases, extracts are made by processes using water, alkalis or acids, or physically by disrupting the seaweed by low-temperature milling to give a micronized suspension of fine particles (Rój et al. 2009; Sharma et al. 2014). For seaweed utilization as fertilizer and biostimulant components, water extraction seems to be the most cost-effective and practicable tool for better release of micro- and macrolements from the biomass (Michalak and Chojnacka 2015). Thus, several reports described the use of water or alkaline extracts from algae as plant growth biostimulants (wheat, tomato, *Arabidopsis*, spinach, *Vigna sinensis,* etc.) under normal and stressed environments. In most cases, such extracts are prepared by autoclaving or heating a previously washed seaweed in distilled water (Sivasankari et al. 2006; Kumar and Sahoo 2011; Nabti et al. 2010; Craigie 2011) or in alkaline solutions (Whapham et al. 1993; Rayorath et al. 2008a, b; Craigie 2011; Fan et al. 2011). In almost all cases, beneficial effects on growth of cereals, pulses, and flowering plants have been reported (Kavipriya et al. 2011).

Based on the application of seaweed extracts, the best results were reported for stimulation of seed germination and root development, enhancement of frost resistance, increased nutrient uptake and control of phytopathogenic fungi (Younes et al. 2009), bacteria (Kulik 1995; Bouhlal et al. 2010; Alves et al. 2016), insects or other pests (Nassar et al. 1999; Ravikumar et al. 2011; Asha et al. 2012) and also for restoration of plant growth under high salinity stress (Nabti et al. 2010; Pacholczak et al. 2016a). The use of marine algae is promising and provides suitable solutions to overcome pollution problems caused by the extensive use of chemical fertilizers and industrialization. However, as is mentioned by many authors, complete details of nutrition and remediation biochemistry, natural bioactive compounds and their activities are lacking. In this review, we present a critical overview about the past and current utilization of seaweeds as biofertilizers in agricultural context and point out possible future research directions.

Main composition of seaweeds

Plant growth promotion by seaweed extracts is often observed, but the mechanisms of stimulation of plant growth are not entirely known in many cases. Several studies have shown that the stimulating effects are due to a variety of major constituents within the seaweed extracts, such as diverse plant nutrients, phytohormones or betains (Karthikai Devi et al. 2009; Alam et al. 2014; Divya et al. 2015a; Michalak and Chojnacka 2015; Shahbazi et al. 2015; Al-Hameedawi 2016; Mirparsa et al. 2016). On the other hand, organic matter contained in seaweed biofertilizers is known to stimulate plant growth due to its nutrient content (Davari et al. 2012). It was also shown that the addition of different seaweeds as organic fertilizers in adequate quantities improved soil condition and growth parameters in field crops (Badar et al. 2015). Seaweeds improve the level of soil nutrients like N, P and K and other minerals necessary for plant growth (Imbamba 1972; Tay et al. 1987; Sethi 2012; Mirparsa et al. 2016). The assessment of mineral composition in various seaweeds belonging to different taxonomic groups like Chlorophyceae (*Chladophora glomerata, Ulva reticulata, Halimeda macroloba*) and Rhodophyceae (*Gelidiella acerosa, Hypenea musciformis*) revealed the content of diverse minerals such as F, Ca, Mg, Na, K, Fe, Mn, Zn, Cu, Ni, Co, Cr, Cd (Anantharaman et al. 2010; El-Said and El-Sikaily 2013; Tuhy et al. 2015). Furthermore, seaweeds are rich in proteins, fiber, fat, cellulose, hemicelluloses, lignin, vitamins, bromine, and iodine (Staden et al. 1994; MacArtain et al. 2007; Crouch and Van Staden 1993; Mohammadi et al. 2013; Shri Devi and Paul 2014; Heltan et al. 2015; Michalak et al. 2015; Mirparsa et al. 2016). Also, they contain a diverse range of organic compounds, at least seventeen amino acids (Qasmi 1991; Oohusa 1993; Yoo 2003; Shevchenko et al. 2007). A higher composition of minerals was found in marine seaweeds as compared to land vegetables (Manivannan et al. 2008; Kumar et al. 2009). Aslem and collaborators studied the mineral composition of a red algal extract (*Lithothatmnion calcareum*) and showed that the richness of minerals led to the use of the algal extract as animal and human food (Aslam et al. 2010) (Table 1).

A high diversity and quantity of polysaccharides are remarkable in diverse marine algae (Tables 1, 2). These carbohydrates constitute cell walls and some are storage compounds within the cell (Murata and Nakazoe 2001; El-deek and Mervat 2009; Cian et al. 2015; Heltan et al. 2015). In general, the different polysaccharides of seaweeds have a chemical structure according to the corresponding taxonomic classification of the algae (Chojnacka et al. 2012). Their high polysaccharide content implies a

Table 1 Mineral composition of three genera of algae (Aslam et al. 2010)

Mineral compounds (µg/g of extract)	Red alga (*Lithothamnion calcareum*)	Green alga (*Ulva lactuca*)	Brown alga (*Stoechospermum marginatum*)
Copper	4.89	0.38	8.64
Manganese	57.50	62.00	8.75
Zinc	15.80	1.01	19.92
Iron	915.00	0.37	858.50
Potassium	5.17	113.00	29.65
Magnesium	25.80	18.30	9.60
Cobalt	0.08	0.06	3.47
Chromium	0.82	nd*	16.60
Lead	0.15	nd*	0.40
Nickel	1.84	10.40	25.20
Cadmium	0.07	2.00	5.90
Sodium	4.15	185.00	39.11
Calcium	351.50	195.26	2053.40

* *nd* not detected

high level of soluble and insoluble fibers. The composition of chemical constituents changes with the seasons and according to different environmental conditions, such as temperature, salinity, light and nutrient availability (Reeta 1993; Marinho-Soriano et al. 2006; Karthikai Devi et al. 2009; Anantharaman et al. 2010; Hanan and Shimaa 2013). In the case of *Ulva*, it was shown that the amount of soluble, insoluble and dietary fiber of both species *Ulva pertusa* and *Ulva intestinalis* ranged from 25.0–39.6%, 21.8–33.5%, and 51.3–62.2% dry weight, respectively (Benjama and Masniyom 2011). A big difference in nutrient composition occurred between the cold and rainy winter and the warm summer season (Benjama and Masniyom 2011). High amounts of lipids, phenols, chlorophyll a and b and total cholorophyll were observed in different species of the genus *Ulva*, in particular *U. rigida* (Satpati and Pal 2011) and *U. lactuca* (Abd El-Baky et al. 2008) (see also Table 2). In additon to carbohydrates, a richness in pigments (chlorophyll, caroteinoids and phycobiliproteins) was also noticed (Chojnacka et al. 2012).

Seaweeds as biofertilizers

Historically, seaweeds had been used since ancient times directly or in composted form as a soil amendment to improve the productivity of crops in coastal regions and for reclamation of alkaline soils, where nutrient deficiencies are frequent (Zodape 2001; Craigie 2011). It is reported that in the second half of the first century, seaweed manure had widely been used (Metting et al. 1990). Seaweeds had been mixed with sand or soil or composted with straw, peat or other organic wastes (Craigie 2011).

The observed benefits of seaweeds as natural bioactive material and source of organic matter and fertilizer nutrients led to their wider application in the agricultural domain (Chapman 1980; Nelson and Van Staden 1984). It has been reported already more than 50 years ago that some brown seaweeds are used to fertilize soil, because they are rich in alginate which is decomposed as additional organic matter by soil microbes (Thivy 1964). Recently, the application of micronutrients from different seaweeds led to increased plant biomass, which is due to the presence of a high amount of zinc (Tuhy et al. 2015). A new generation of seaweed liquid fertilizer was developed as natural organic fertilizer rich in nutrients which promote, e.g., faster generation of seeds, increase crop yields and stimulate pathogen resistance of many crops (Sathya et al. 2010). Therefore, liquid fertilizers based on seaweed extracts, originally introduced by Milton in (1952), are now successfully used as fertilizers in horticulture and agriculture (Hurtado et al. 2009; Srijaya et al. 2010; Shahbazi et al. 2015; Ciepiela et al. 2016).

In the following, further examples for the application of seaweeds as biofertilizers are given. In some cases, marine macroalgae are not only used as biofertilizers but also as soil stabilizers (Abdel-Raouf et al. 2012; Bhardwaj et al. 2014; Arioli et al. 2015). Temple and Bomke (1988) reported that fresh kelp (*Macrocystis integrifolia*) has an excellent effect in fine-textured soil on crop growth and nutritional response. Fertilizers derived from seaweeds (*Fucus*, *Laminaria*¸ *Ascophyllum, Sargassum* etc.) are biodegradable, non-toxic, non-polluting and non-hazardous to human, farm animals and birds (Dhargalkar and Pereira 2005). Nedzarek and Rakusa-Suszczewski (2004) showed that a mixture of macroalgae released high quantities of

Table 2 Carbohydrates and amino acid composition of algae (Qasmi 1991; Castro-Gonzalez et al. 1996; Shevchenko et al. 2007; Cian et al. 2015)

	Red algae (Rhodophyceae)	Green algae (Chlorophyceae)	Brown algae (Phaeophyceae)
Polysaccharides	Agars, agaroids	Amylase	Alginates
	Carrageenans	Amylopectin	Cellulose
	Cellulose	Cellulose	Complex sulfated heteroglucans
	Complex mucilage's	Complex hemicelluloses	Fucose containing glycans
	Furcellaran	Glucomannans	Fucoidans
	Glycogen (floridean starch)	Mannans	Glucuronoxylofucans
	Mananas	Inulin	Laminarans
	Xylans, rhodymenan	Laminaran	Lichenan-like glucan
		Pectin	
		Sulfated mucilages (glucuronoxylorhamnans)	
		Xylans	
Amino acids			
Alanine	+++	+++	++
Glycine	+++	++	++
Valine	++	++	++
Leucine	++	++	+
Isoleucine	++	++	+
Serine	++	++	+
Threonine	+++	+++	+
Cystein	+	+	+
Methionine	+	+	+
Aspartate	+++	+++	++
Glutamate	+++	+++	++
Lysine	++	++	+
Arginine	+++	++	+
Phenylalanine	+	++	++
Tyrosine	+++	++	+
Proline	+++	+++	++
Histidine	+++	+	+

"+++" high quantity >60 mg/g total nitrogen; *"++" average quantity* 20–60 mg/g; *"+" low quantity* <20 mg/g

organic matter and different nutrients, especially very rich in NH_4^-, NO_3^- and NO_2^-, and phosphate. Furthermore, growth stimulation of okra was found after foliar application (Abbasi et al. 2010), stimulation of *Vigna mungo* by *Sargassum myriocystum* extracts (Kalaivanan and Venkatesalu 2012), induction of amylase acitivity in barley (Rayorath et al. 2008a), effect of *Ulva fasciata* on seed germination, growth parameters, pigment and carbohydrate content of wheat var. Charman (Shahbazi et al. 2015), enhancement of rice and maize growth by seaweed sap (Singh et al. 2015a, b, 2016), and improvement of root and shoot length with increased numbers of leaves. Very recently, overall growth stimulation of *Vigna* sp. by using different macroalgae as biofertilizers (Reddy et al. 2016; Vyomendra and Kumar 2016; Gopalakrishnan and Binumol 2016) was found. The treatment with a commercial extract from *Ascophyllum nodosom* affected the regulation of phytohormone biosynthesis and accumulation in *Arabidopsis* (Wally et al. 2012). Aslo, the induction of cytokinin-like activity in *Arabidopis thaliana* due to the application of extracts from brown macroalga *Aqcophylum nodosum* (Khan et al. 2011) was reported. Many more different seaweeds were studied as sources of biofertilizers (Reitz and Trumble 1996; Kavipriya et al. 2011; Lola-luz et al. 2013; Pramanick et al. 2013; Zamani et al. 2013; Jayasinghe et al. 2016).

Phytohormones content of seaweeds

Seaweeds and their extracts have been used for centuries in agriculture to improve plant growth and stress tolerance. It was concluded that their phytohormonal compounds may modulate innate pathways for phytohormone biosynthesis in plants (Wally et al. 2012; Divya et al. 2015ab). Seaweed extracts are known to promote and enhance vegetables, fruits and various other crops because of their richness in growth regulators such as auxins (IAA and IBA), gibberellins and cytokinin, in addition to osmoprotectant betains and micronutrients (Ghoul et al. 1995; Renuka Bai et al. 2007; Divya et al. 2015a, b; Mathur et al. 2015; Pacholczak et al. 2016b).

Liquid fertilizers based on different seaweed extracts are useful for achieving higher agricultural production, because the extract contains growth-promoting hormones, like cytokinins or gibberellins—in addition to trace elements, vitamins, amino acids and antibiotics (Craigie et al. 2007; Sathya et al. 2010; Wally et al. 2012; Divya et al. 2015a; Mirparsa et al. 2016). Also Zodape et al. (2010) concluded in their studies that the effect of seaweed extract is due to plant growth regulators such as cytokinins. *Ascophyllum nodosum* extracts have been used as biostimulant to promote growth and productivity in a number of agricultural production systems (Rayorath et al. 2008b). It is well established that gibberellic acid (GA_3) is responsible for the stimulation of seed germination of different plants (Brink and Cooper 1947). This substance induces hydrolytic enzymes in the aleurone layer surrounding the endosperm (Cooper and Brink 1945; Scott et al. 1998). Jennings (1968) confirmed that green and brown algae are very rich in gibberellic acid, which is involved in seed germination. In fact, gibberellic acid acts as a signal in the germinating process of seeds by activating amylase genes in aleurone cells (Sun and Gubler 2004). Rayorath et al. (2008a) reported that the organic components of *Ascopyllum nodosum* induce gibberellic acid (GA_3)-independent amylase activity in barley. The analyzed *Ascopyllum nodosum* extracts revealed high concentrations of cytokinins (CKs), particularly trans-zeatin-type CK, and abscisic acid (ABA) (Wally et al. 2012). Since many phytohormones stimulate root development, the reported increased plant growth and vigor after application of seaweeds may be through increased efficiency of nutrients and water uptake (Russo and Berlyn 1990). Thus, seaweed cultivation and its utilization is an economically successful approach in agricultural production (Sridhar and Rengasmay 2011; Gireesh et al. 2011; Michalak et al. 2016a).

Seaweed extracts stimulate various aspects of plant development (Pramanick et al. 2013; Ismail and El-Shafay 2015). Drought generates oxidative stress and increased cell membrane leakage in stressed wheat plants resulting in an increased need for antioxidant (enzymatic and non-enzymatic) activities. Physiological effects of the application of seaweeds during drought on *Triticum aestivum* were evaluated in the presence and absence of different seaweed extracts (*Sargassum latifolium*, *Ulva lactuca* and their mixture) (Kasim et al. 2015). A pretreatment with seaweed extract led to a stimulation of antioxidant activities and thus to the alleviation of the damaging effects of drought on the vegetative stage of *Triticum aestivum*. *Sargassum* or *Ulva* extracts antagonize the oxidative damaging effects of drought not only directly through activating the antioxidative system (catalase, peroxidase and ascorbate), but also through providing phytohormones and micro-nutrients essential for wheat growth (Kasim et al. 2015).

When seeds of *Phaseolus aureus* were treated with extracts from the red marine algae *Asparagopsis taxiformis*, a promotion of root and internode length of shoot, as well as on petiole and leaf surface area, were reported by Renuka Bai et al. (2007). These authors suggested that plant growth stimulation by extracts of these red algae is due to high quantities of cytokinins. Many studies concerning the composition of liquid seaweed fertilizers demonstrated that they are rich in plant growth regulators such as the auxin indole acetic acid (IAA), kinetin, zeatin, gibberellin, cytokinins, abscisic acid, ethylene, in addition to betaines and polyamines (Kingman and Moore 1982; Nelson and Van Staden 1985; Crouch and Van Staden 1993; Zahid 1999; Tarakhovskaya et al. 2007; Zhang and Ervin 2008; Zodape et al. 2008). Savasangari et al. (2011) concluded that the growth enhancement of the cluster plant *Cyamopsis tetragonolaba* (L.) Taub. is due to the presence of cytokinin and magnesium, which are considered as an essential growth-promoting hormone and chief constituent in chlorophyll biosynthesis, respectively. The same explanation about the richness in phytohormones (auxin and cytokinins) in seaweeds liquid fertilizers was reported by Sridhar and Rengasamy (2010b). Similarly, Stirk et al. (2014) showed that *Ecklonia maxima* extracts present a high potential for application in agriculture due to its high content of several plant hormones such as abscisic acid, gibberelins, brassinosteroids and castasterone. It was also observed that the enhancement of germination, growth and productivity of brinjal by using *Sargassum wightii* liquid fertilizer is related to the presence of high levels of several phytohormones in this extract (Divya et al. 2015b).

Liquid seaweed extracts also have been successfully applied to restore plant growth at hardness conditions such as high pH and temperature conditions (Briceño-Domínguez et al. 2014; Bradáčová et al. 2016) as well as at very low pH and water content (Arthur et al. 2013). It was commonly reported in these studies that the main effect of seaweeds extracts against environmental stresses is due to cytokinins as well as gibberellic and abscisic acid, which help to support plant growth under nutrient-stressed conditions and to recover plants after damage (Reitz and Trumble 1996; El Shoubaky and Salem 2016).

Biostimulant effects

Liquid extracts of brown and green algae are being sold as biostimulants or biofertilizers in different brands (Kavipriya et al. 2011; Sharma et al. 2012; Divya et al. 2015a; Shahbazi et al. 2015; Gopalakrishnan and Binumol 2016; Mirparsa et al. 2016). Algae, particularly seaweeds, are used as biofertilizers, resulting in less runoff of nitrogen and phosphorus fertilizers after application of livestock manure (Abdel-Raouf et al. 2012), which could be due to stimulated nutrient uptake in crop plants. Many results were obtained with seaweed extracts such as improvements of seed germination and root development, frost resistance, nutrients uptake, increased resistance to pathogenic fungi, reduced incidence of insect attack and salt stress (Abetz 1980; Nabti et al. 2010; Battacharyya et al. 2015).

Adequate amounts of potassium, nitrogen, micronutrients, humic acid, polysaccharides laminarin, alginates and carrageenans, in addition to growth-promoting phytohormones, present in seaweeds, makes them excellent biofertilizers (Sathya et al. 2010; du Jardin 2015). The application of seaweed saps in green gram (Pramanick et al. 2013) resulted in growth and yield increases. An increase in chlorophyll content was achieved in different crops (tomato, dwarf French bean, wheat, barley and maize) treated with *Ascophyllim nodosum* alkaline extracts. The authors explained this increase in chlorophyll content by the presence of betaines in the seaweed extracts (Blunden et al. 1997). In addition, when *Ecklonia maxima* extracts was applied as a foliar spray or a root drench for promotion of growth and development of marigold *Tagetes patula*, significative enhancement of both vegetative and reproductive growth could be demonstrated (Staden et al. 1994). A seaweed-based liquid fertilizer of *Rosenvingea intricata* was used successfully to increase growth and pigment concentration in *Cyamopsis tetrogonolaba* and *Abelmoschus esculentus* (Thirumaran et al. 2009a, b). A growth stimulation of egg plants (*Solanum melongena* L) by *Ascophyllum nodosum* extracts (Bozorgi 2012) and enhancement of seed germination of fenugreek by seaweed extracts were reported (Sabale and Pise 2010). Sridhar and Rengasamy (2010a) successfully applied *Sargassum wightii* (brown seaweed) mixed with *Ulva lactuca* (green marine alga) to increase peanut growth (*Arachis hypogaea*). Additonally, a combination of *Azotobacter chrococum* and *Bacillus megaterium var. phosphaticum* mixed with marine algal extracts stimulated growth of bitter orange seedlings (Ismail et al. 2011). Furthermore, *Azospirillum brasilense* strain NH combined with *Ulva lactuca* extracts was able to enhance the development of durum wheat under saline and non-saline conditions (Nabti et al. 2010). Moreover, a commercial algal extract of *Ascophyllum nodosum* was proven as potential bioregulator which improved the size and quality of fruits and reduced variations in fruit yield during different seasons in apple trees (Spinelli et al. 2009). Recent studies also showed that some algal extracts exert potent biostimulation of vegetative growth and yield of fig trees (*Ficus carica* L.) (Al-Hameedawi 2016).

Application of a variety of liquid seaweed fertilizers were repeatedly reported to be able to decrease application doses of nitrogen, phosphorus and potassium as well as to stimulate plant growth and yields of many crop plants. There are at least 59 species of seaweeds that were shown to stimulate germination, growth and yields of some horticultural and legume plants (Sunarpi et al. 2010). Sunarpi obtained satisfactory results when using a mixture of 10 seaweeds to improve growth and production of rice. Seaweeds are much better than chemical fertilizer to improve soil fertility, because they contain a high quantity of organic matter which additionally improves available water and mineral uptake in the upper soil level (Ramarajan et al. 2012). Seaweed liquid fertilizer of *Sargassum wightii*, *Ulva lactuca* and *Enteromorpha intestinalis* enhanced seed germination, growth, and biochemical features of legume plant *Glycine max* (Mathur et al. 2015). These extracts were shown to induce seed germination and growth parameters more strongly than chemical fertilizers (Ramarajan et al. 2012; Godlewska et al. 2016). Finally, Partani (2013) showed an extraordinary effect of seaweed extract on corn growth and performance.

Osmoprotective effects

Soil salinity constitutes a major obstacle for agriculture in arid and semiarid regions. 20% of the world's cultivated area and almost half of the world's irrigated soils are severely affected by the lack of water and increased salinity and are thus lost for agriculture (Nabti et al. 2010).

Salt stress leads to yield decreases by inhibition of different plant growth parameters such as seed germination (Sharma et al. 2004), photosynthesis and transpiration rates (Sharma et al. 2005), as well as biosynthesis of phytohormones and plant growth regulators (Sarin and Narayanan 1968). High osmolarity can also affect plant growth by inhibiting plant growth-promoting rhizobacteria (PGPR), because rhizospheric microorganisms play an important role in soil processes that determine and modulate plant productivity (Tilak et al. 2005). Hence, in order to overcome salinity problem, osmotolerant PGPR were applied to develop tolerance toward salt stress through strategies of osmoregulatory mechansims (Hartmann et al. 1991; Galinski and Trüper 1994; Miller and Wood 1996). The direct application of osmolytes turned out to be not sufficient or not of practical relevance in this respect. However, due to their high contents and diversity of osmoprotective molecules, seaweeds can be used as solution for reclamation of saline soils and to overcome osmotic stress affecting plant growth.

Seaweeds living in marine waters are exposed to a continuous salt stress because of the high salinity of the marine environment. Under hyperosmotic conditions, organic compounds such as proline, betaines, as well as polyamins and sorbitol are synthesized and accumulated at high concentrations which are intimately involved in the osmotic stress adjustment in macroalgae (Brown and Hellebust 1978; Karsten et al. 1991; Karamanos 1995; Van Alstyne et al. 2003; El Shoubaky and Salem 2016; Ghoul et al. 1995; Kiene et al. 1998; Van Bergeijk et al. 2002). It also has been revealed that many marine algae produce 3-dimethylsulfoniopropionate (DMSP), a potent osmoprotective compound; its degradation product dimethylsulfide plays a central role in the biogeochemical S-cycle (Pichereau et al. 1998; Summers et al. 1998). Tertiary sulphonium (DMSP) and quaternary ammonium (like glycine betaine) compounds were reported as efficient osmoprotectants for agricultural bacteria and plants as well (Reed 1983; Rhodes and Hanson 1993; Fang et al. 1996; Asma et al. 2006; Rezaei et al. 2012; Manaf 2016).

In order to make best use of particularly osmoprotective substances of seaweeds, many experiments have been performed in order to restore plant growth under saline conditions by using different algal extracts. It could be shown that, e.g., *U. lactuca* was able to restore the leaf area and pigment content in soy bean under saline stress conditions (Ramarajan et al. 2013). Furthermore, maize growth under cold stress has been restored after addition of seaweeds extract (Bradáčová et al. 2016). It could also be demonstrated that the addition of extracts of *Sargassum vulgare* improved the germination behavior of two bean cultivars (*Phaseolus* vulgaris) under salt stress (Latique et al. 2014). Other examples for successful use of seaweed extracts are: application of seaweed extracts of *Ascophyllum nodosum* to *Amaranthus tricolor* enhancing flowering and its chemical constituents under high salinity conditions (Abdel Aziz et al. 2011), the utilization of seaweed extracts to stimulate germination and growth of tomato (*Lycopersicon* spp.) seedlings under salt stress (Alalwani et al. 2012), and the application of liquid extracts of *U. lactuca* at high salinity conditions to restore growth of durum wheat (*Triticum durum* var waha) (Nabti et al. 2007, 2010). Finally, *Durvillaea plantarum* application could substantially improve growth and yield of bean plants under water suppression (Bastos et al. 2016).

Biocontrol activities

Seaweeds are generally known as a rich source of a high diversity of natural molecules. Seaweeds can produce high amounts of secondary metabolites, including terpenes, lipid-, steroid-, and aromatic-like compounds, acetogenins, amino acid derived products, phlorotannin and other polymeric substances (Ballantine et al. 1987; Febles et al. 1995; Ozdemir et al. 2004; Zbakh et al. 2012; Thinakaran and Sivakumar 2013; Shri Devi and Paul 2014). Marine algae produce also bioactive metabolites in response to microbial activities (Taskin et al. 2007; Younes et al. 2009; Alam et al. 2014; Michalak et al. 2015; Watee et al. 2015; Pérez et al. 2016; Sahnouni et al. 2016), insects (Cetin et al. 2010; Asha et al. 2012; Holden and Ross 2012; Abbassy et al. 2014), and viruses (Serkedjieva 2000; Mendes et al. 2010). It was revealed, that red macroalgae show the best production of halogenated compounds (Pereira and Teixeira 1999). However, studies concerning products of green algae utilized against microbial activities are relatively scarce.

Numerous studies have been performed about antimicrobial activities of seaweed extracts, such as antifungal activities. It has been demonstrated that the strong antimicrobial activities of many seaweed algae is due to the presence of terpenes (Paulert et al. 2009; Peres et al. 2012). Activities against fungal phytopathogens were also demonstrated for different algal extracts (Coşoveanu et al. 2010; Thinakaran and Sivakumar 2013). In this way, six organic extracts of five seaweeds belonging to *Phaeophyta* (*Sargassum vulgare, Cystoseira barbata, Dictyopteris membranacea, Dictyota dichotoma* and *Colpomenia sinuosa*) were tested for their antagonistic effect on eight fungal species (*Alternaria alternata*, *Cladosporium cladosporioides*, *Fusarium oxysporum*, *Epicoccum nigrum*, *Aspergillus niger*, *Aspergillus ochraceus, Aspergillus flavus, and Penicillium citrinum*). These experiments showed that a variety of seaweeds from different sites had pronounced antifungal activities (Khallil et al. 2015).

The capacity to utilize seaweeds as biocides was also revealed after using extracts of green marine algae of *Ulva fasciata* and *Ulva lactuca* against nymph and adults of cotton pest (*Dysdercus cingulatus*) (Asha et al. 2012). Many brown seaweed species were shown to be effective in controlling plant diseases (Peres et al. 2012). Extracts of different marine algal species like *Sargasssum tenerrimum*, *Padina tetrastromatica* and *Melanothamnus afaqhusainii* were used for nematicidal activity tests against the root-knot nematode *Meloidogyne javanica* (egg hatching and larval mortality), which showed maximum egg hatching (96%) and larval mortality (99%) (Khan et al. 2015).

Some seaweeds have only low antifungal activities. However, when combined with some plant growth promoting bacteria, they show a significantly higher activity. This is, e.g., the case with some seaweed species when associated with *Bradyrhizobium japonicum* and *Paecilomyces lilacinus* protecting roots of sunflower (Ara et al.

1996). Thus, seaweed application in biological control studies is currently a much advanced area of biotechnological research (Abdel-Raouf et al. 2012). A very recent study revealed that polysaccharides, fatty acids, phlorotannins, pigments, lectins, alkaloids, terpenoids and halogenated compounds isolated from green, brown and red algae have potent antimicrobial activities (Pérez et al. 2016). A mixture of brown, red and green seaweeds was successfully used, e.g., to control root-infecting fungi on okra seedlings, demonstrating a highly effective inhibition of plant pathogenic fungi by seaweeds (Sultana et al. 2005). Foliar sprays of seaweed extracts were able to inhibit fruit rot and to increase yields of strawberry, as well as to efficiently reduce the gray mold development (Washington et al. 1999).

Seaweed extracts are readily commercially available and their impact on yield and health of different crops is very significant (Norrie et al. 2002). The addition of *Ascophyllum nodosum* extracts to carrot plants inoculated with the fungal pathogens *Alternaria radicina* and *Botrytis cinerea* resulted in a strong inhibition of disease phenotype. In parallel, the activity of certain defense-related enzymes, such as peroxidase, polyphenoloxidase, phenylalanine ammonia lyase, chitinase, and β-1,3-glucanase was significantly increased after seaweed extracts application. These latter efficiently enhanced disease resistance in carrot probably through defense-related genes and proteins induction (Jayaraj et al. 2008). Studies about biocontrol activities of seaweed extracts and their effects on disease control require more detailed assessments in several respects in future. Detailed studies on the induction of systemic resistance in addition to direct inhibition of pathogen development need to be performed. For example, in biocontrol active Bacilli it has been shown that antibiotically active secondary metabolites not only inhibit phytopathogens but are also able to trigger plant resistance mechanisms (Chowdhury et al. 2015).

Recovery of polluted soils

Various industries, such as mining, leaching, surface finishing industry, energy and fuel production, fertilizer and pesticide industry, metallurgy, iron and steel factories, electroplating, electrolysis, electro-osmosis, leather working, photography and electrical appliance manufacturing industries, discharge heavy metals into the environment, which leads to locally dramatic ecosystem pollution (soil, surface water, ground water) (Davis et al. 2000; Nahmani et al. 2003; Tamilselvan et al. 2013). Heavy metals are major pollutants in marine ecosystems, lakes and groundwaters, originating from industrial effluents even if they are treated for contaminant reduction. Biosorption is an inexpensive and reliable method to remove, for example, cadmium and lead ions from aqueous solution using dry seaweed biomass as adsorbents (Vinoj Kumar and Kaladharan 2006). Therefore, seaweeds offer great opportunities for biosorption because their macroscopic structure provides a convenient basis for production of biosorbent particles suitable for applications as sorption material (Vieira and Volesky 2000; Michalak et al. 2016b).

Novel methods were recently used to characterize and determine the detailed mechanisms, how seaweeds are capable to remove heavy metals; “green synthesis” of iron oxide (Fe_3O_4) nanoparticles together with brown seaweeds contributed to successful lead bioremediation (El-Kassas et al. 2016). Furthermore, heavy metal adsorption studies using *Kappaphycus sp.* from aqueous solutions showed clearly that this red seaweed can be used as a potentially low-cost biosorbent for removal of heavy metal ions from aqueous solutions (Rahman and Sathasivam 2015). Some seaweeds, such as *Gracilaria corticata varcartecala* and *Grateloupia lithophila*, were also shown to efficiently remove heavy metals (Cr(VI), Cr(III), Hg(II), Pb(II), Co and Cd (II)) by a biosorption process (Tamilselvan et al. 2013; Duraipandian et al. 2016). A mixture of green, red and brown algae was prepared to eliminate chromium pollution by biosorption. Seaweed material analysis revealed that chromium was adsorbed by two functional groups of polysaccharides at seaweed surface (Abirami et al. 2013). Other species of seaweeds (*Kappaphycus alvarezii* and *Eucheuma ddenticulatum*) were also utilized successfully for Cadmium (II) biosorption (Figueira et al. 2000; Kang et al. 2012). In addition, a red algal extract named “Acadian” was successfully applied to remove lead pollution (Abdalla and El-Khoshiban 2012).

Some researchers found that DDT [1,1,1-trichloro-2,2-bis (p-chlorophenyl) ethane], which is a major environmental pollutant, is progressively biodegraded after the application of seaweed extracts. Probably, it is due to the high level of dissolved organic carbon present in soil amended with seaweed, which significantly retarded DDT biodegradation (Kantachote et al. 2014; Michalak et al. 2016b). It is known that seaweed amendments modify soil conditions including dissolved organic carbon (DOC) of soils, ionic strength, redox potential and pH. These significant physicochemical changes influence the increase in DDT bioavailability and transformation in seaweed-amended soils compared to the unamended soil (Sudharsan et al. 2013). However, it remains an open question, whether a considerable part of the added DDT, which was not detectable as original compound or metabolites, is already completely mineralized to CO_2 or is still tightly bound to soil components as so-called bound residue. More detailed studies using radiolabeled DDT may allow to answer these questions. Investigating the bioremediation efficiency of organic pollutions from shrimp hatcheries using the green alga *Ulva reticulata,* the authors found that this green macroalga could successfully be used as effective biofilter for nutrient removal from shrimp hatchery effluents (Rabiei et al. 2014).

Possible limitations of seaweed applications

Until now, no severe general limitations of the application of seaweeds as biofertilizer are known. However, due to the high salt content of seaweeds (Na^+, Cl^-, K^+, and Ca^{2+}, etc.) the long-term or excessive application of seaweeds may contribute to the development of saline soils and may increase the salt content in plant tissues. Such problems could be avoided by including intermitting pauses of seaweed application and allowing rain-rinsing periods to decrease the salt content of soils (Angus and Dargie 2002; Ruperez 2002; MacArtain et al. 2007). Furthermore, if enriched subfractions or purified preparations of seaweed extracts are used instead of crude seaweed extracts, this problem can be minimized. Since seaweeds are known as potent accumulators of heavy metals and other contaminants in marine environments (Vasquez and Guerra 1996; Fourest and Volesky 1997; Dadolahi-Sohrab et al. 2011; Karthicka et al. 2012; Sudharsan et al. 2012), the application of seaweeds collected from contaminated sites in agricultural soils would increase the content of these contaminants in both soils and plants (Wosnitza and Barrantes 2003). Therefore, the contaminant levels of seaweeds need to be examined routinely before application and contaminated seaweeds should not be applied. Furthermore, the anaerobic decomposition of sulfated organic compounds of seaweeds was reported to lead to the production of sulfides. The microbial oxidation of these sulfides to sulfate increases the concentrations of protons in soils and hence may create soil acidification (Brady and Weil 2008).

The typical organic compounds of seaweeds, like carrageenans, laminarins and ulvans, are different from the major polymeric carbon compounds of terrestrial plant, such as cellulose, hemicellulose and lignin, and expose the soil microbial community to novel and possibly less readily degradable compounds (Jiménez-Escrig and Sánchez-Muniz 2000; Jaulneau et al. 2010). In addition, alginate, a brown seaweed molecule that acts as a water-holding compound, may affect water distribution within the soil (Fourest and Volesky 1997; Jiménez-Escrig and Sánchez-Muniz 2000). In this context, a thorough examination of the effect of long-term or excessive application of seaweeds on the microbial community of soils using DNA-based deep sequencing high throughput approaches should be performed to follow up consequences for the whole microbial ecosystem. Furthermore, since seaweeds are colonized by complex microbial communities, which themselves produce, e.g., antimicrobial compounds (Egan et al. 2013; Singh et al. 2015), it would be important to examine, whether or to which extent these seaweed-associated microbes establish themselves in the soil. This seaweed-influenced soil microbial community may finally even exhibit improved functions of nutrient turnover in soils, which could be the basis to benefit plant development and soil health.

Soil conditioner in organic farming

Seaweed extracts have gained significant attractiveness worldwide as liquid fertilizers in recent years (Khan et al. 2009; Kumar and Sahoo 2011; Shah et al. 2013), although their successful application as agricultural biofertilizer goes back to its original application as soil conditioner for horticultural crops (Aitken and Senn 1964). Nowadays, the forms of application of seaweeds as fertilizer include foliar spray, granules, powder and manure (Kumari et al. 2011, 2013; Gharakhani et al. 2016). Recent trends of organic farming and increased demands of organic foods have opened a wide window of opportunities for seaweed reinvestigation for its potential applications as a soil conditioner, biofertilizer and biostimulant (Khan et al. 2009) (Table 3). Seaweeds are known to contain several organic contents, particularly carbohydrates, proteins and fatty acids which are helpful in retaining moisture and nutrients in the upper layers of soil. Numerous studies reported the beneficial impacts of seaweed-based fertilizer on soil and crop growth by increasing water-holding

Table 3 Commercial seaweed products used in agriculture (Khan et al. 2009)

Product name	Seaweed name	Application
Acadian	*Ascophyllum nodosum Ascophyllum*	Plant growth stimulant
Agri-Gro Ultra	*Nodosum Macrocystis pyrifera*	Plant growth stimulant
AgroKelp	*Ascophyllum nodosum*	Plant growth stimulant
Bio-Genesis™ High Tide™	Unspecified	Plant growth stimulant
Fartum	*Ecklonia maxima*	Biofertilizer
Kelpak	*Durvillea antarctica* unspecified	Plant growth stimulant
Profert	Unspecified	Plant biostimulant
Sea Winner	*Durvillea potatorum*	Plant biostimulant
Seanure		Plant growth stimulant
Seasol		Plant growth stimulant

capacity, stimulation of microorganisms' activity and improving soil texture. Seaweed fertilizers are helping soil to create an environment suitable for root growth by increasing microbial diversity and improving biological activities like respiration and nitrogen mobilization and mineralization of mineral nutrients (Haslam and Hopkins 1996; Selvaraj et al. 2004; Battacharyya et al. 2015).

Conclusion

In this review, main beneficial roles of the exploitation of seaweeds as biostimulants in agriculture are emphasized. Trends toward organic farming and increased demands of organic foods have increased the demand for biofertilization and created also new opportunities to reinvestigate the potentials and limitations of seaweed applications as a soil conditioner and biofertilizer. It is well established that marine algae are very rich in different secondary metabolite compounds, which make them resistant to different climatic and environmental stress conditions and which could also improve the fertility of agricultural soils and foster plant growth. Due to the diversity of these compounds, seaweeds or seaweed-derived products are also being utilized successfully in many different applications in industry, medicine, food and agriculture. However, many of these applications could still be improved and the fields of applications diversified. On the other hand, more basic microbiological and soil ecological investigations about the influence of seaweed applications on the soil microbial community and its functions and processes are necessary to find out ways to more effectively apply this type of biofertilizer. This is certainly one of the tasks for future research work.

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