J Plant Growth Regul (2009) 28:386–399
DOI 10.1007/s00344-009-9103-x

REVIEWS

Seaweed Extracts as Biostimulants of Plant Growth and Development

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Received: 24 October 2008 / Accepted: 18 March 2009 / Published online: 8 May 2009

Abstract Marine algal seaweed species are often regarded as an underutilized bioresource, many have been used as a source of food, industrial raw materials, and in therapeutic and botanical applications for centuries. Moreover, seaweed and seaweed-derived products have been widely used as amendments in crop production systems due to the presence of a number of plant growth-stimulating compounds. However, the biostimulatory potential of many of these products has not been fully exploited due to the lack of scientific data on growth factors present in seaweeds and their mode of action in affecting plant growth. This article provides a comprehensive review of the effect of various seaweed species and seaweed products on plant growth and development with an emphasis on the use of this renewable bioresource in sustainable agricultural systems.

Keywords Seaweed · Biostimulants · Plant growth · Plant development · Biotic and abiotic stresses · Plant-microbe interactions

Introduction

Seaweeds form an integral part of marine coastal ecosystems. They include the macroscopic, multicellular marine algae that commonly inhabit the coastal regions of the world's oceans where suitable substrata exist. It has been estimated that there are about 9,000 species of macroalgae broadly classified into three main groups based on their pigmentation (for example, Phaeophyta, Rhodophyta, and Chlorophyta; or the brown, red, and green algae, respectively). Brown seaweeds are the second most abundant group comprising about 2,000 species which reach their maximum biomass levels on the rocky shores of the temperate zones. They are the type most commonly used in agriculture (Blunden and Gordon 1986) and, among them, *Ascophyllum nodosum* (L.) Le Jolis is the most researched (Ugarte and others 2006). Besides *A. nodosum*, other brown algae such as *Fucus* spp., *Laminaria* spp., *Sargassum* spp., and *Turbinaria* spp. are used as biofertilizers in agriculture (Hong and others 2007).

The benefits of seaweeds as sources of organic matter and fertilizer nutrients have led to their use as soil conditioners for centuries (Blunden and Gordon 1986; Metting and others 1988; Temple and Bomke 1988). Some 15 million metric tonnes of seaweed products are produced annually (FAO 2006), a considerable portion of which is

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Table 1 Commercial seaweed products used in the agriculture and horticulture industries

Product name	Seaweed name	Company	Application
Acadian®	*Ascophyllum nodosum*	Acadian Agritech	Plant growth stimulant
Acid Buf	*Lithothamnium calcareum*	Chance & Hunt Limited	Animal feed
Agri-Gro Ultra	*Ascophyllum nodosum*	Agri Gro Marketing Inc.	Plant growth stimulant
AgroKelp	*Macrocystis pyrifera*	Algas y Bioderivados Marinos, S.A. de C.V.	Plant growth stimulant
Alg-A-Mic	*Ascophyllum nodosum*	BioBizz Worldwide N.V.	Plant growth stimulant
Bio-Genesis™ High Tide™	*Ascophyllum nodosum*	Green Air Products, Inc.	Plant growth stimulant
Biovita	*Ascophyllum nodosum*	PI Industries Ltd	Plant growth stimulant
Emerald RMA	Red marine algae	Dolphin Sea Vegetable Company	Health product
Espoma	*Ascophyllum nodosum*	The Espoma Company	Plant growth stimulant
Fartum®	Unspecified	Inversiones Patagonia S.A.	Biofertilizer
Guarantee®	*Ascophyllum nodosum*	MaineStream Organics	Plant growth stimulant
Kelp Meal	*Ascophyllum nodosum*	Acadian Seaplants Ltd	Plant growth stimulant
Kelpak	*Ecklonia maxima*	BASF	Plant growth stimulant
Kelpro	*Ascophyllum nodosum*	Tecniprocesos Biologicos, S.A. de C.V.	Plant growth stimulant
Kelprosoil	*Ascophyllum nodosum*	Productos del Pacifico, S.A. deC.V.	Plant growth stimulant
Maxicrop	*Ascophyllum nodosum*	Maxicrop USA, Inc.	Plant growth stimulant
Nitrozime	*Ascophyllum nodosum*	Hydrodynamics International Inc.	Plant growth stimulant
Profert®	*Durvillea antarctica*	BASF	Plant biostimulant
Sea Winner	Unspecified	China Ocean University Product Development Co., Ltd	Plant biostimulant
Seanure	Unspecified	Farmura Ltd.	Plant growth stimulant
Seasol®	*Durvillea potatorum*	Seasol International Pty Ltd	Plant growth stimulant
Soluble Seaweed Extract	*Ascophyllum nodosum*	Technaflora Plant Products, LTD	Plant growth stimulant
Stimplex®	*Ascophyllum nodosum*	Acadian Agritech	Plant growth stimulant
Synergy	*Ascophyllum nodosum*	Green Air Products, Inc.	Plant growth stimulant
Tasco®	*Ascophyllum nodosum*	Acadian Agritech	Animal feed

used for nutrient supplements and as biostimulants or biofertilizers to increase plant growth and yield. A number of commercial seaweed extract products are available for use in agriculture and horticulture (Table 1).

Numerous studies have revealed a wide range of beneficial effects of seaweed extract applications on plants, such as early seed germination and establishment, improved crop performance and yield, elevated resistance to biotic and abiotic stress, and enhanced postharvest shelf-life of perishable products (Beckett and van Staden 1989; Hankins and Hockey 1990; Blunden 1991; Norrie and Keathley 2006) (Fig. 1).

Modes of Action of Growth Stimulatory Factors in Seaweed Extracts

Seaweed products exhibit growth-stimulating activities, and the use of seaweed formulations as biostimulants in crop production is well established. Biostimulants are defined as "materials, other than fertilizers, that promote plant growth when applied in small quantities" and are also referred to as "metabolic enhancers" (Zhang and Schmidt 1997). Seaweed components such as macro- and microelement nutrients, amino acids, vitamins, cytokinins, auxins, and abscisic acid (ABA)-like growth substances affect cellular metabolism in treated plants leading to enhanced growth and crop yield (Crouch and others 1992; Crouch and van Staden 1993a; Reitz and Trumble 1996; Durand and others 2003; Stirk and others 2003; Ördög and others 2004). Seaweed extracts are bioactive at low concentrations (diluted as 1:1000 or more) (Crouch and van Staden 1993a). Although many of the various chemical components of seaweed extracts and their modes of action remain unknown, it is plausible that these components exhibit synergistic activity (Fornes and others 2002; Vernieri and others 2005).

Chemical Components of Seaweed that Affect Plant Growth

Carbohydrates, Minerals, and Trace Elements

Seaweeds, particularly the red and brown algae, are a source of unusual and complex polysaccharides not present

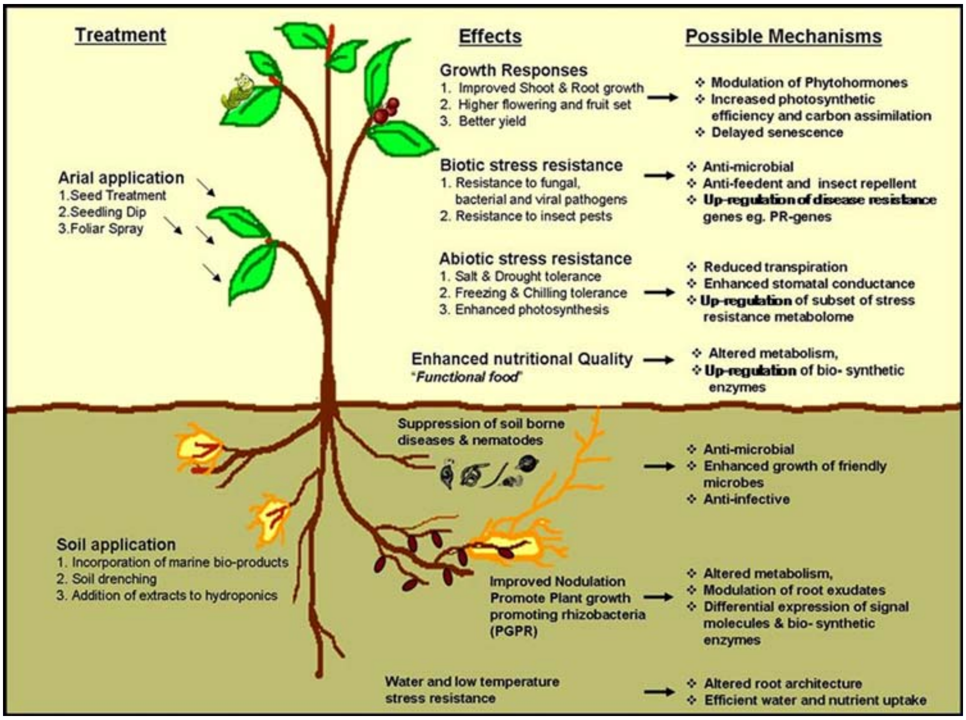

Fig. 1 Schematic representation of physiological effects elicited by seaweed extracts and possible mechanism(s) of bioactivity

in land plants (Siegel and Siegel 1973; Painter 1983; Blunden and Gordon 1986; Craigie 1990; Chizhov and others 1998; Duarte and others 2001) (Table 2). For example, the brown seaweeds *Ascophyllum nodosum*, *Fucus vesiculosus*, and *Saccharina longicruris* contain the polysaccharides laminaran, fucoidan, and alginate (Painter 1983; Lane and others 2006). Laminaran is a (1,3)-β-D-glucan with β-(1,6) branching (Nelson and Lewis 1973; Zvyagintseva and others 1999). Although the precise structures of fucoidans are not fully established, fucoidan from *A. nodosum* consists primarily of sulfated fucose linked in α-(1,3) and α-(1,4) configuration (Chevolot and others 1999; Chevolot and others 2001; Daniel and others 2001; Marais and Joseleau 2001). Alginate is a block copolymer structure composed of D-mannuronic and L-guluronic acids with β-(1,4)-glycosidic linkages. The properties of the various alginates differ depending on the position of each monomeric unit in the chain, the average molecular weight of the polymer, and the nature of its associated counter ions. The monomers may alternate in some regions of the alginate (heteropolymeric), or they may occur in contiguous groups to produce homopolymeric sections with either monomer within the alginate molecule (Painter 1983; Rioux and others 2007). Of these three polysaccharides, laminaran and fucoidan exhibit a wide range of biological activities (Rioux and others 2007). Direct effects of fucoidan on plants have not yet been reported but sulfated fucoidans from brown algae have evinced biological activities in mammalian systems (McClure and others 1992; Angstwurm and others 1995; Mauray and others 1995). Laminarin has been shown to stimulate natural defense responses in plants and is involved in the induction of genes encoding various pathogenesis–related (PR) proteins with antimicrobial properties (Fritig and others 1998; van Loon and van Strien 1999).

Growth Hormones

The concentration of mineral nutrient elements present in commercial seaweed concentrates (SWCs) alone cannot account for the growth responses elicited by seaweed extracts (Blunden 1972, 1991). Beneficial effects observed in various plant growth bioassays have led to speculation that SWCs contain plant growth-regulatory substances (Williams and others 1981; Tay and others 1985; Mooney and van Staden 1986). Furthermore, the wide range of growth responses induced by seaweed extracts implies the presence of more than one group of plant growth-promoting substances/hormones (Tay and others 1985; Crouch and van Staden 1993a).

Cytokinins have been detected in fresh seaweeds (Hussein and Boney 1969) and seaweed extracts (Brain and others 1973). The cytokinins present in seaweed formulations include *trans*-zeatin, *trans*-zeatin riboside, and dihydro derivatives of these two forms (Stirk and van Staden 1997). Liquid chromatography/mass spectroscopy (LC/MS) analysis of 31 seaweed species representing various groups revealed that zeatin (Z) and isopentenyl (IP) conjugates of cytokinins are the predominant cytokinins

Table 2 Selected polysaccharide constituents of green, red, and brown seaweeds

Seaweed	Polysaccharides
Chlorophyceae (Green)	Amylose, amylopectin
	Cellulose
	Complex hemicellulose
	Glucomannans
	Mannans
	Inulin
	Laminaran
	Pectin
	Sulfated mucilages (glucuronoxylorhamnans)
	Xylans
Rhodophyceae (Red)	Agars, agaroids
	Carrageenans
	Cellulose
	Complex mucilages
	Furcellaran
	Glycogen (floridean starch)
	Mannans
	Xylans, rhodymenan
Phaeophyceae (Brown)	Alginates
	Cellulose
	Complex sulfated heteroglucans
	Fucose containing glycans
	Fucoidans
	Glucuronoxylofucans
	Laminarans
	Lichenan-like glucan

(Stirk and others 2003). Seaweed concentrates also contained aromatic cytokinins BAP (benzyl amino purine) and topolin (6-[3-hydroxybenzyl-amino] purine) derivatives) (Stirk and others 2004).

Marine algae are also reportedly rich in auxins and auxin-like compounds (Crouch and van Staden 1993a). An *A. nodosum* extract had as high as 50 mg IAA (indole acetic acid) per gram of dry extract (Kingman and Moore 1982). Similarly, an extract of *Ecklonia maxima* exhibited a remarkable root-promoting activity on mung bean, an effect reminiscent of auxins (Crouch and van Staden 1991). Gas chromatography/mass spectroscopy (GC/MS) analysis of the extract revealed the presence of indole compounds, including IAA in SWC (Crouch and others 1992).

Auxins have been detected in other algal species like *Porphyra perforata,* but the levels found were low (Zhang and others 1993). In higher plants IAA occurs as an inactive conjugate with carboxyl groups, glycans, amino acids, and peptides, which, upon hydrolysis, are converted to free active IAA (Bartel 1997). Stirk and others (2004) found four amino acid and three indole conjugates of IAA in the extracts of two seaweeds, *E. maxima* and *Macrocystis pyrifera*. Biologically active auxin-like compounds other than IAA were reported in alkaline hydrolyzates of *A. nodosum*, *Fucus vesiculosus*, and other seaweeds (Buggeln and Craigie 1971).

The water-soluble growth inhibitors extracted from *Laminaria digitata* and *A. nodosum* resulted in marked inhibition of lettuce hypocotyl growth (Hussain and Boney 1973). One of these substances seemed to be similar to ABA as revealed by bioassay, thin-layer, and gas-liquid chromatography analysis. Presence of ABA in seaweeds has also been reported by others such Tietz and others (1989) (green algae) and Kingman and Moore (1982) (*A. nodosum*).

Betaines

Ascophyllum nodosum extracts contain various betaines and betaine-like compounds (Blunden and others 1986). In plants, betaines serve as a compatible solute that alleviates osmotic stress induced by salinity and drought stress; however, other roles have also been suggested (Blunden and Gordon 1986), such as enhancing leaf chlorophyll content of plants following their treatment with seaweed extracts (Blunden and others 1997). This increase in chlorophyll content may be due to a decrease in chlorophyll degradation (Whapham and others 1993). Yield enhancement effects due to improved chlorophyll content in leaves of various crop plants have been attributed to the betaines present in the seaweed (Genard and others 1991; Whapham and others 1993; Blunden and others 1997). It has been indicated that betaine may work as a nitrogen source when provided in low concentration and serve as an osmolyte at higher concentrations (Naidu and others 1987). Betaines have been shown to play a part in successful formation of somatic embryos from cotyledonary tissues and mature seeds of tea (Wachira and Ogada 1995; Akula and others 2000).

Sterols

As with many other eukaryotic cells, sterols are an essential group of lipids. Generally, a plant cell contains a mixture of sterols, such as β-sitosterol, stigmasterol, 24-methylenecholesterol, and cholesterol (Nabil and Cosson 1996). Brown seaweed chiefly contains fucosterol and fucosterol derivatives, whereas red seaweeds primarily contain cholesterol and cholesterol derivatives. Green seaweed accumulates mainly ergosterol and 24-methylenecholesterol (Ragan and Chapman 1978; Hamdy and Dawes 1988; Govindan and others 1993; Nabil and Cosson 1996) (Table 3).

Table 3 Common sterol constituents of green, red, and brown seaweeds

Seaweed	Type of sterol
Chlorophyceae (Green)	22-Dehydrocholesterol
	24-Methylenecholesterol
	24-Methylenecycloartanol
	28-Isofucosterol
	Brassicasterol
	Cholesterol
	Clerosterol
	Clionasterol
	Codisterol
	Cycloartannol
	Cycloartenol
	Decortinol
	Decortinone
	Ergosterol
	Fucosterol
	Isodecortinol
	Ostreasterol
	ß-Stitosterol
	Zymosterol
	Chondrillasterol
	Δ^5 - Ergostenol
	Δ^7 - Ergostenol
	Poriferastenol
	24-Methylenophenol
Rhodophyceae (Red)	22-Dehydrocholesterol
	24-Methylenecholesterol
	Campesterol
	Cholesterol
	Cycloartenol
	Desmosterol
	Fucosterol
	Stigmasterol
	Brassicasterol
	5-Dihydroergosterol
	Δ^5 - Ergostenol
	Obusifoliol
	$\Delta^{4,5}$ - Ketosteroids
	Sitosterol
Phaeophyceae (Brown)	22-Dehydrocholesterol
	Cycloartenol
	24-Methylenecycloartenol
	24-Methylenecholesterol
	Fucosterol
	Cholesterol
	Campesterol
	Stigmasterol
	Brassicasterol
	Clionasterol
	Porifasterol

Effect on Soil Health

Soil Structure and Moisture Retention

Besides eliciting a growth-promoting effect on plants, seaweeds also affect the physical, chemical, and biological properties of soil which in turn influence plant growth. Seaweeds and seaweed extracts enhance soil health by improving moisture-holding capacity and by promoting the growth of beneficial soil microbes. Brown seaweeds are rich in polyuronides such as alginates and fucoidans. The gelling and chelating abilities of these polysaccharides coupled with their hydrophilic properties make these compounds important in food processing and in the agricultural and pharmaceutical industries (Cardozo and others 2007). Alginate occurs in the cell walls of seaweeds as a mixed salt with the major cations being Na, Ca, Mg, and K together with a number of minor metal counterions. The molecular mass of alginate isolated from *A. nodosum*, *F. vesiculosus*, and *S. longicruris* varies between 106.6 and 177.3 kDa (Rioux and others 2007). Alginates possess unique and valuable properties attributable to the varying proportions of their two monomeric units (D-mannuronic acid and L-guluronic acid) that are arranged in block copolymer structures. The free acid form, alginic acid, is insoluble in water, as are alginates of certain divalent and polyvalent metal ions. Knowledge of these properties together with that of chain lengths and copolymer composition are used to control the gel structure and porosity of alginates for agricultural, pharmaceutical, and industrial uses (Lewis and others 1988; Skjak-Braek and others 1989). For example, alginates are widely used in formulating slow-release pharmaceuticals (Kim and others 2005; Chan and Heng 2002; Wong and others 2002) and pesticides (Vollner 1990; Davis and others 1996; Gonzalez-Pradas and others 1999; Kumbar and others 2003). The widespread interest in alginate is due in part to its biodegradable nature and the relatively non toxic nature of this natural compound.

Salts of alginic acid combine with the metallic ions in the soil to form high-molecular-weight complexes that absorb moisture, swell, retain soil moisture, and improve crumb structure. This results in better soil aeration and capillary activity of soil pores which in turn stimulate the growth of the plant root system as well as boost soil microbial activity (Eyras and others 1998; Gandhiyappan and Perumal 2001; Moore 2004). The polyanionic properties of seaweeds and unicellular algae have proved valuable in remediation of soils, especially those contaminated with heavy metals (Metting and others 1988; Blunden 1991).

Effect on Rhizosphere Microbes

Application of seaweeds and seaweed extracts triggers the growth of beneficial soil microbes and secretion of soil-conditioning substances by these microbes. As mentioned, alginates affect soil properties and encourage growth of beneficial fungi. Ishii and others (2000) observed that alginate oligosaccharides, produced by enzymatic degradation of alginic acid mainly extracted from brown algae, significantly stimulated hyphal growth and elongation of arbuscular mycorrhizal (AM) fungi and triggered their infectivity on trifoliate orange seedlings. Extracts of various marine brown algae [*Laminaria japonica* Areschoug and *Undaria pinnatifida* (Harvey) Suringar] could be used as an AM fungus growth promoter (Kuwada and others 2006). Kuwada and others (1999) previously showed that methanol extracts of brown algae fractionated by flash chromatography promoted in vitro AM hyphal growth as well as improved root colonization by AM fungi on trifoliate orange, *Poncirus trifoliate* (Linn.) Raf., seedlings. Indigenous AM fungi demonstrated a 27% improvement in root colonization, while spore number was increased about 21% over the controls when liquid fertilizer containing tangle (*L. japonica*) extracts was applied via a sprinkler system in a citrus orchard (Kuwada and others 2000). Kuwada and others (2006) reported that organic fractions (25% MeOH eluates) of red and green algae considerably improved *in vitro* hyphal growth of AM fungi. Their results showed that application of the 25% MeOH eluates of red and green algal extracts to roots of papaya (*Carica papaya* Linn.) and passion fruit (*Passiflora edulis* Sims.) improved mycorrhizal development more than the control treatment. Kuwada and others (2006) implied that both red and green algae have AM stimulatory compounds which play a part in mycorrhizal development in higher plants.

Limited research has been conducted on the effects of seaweed extracts on other beneficial AM fungi.

Effect on Plant Growth and Health

Root Development and Mineral Absorption

Seaweed products promote root growth and development (Metting and others 1990; Jeannin and others 1991). The root-growth stimulatory effect was more pronounced when extracts were applied at an early growth stage in maize, and the response was similar to that of auxin, an important root-growth-promoting hormone (Jeannin and others 1991). SWC applications reduce transplant shock in seedlings of marigold, cabbage (Aldworth and van Staden 1987), and tomato (Crouch and van Staden 1992) by increasing root size and vigor. SWC treatment enhanced both root:shoot ratios and biomass accumulation in tomato seedlings by stimulating root growth (Crouch and van Staden 1992). Similarly, wheat plants treated with SWC Kelpak® (Table 3) exhibited an increase in root:shoot dry mass ratio, indicating that the components in the seaweed had a considerable effect on root development (Nelson and van Staden 1986). This stimulatory activity was lost on ashing, suggesting that the active principles in the seaweed extract were organic in nature (Finnie and van Staden 1985). The root-growth-promoting activity was observed when the seaweed extracts were applied either to the roots or as a foliar spray (Biddington and Dearman 1983; Finnie and van Staden 1985). The concentration of kelp extract is a critical factor in its effectiveness as Finnie and van Staden (1985) showed for tomato plants in which high concentrations (1:100 seaweed extract:water) inhibited root growth but stimulatory effects were found at a lower concentration (1:600). Biostimulants in general are capable of affecting root development by both improving lateral root formation (Atzmon and van Staden 1994; Vernieri and others 2005) and increasing total volume of the root system (Thompson 2004; Slàvik 2005; Mancuso and others 2006).

An improved root system could be influenced by endogenous auxins as well as other compounds in the extracts (Crouch and others 1992). Seaweed extracts improve nutrient uptake by roots (Crouch and others 1990), resulting in root systems with improved water and nutrient efficiency, thereby causing enhanced general plant growth and vigor.

Effect on Shoot Growth and Photosynthesis

Seaweeds and seaweed products enhance plant chlorophyll content (Blunden and others 1997). Application of a low concentration of *Ascophyllum nodosum* extract to soil or on foliage of tomatoes produced leaves with higher chlorophyll content than those of untreated controls. This increase in chlorophyll content was a result of reduction in chlorophyll degradation, which might be caused in part by betaines in the seaweed extract (Whapham and others 1993). Glycine betaine delays the loss of photosynthetic activity by inhibiting chlorophyll degradation during storage conditions in isolated chloroplasts (Genard and others 1991).

In a recent study (Rayorath and others 2008), extracts of *A. nodosum* have been shown to affect the root growth of *Arabidopsis* at very low concentrations (0.1 g L^{-1}), whereas plant height and number of leaves were affected at concentrations of 1 g L^{-1}. Plants treated with extracts showed growth enhancement effects over control plants; for example, plants treated with *A. nodosum* extract were at a more advanced developmental stage when compared with untreated plants and the effect was concentration dependent (Fig. 2; unpublished results).

Although they may contain different levels of minerals, biostimulants are unable to provide all the nutrients needed by a plant in required quantities (Schmidt and others 2003); however, their main benefit is to improve plant mineral uptake by the roots (Vernieri and others 2005) and in the leaves (Mancuso and others 2006).

Effect on Crop Yield

Seaweed concentrate triggers early flowering and fruit set in a number of crop plants (Abetz and Young 1983; Featonby-Smith and van Staden 1987; Arthur and others 2003). For example, tomato seedlings treated with SWC set more flowers earlier than the control plants and this was not considered to be a stress response (Crouch and van Staden 1992). In many crops yield is associated with the number of flowers at maturity. As the onset and development of flowering and the number of flowers produced are linked to the developmental stage of plants, seaweed extracts probably encourage flowering by initiating robust plant growth. Yield increases in seaweed-treated plants are thought to be associated with the hormonal substances present in the extracts, especially cytokinins (Featonby-Smith and van Staden 1983a, b, 1984). Cytokinins in vegetative plant organs are associated with nutrient partitioning, whereas in reproductive organs, high levels of cytokinins may be linked with nutrient mobilization. Fruit ripening generally causes an increase in transport of nutrient resources within the developing plant (Hutton and van Staden 1984, Adams-Phillips and others 2004) and the fruits have the capacity to serve as strong sinks for nutrients (Varga and Bruinsma 1974; Adams-Phillips and others 2004). Photosynthate distribution could be shifted, perhaps markedly, moving from vegetative parts (roots, stem, and young leaves) to the developing fruit, to be utilized in fruit development (Nooden and Leopold 1978). Fruit treated with seaweed extracts had higher concentrations of cytokinins compared to untreated fruit in tomato (Featonby-Smith and van Staden 1984). Cytokinins have been implicated in nutrient mobilization in vegetative plant organs (Gersani and Kende 1982) as well as reproductive organs (Davey and van Staden 1978). Such a response indicates that seaweed extracts are involved either in enhancing the mobilization of cytokinins from the roots to the developing fruit, or, more likely, by improving the amount or synthesis of endogenous fruit cytokinins (Hahn and others 1974). Higher root cytokinin levels have also been found in seaweed extract-treated plants (Featonby-Smith 1984). This increase in cytokinin availability will eventually result in a greater supply of cytokinins to the maturing fruit. Developing fruits and seeds demonstrated increased endogenous cytokinin levels (Crane 1964; Nitsch 1970; Letham 1994). It has been reported that the increased cytokinin concentration is associated with translocation of cytokinin from roots to other plant parts (Stevens and Westwood 1984; Carlson and others 1987).

Fig. 2 *Arabidopsis thaliana* plants treated with different *A. nodosum* extracts (1 g L^{-1}) showed growth enhancement effects over the control plants 3 weeks after treatment

Seaweed extract increased fruit yield when sprayed on tomato plants during the vegetative stage, producing large-sized fruits (30% increase in fresh fruit weight over the controls) with superior quality (Crouch and van Staden 1992). The number of flowers and seeds per flower head increased (as much as 50% over the control) (van Staden and others 1994) when marigold seedlings were treated with SWC Kelpak immediately after transplanting (Aldworth and van Staden 1987). Application of Maxicrop® enhanced harvestable yield in lettuce, whereas an increase in the heart size of the florets and curd diameter was observed in cauliflower (Abetz and Young 1983). Similarly, a substantial increase in yield was achieved in barley (Featon-Smith and van Staden 1987) and peppers (Arthur and others 2003) after treatment with Kelpak.

Foliar application of seaweed liquid extract (Kelpak 66) enhanced bean yield by 24% (Nelson and van Staden 1984). Kelpak 66 also had a similar effect on the yield of wheat under potassium stress, although its application had no significant effect on the plants receiving an adequate K supplement (Beckett and van Staden 1989). Norrie and Keathley (2006) have reported that *A. nodosum* extracts showed positive effects on the yield of 'Thompson seedless' grape (*Vitis vinifera* L.) consistently over a 3-year period. They observed that the *A. nodosum*-treated plants always outperformed (in terms of berries per bunch, berry size, berry weight, rachis length, and the number of primary bunches per plant) the controls maintained under the regular crop management program, and resulted in improved fruit size (13% increase), weight (39% increase), and yields (60.4% increase over the control).

Vegetative Propagation

Seaweed products are exploited in conventional vegetative propagation in many crop species (Crouch and van Staden 1991; Atzmon and van Staden 1994; Kowalski and others 1999). It is common practice to apply auxins exogenously to enhance rooting in cuttings in certain species that are difficult to root. It has been observed that treating cuttings of some flowering plants like marigold (*Tagetus patula*) for about 18 h with 10% SWC Kelpak increased the number and dry weight of roots (Crouch and van Staden 1991). Similarly, Kelpak, when applied at a 1:100 dilution, increased the number of rooted cuttings and improved the vigor of the roots in difficult-to-root cuttings of *Pinus pinea* (Atzmon and van Staden 1994). In another study, Leclerc and others (2006) observed that foliar application of commercial liquid seaweed extract from *Ascophyllum nodosum* (Acadian Seaplants Limited), supplemented with BA and IBA, enhanced the number of propagules (crown divisions) per plant in the ornamental herbaceous perennial *Hemerocallis* sp.

Resistance to Environmental Stresses

Effects of SWCs in Alleviating Abiotic Stress in Crop Plants

Abiotic stresses such as drought, salinity, and temperature extremes can reduce the yield of major crops (Wang and others 2003) and limit agricultural production worldwide. For example, salinity and drought are becoming widespread in many regions of the world, with an estimated 50% of all arable lands possibly being salinized by 2050 (Flowers and Yeo 1995). Many abiotic factors such as drought, salinity, and temperature are manifested as osmotic stress and cause secondary effects like oxidative stress, leading to an accumulation of reactive oxygen species (ROS) such as the superoxide anion ($O_2^{\bullet -}$) and hydrogen peroxide (H_2O_2) (Mittler 2002). These are known to damage DNA, lipids, carbohydrates, and proteins and also cause aberrant cell signaling (Arora and others 2002).

Seaweed extracts from *Ascophyllum nodosum* have been shown to contain betaines, including gamma-aminobutyric acid betaine, 6-aminovaleric acid betaine, and glycine betaine (Blunden and others 1986). To test whether the increased chlorophyll content in leaves caused by seaweed extract treatment may be due in part to the betaines present in the extract, the effects of Algifert 25, an alkaline extract of *A. nodosum*, were compared with those of a mixture of known betaine constituents of *A. nodosum* (Blunden and others 1997). Blunden and others (1986) used a betaine mixture in the same concentrations as those present in the diluted seaweed extract (gamma-aminobutyric acid betaine, 0.96 mg L^{-1}; 6-aminovaleric acid betaine, 0.43 mg L^{-1}; glycine betaine, 0.34 mg L^{-1}). Results showed that similar leaf chlorophyll levels were recorded in both seaweed- and betaine-treated plants. Sixty-three and 69 days after application of SWC, leaf chlorophyll contents, as expressed in SPAD (soil-plant analysis development; Minolta Corporation, Japan) units, were 27.70 and 26.48, respectively, for seaweed extract and 27.30 and 23.60, respectively, for the betaine treatment. Both treatments resulted in higher chlorophyll levels versus controls measured on both days. The results imply that the enhanced leaf chlorophyll content of plants treated with SWC might depend on betaines present in the extract (Blunden and others 1997).

Plants sprayed with seaweed extracts also exhibit enhanced salt and freezing tolerance (Mancuso and others 2006). Commercial formulations of *Ascophyllum* extracts (Seasol®) improved freezing tolerance in grapes. Grapevines sprayed with Seasol (0.8%) showed a reduction in leaf osmotic potential, a key indicator of osmotic tolerance. The treated plants showed an average osmotic potential of −1.57 MPa after 9 days of seaweed extract treatment, whereas it was −1.51 MPa in untreated controls (Wilson 2001). Field studies on winter barley (*Hordeum vulgare* cv Igri) have shown that application of seaweed extract (Maxicrop) improves winter hardiness and increases frost resistance (Burchett and others 1998).

Taken collectively, these studies suggest that seaweed products elicit abiotic stress tolerance in plants and that the bioactive substances derived from seaweeds impart stress tolerance and enhance plant performance. The chemistry of bioactive compounds in the seaweed and the physiologic mechanism of action of the compounds that impart this tolerance are largely unknown. However, a number of reports suggest that the beneficial antistress effects of seaweed extracts may be related to cytokinin activity. For example, Zhang and Ervin (2004) conducted experiments to confirm the action of seaweed extracts (*Ascophyllum nodosum*) on drought tolerance in creeping bentgrass. Drought-stressed plants treated with a combination of humic acid and seaweed extract had root mass enhanced by 21–68%, foliar tocopherol by 110%, and endogenous zeatin riboside (ZR) by 38%. A systematic analysis of cytokinins, namely, ZR and isopentenyl adenosine (iPA), was then performed on *A. nodosum* extract using enzyme-linked immunosorbent assay (ELISA). Seaweed extract contained substantial amounts of cytokinins amounting to 66 μg g^{-1} as zeatin riboside. Ashing of the seaweed extract reduced the effectiveness of the treatments suggesting the organic nature of the bioactive compound (Zhang and Ervin 2004). Cytokinins mitigate stress-induced free radicals by direct scavenging and by preventing reactive oxygen species (ROS) formation by inhibiting xanthine oxidation (McKersie and Leshem 1994; Fike and others 2001). It was hypothesized that seaweed extract-induced heat tolerance in creeping bent grass might be attributed largely to the cytokinin components in the seaweed extracts (Ervin and others 2004; Zhang and Ervin 2008). However, it has also been reported that Kelpak seems to mediate stress tolerance by enhancing K^+ uptake, although synthetic benzylaminopurine (BA), at a similar concentration to natural cytokinin present in Kelpak, showed no effect on yield, irrespective of the K^+ supply. Hence, the beneficial effects of seaweed extract against abiotic stress could also be partly elicited by bioactive chemicals other than cytokinin (Beckett and van Staden 1989).

Reactive oxygen species (ROS) are a common factor in many abiotic stresses such as salinity, ozone exposure, UV irradiation, temperature extremes, and drought (Hodges 2001). Application of an *A. nodosum* extract (Tasco®) to unstressed turf grasses increased the activity of the antioxidant enzyme superoxide dismutase (SOD), which scavenges superoxide (Fike and others 2001). In another study, tall fescue (*Festuca arundinacea*) treated with 0, 1.7, or 3.4 kg ha^{-1} of *A. nodosum* extract exhibited increased SOD activity in all 3 years of the study by an average of approximately 30% (Zhang 1997). Similarly, Ayad (1998) reported an increase in SOD, glutathione reductase (GR), and ascorbate peroxidase (AsPX) activities in genetically similar endophyte-infected and endophyte-free tall fescue in response to 3.4 kg Tasco ha^{-1}. Thus, the primary effect of Tasco application to tall fescue in these experiments seems to be through an increase in antioxidant capacity (Fike and others 2001).

Effect of SWC in Alleviating Biotic Stress

Seaweed extracts have been shown to enhance plant defense against pest and diseases (Allen and others 2001). Besides influencing the physiology and metabolism of plants, seaweed products promote plant health by affecting the rhizosphere microbial community.

Nematodes Seaweed extracts were found to have an impact on the population of nematodes in the soil (Wu and others 1997). Plants treated with seaweed extracts caused a reduction in nematode infestation (Featonby-Smith and van Staden 1983a; Wu and others 1997). Root knot nematode infestation in tomato was reduced in soil amended with commercial seaweed extracts from *Ecklonia maxima* (Featonby-Smith and van Staden 1983a; Crouch and van Staden 1993b). Interestingly, seaweed extract treatment did not affect the nematode population in the rhizosphere (Featonby-Smith and van Staden 1983a) and did not show a direct nematicidal effect. Taken together, these results suggest that seaweed extract imparts nematode resistance possibly by altering the auxin:cytokinin ratio in the plant. An *in vitro* experiment in which excised maize roots were treated with seaweed extract showed reduction in the reproduction of the nematode *Pratylenchus zeae* by 47–63%. However, in a pot experiment, the reproduction of *P. zeae* was not influenced by seaweed extracts (De Waele and others 1988).

Fungal and bacterial pathogens Marine algae can serve as an important source of plant defense elicitors (Cluzet and others 2004). Plants protect themselves against pathogen invasion by the perception of signal molecules called elicitors which include a wide variety of molecules such as oligo- and polysaccharides, peptides, proteins, and lipids, often found in the cell wall of attacking pathogens (Boller 1995; Côté and others 1998). A variety of polysaccharides present in algal extracts include effective elicitors of plant defense against plant diseases (Kloareg and Quatrano 1988). Although red algae typically contain agars and carrageenans in their cell walls, extracts of brown algae contain alginates, laminarans, sulfated fucans, and other complex mucilages, and green algae (e.g., *Ulva* spp.) contain mucilages composed of units such as rhamnose, uronic acid, and xylose (Cluzet and others 2004). Laminaran, a linear β-(1,3)-glucan, and sulfated fucans from brown algae elicit multiple defense responses in alfalfa and tobacco (Kobayashi and others 1993; Klarzynski and others 2000, 2003). Similarly, carrageenans, a family of sulfated linear galactans, are effective elicitors of defense in tobacco plants (Mercier and others 2001). Foliar sprays of *A. nodosum* extract reduced *Phytophthora capsici* infection in *Capsicum* and *Plasmopara viticola* in grape (Lizzy and others 1998). Soil application of liquid seaweed extracts to cabbage stimulated the growth and activity of microbes that were antagonistic to *Pythium ultimum,* a serious fungal pathogen that causes damping-off disease of seedlings (Dixon and Walsh 2002). Seaweeds are a rich source of antioxidant polyphenols with bactericidal properties (Zhang and others 2006). The application of *A. nodosum* extract and humic acid to bentgrass (*Agrostis stolonifera*) increased SOD activity, which in turn significantly decreased dollar spot disease caused by *Sclerotinia homoeocarpa*.

A study using extracts of *Ulva* spp. against *Colletotrichum trifolii* in *Medicago truncatula* showed disease resistance without the elicitation of necrotic lesions (Cluzet and others 2004). *Ulva* extract elicited the expression of the PR-10 gene. The PR-10 gene belongs to the group of pathogenesis-related genes (PR) important for active defense against diseases following pathogen attack (van Loon and others 2006). Treatment of alfalfa with the algal extracts prior to pathogen challenge resulted in an increased resistance to *Colletotrichum.* cDNA array revealed that the algal extract caused upregulation of 152 genes, mostly plant defense genes such as those involved in phytoalexin, PR proteins, cell wall proteins, and oxylipin pathways (Cluzet and others 2004).

Bacterial quorum sensing and effect of seaweed on quorum sensing Quorum sensing (QS) is a communication mechanism used by bacterial populations that are dependent on cell density which, in turn, triggers and controls gene expression that regulates various physiologic functions and responses (Brelles-Marino and Bedmar 2001; Winzer and Williams 2001; Dong and Zhang 2005). This response is mediated by low-molecular-weight signal molecules called acylated-homoserine lactones (acyl-HSL).

The virulence of pathogenic bacteria is under the control of the QS system. Agents that affect the QS system can potentially alter pathogenicity. The marine red alga *Delisea pulchra* synthesizes halogenated furanones and enones that are homologous to acyl-HSL. They bind to the LuxR in the acyl-HSL binding site and prevent the binding of acyl-HSL autoinducers, thereby inhibiting the process of QS. These furanones in nature seem to interfere with QS in marine bacteria such as *Serratia liquefaciens*, *Vibrio fischeri*, and *Vibrio harveyi* (Rasmussen and others 2000; Manefield and others 2002).

Other pests Aphids and other sap-feeding insects generally avoid plants treated with seaweed extracts (Stephenson 1966; Hankins and Hockey 1990). Hydrolyzed seaweed extracts sprayed onto apple trees reduced red spider mite populations (Stephenson 1966), and 2–3 years of seaweed extract application resulted in a level of control similar to that of acaricides (Stephenson 1966). Futhermore, it was observed that the use of Maxicrop on strawberry plants (*Fragaria* sp.) greatly reduced the two-spotted red spider mite (*Tetranychus urticae*) population (Hankins and Hockey 1990). It has been suggested that seaweed extracts might contain chelated metals that have been shown to reduce the population of red spider mites (Terriere and Rajadhyaksha 1964; Abetz 1980).

Conclusions and Future Perspectives

Seaweeds and seaweed products are increasingly used in crop production. However, the mechanism(s) of actions of seaweed extract-elicited physiological responses are largely unknown. As genomes of a number of plants are now completely sequenced or nearing completion, it is possible to look at the effects of seaweed extracts and components of the seaweeds on the whole genome/transcriptome of plants to better understand the mechanisms of action of seaweed-induced growth response and stress alleviation. For example, the use of model plants *Arabidopsis thaliana* and *Medicago truncatula* could potentially unravel the molecular mechanism(s) of action of seaweed extracts (Rayorath and others 2008). The recent challenges to food production due to the increasing occurrence of biotic and abiotic stresses is likely due to climate change and will further reduce yields and/or will have an impact on crops in the 21st century (IPCC 2007). Therefore, research into developing sustainable methods to alleviate these stresses should be a priority. Recent studies have shown that seaweed extracts protect plants against a number of biotic and abiotic stresses and offers potential for field application. Further, seaweed extracts are considered an organic farm input as they are environmentally benign and safe for the health of animals and humans.

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