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Review

# Seaweed extracts as biostimulants in horticulture

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ABSTRACT

Seaweeds are green, brown and red marine macroalgae. Extracts of brown seaweeds are widely used in horticulture crops largely for their plant growth-promoting effects and for their ameliorating effect on crop tolerance to abiotic stresses such as salinity, extreme temperatures, nutrient deficiency and drought. The chemical constituents of seaweed extract include complex polysaccharide, fatty acids, vitamins, phytohormones and mineral nutrients. Recent researches have shed light on the possible molecular mechanisms activated by seaweed extracts. In this review we give an update of the current state of our understanding of the chemical constituents of brown seaweed extracts and the physiological effects they induce on plants with particular reference to horticultural crops.



**Contents**



## 1. Introduction

Macroalgae (seaweeds) comprise nearly 10,000 species and contribute to approximately 10% of the total world marine productivity. The large biomass species can be free-floating such as members of the brown algal genus *Sargassum* (viz. Sargasso Sea), however the majority are benthic, attached to hard substrata by holdfasts the fucoids and 'kelps' are perhaps the best known and most easily observed by the casual observer on the shoreline. Seaweeds are quintessential members of inshore, marine ecosystems as they provide shelter and food to numerous marine biota and can even contribute to the modification of physicochemical properties of seawater. A relatively small proportion of the total number of seaweed species are of significant importance as animal and human food/supplements and also in agriculture as mulches/manure and modified extracts (Craigie 2011; Khan et al., 2009; Rönnbäck et al., 2007; Rayorath et al., 2009).

The earliest evidence of human use of seaweeds was found in 15,000-year old organic remains recovered from pre-historic sites in Monte Verde, Sothern Chile, where an ancient migratory group of coastal origin settled down and consumed seaweeds in

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**Table 1**
Effects of seaweed extracts on vegetable crops.

| Crop | Seaweed extract | Effects | Reference |
|---|---|---|---|
| Bean | *A. nodosum* | Increased in germination | Carvalho et al. (2013) |
| Broccoli | *A. nodosum*<br>*A. nodosum* and, *Durvillaea potatorum* | Increased in antioxidant activity, flavonoids, phenolic and, isothiocynate<br>Increased in stem diameter, leaf area, biomass, enhanced early growth and reduced white blister (*Albugo candida*) | Lolo-Luz et al. (2014)<br>Mattner et al. (2013) |
| Cabbage | *A. nodosum* commercial extracts | Increased in concentration of flavonoids and, phenolics | Lolo-Luz et al. (2013) |
| Carrot | *A. nodosum* | Increased *peroxidase, phenylalanine ammonia lyase, chitinase, PR1 and PR5; reduced growth of Alternaria radicina and, Botrytis cinerea* | Jayaraj et al. (2008) |
| Cauliflower | *A. nodosum* | Increased in yield and, curd diameter | Abetz and Young (1983) |
| Cucumber | Green alga (*E. intestinelis*), red alga (*G. pectinutum*), *Ecklonia maxima*<br>*A. nodosum* | Increased in yield, Fe, Zn and Mn content<br>Increased in yield, fruit per plant and, fruit weight | Ahmed and Shalaby (2012)<br>Nelson and Van (1984)<br>Sarhan (2014) |
| Eggplant | *A. nodosum*<br>Hypnea musciformis and *Gracilaria textorii* | Increased in vegetative growth and yield<br>Increased in seed germination and, yield | Abd El-Gawad and Osman (2014)<br>Rao and Chatterjee (2014) |
| Lettuce | A commercial extract of *E. maxima* | Increased in yield, K, Mg and Ca uptake | Crouch et al. (1990) |
| Gram Mung bean | *Sargassum wightii* | Increased in total protein, total carbohydrate and, total lipid; increased in shoot and root length | Ashok Kumar et al. (2012) |
| Okra | *Rosenvigea intricate*<br>Kappaphycus alvarezii | Increased in yield, chlorophyll and, carotenoids<br>Increased in fruit yield, fruit length, fruit diameter and, nutritional quality | Thirumaran et al. (2009)<br>Zodape et al. (2008)<br>Papenfus et al. (2013) |
| Onion | *A. nodosum* | Increased in yield and, reduced severity of downy mildew | Dogra and Mandradia (2014) |
| Pepper | *A. nodosum*<br>*A. nodosum* commercial extract | Increased in yield, fruit diameter, length and, chlorophyll content<br>Increased in yield, ascorbic acid and, chlorophyll content | Eris et al. (1995)<br>Manna et al. (2012)<br>Arthur et al. (2003) |
| Potato | *E. maxima* | Improved seedling establishment after transplanting | Kowalski et al. (1999) |
| Spinach | *A. nodosum* | Increased in antioxidant activity, flavonoids, phenolic content and, $Fe^{2+}$ chelating ability | Fan et al. (2010, 2014) |
| Tomato | *E. maxima*<br>A commercial extract of brown seaweeds<br>*Ulva lactuca* and *P. gymnospora*<br>*Hypnea musciformis* and *Gracilaria textorii* | Increased Mn uptake<br>Increased in Zn, Fe and, chlorophyll content<br>Enhanced germination, height and, fruit weight<br>Increased in germination and yield | Crouch et al. (1990)<br>Eyras et al. (2008); Dobromilska et al. (2008); Khan et al. (2009)<br>Hernández-Herrera et al. (2014); Crouch and Van Staden (1992)<br>Rao and Chatterjee (2014) |
| Watermelon | *A. nodosum* | Increased in yield | Abdel-Mawgoud et al. (2010) |

**Table 2**
Effects of seaweed extracts on fruit crops.

| Crop | Seaweed extract | Effects | Reference |
|---|---|---|---|
| Apple | A commercial extract of *A. nodosum* | Reduced alternate bearing | Spinelli et al. (2009) |
| Banana | *Ochtodes secundiramea* and, *Laurencia dendroidea* | Inhibited anthracnose | Machado et al. (2014) |
| Clementine | *A. nodosum* extract | Increased in yield | Fornes et al. (2002) |
| Grape | *A. nodosum* commercial extract<br>*A. nodosum*<br>*A. nodosum* | Increased in Cu uptake, $K^{+}$ and $Ca^{2+}$ influx<br>Increased in berry size, weight and firmness<br>Increased in yield, uniform ripening | Turan and Kose (2004); Mancuso et al. (2006)<br>Norrie et al. (2001)<br>Holden et al. (2008) |
| Olive | *A. nodosum* | Increased in yield, oil content, linolenic, oleic acid and, accelerated maturation; reduced palmitoleic, stearic and, linoleic acid content | Chouliaras et al. (2009) |
| Orange | *A. nodosum*<br>Seaweed extract<br>*A. nodosum* | Increased in growth under drought stress<br>Increased in fruit weight, quality, total soluble solids and, sugar<br>Early maturity | Spann and Little (2011)<br>Kamel (2014)<br>Fornes et al. (1993)<br>Omar (2014) |
| Papaya | *Ochtodes secundiramea* and, *Laurencia dendroidea* | Inhibited anthracnose | Machado et al. (2014) |
| Pear | *A. nodosum* | Increased in yield, fruit diameter, fruit weight and, number of cells per area of parenchymatous tissue | Colavita et al. (2010) |
| Strawberry | A commercial extract of *A. nodosum* | Increased in fruit yield, size and, total anthocyanin | Spinelli et al. (2010)<br>Alam et al. (2013)<br>Roussos et al. (2009) |

**Table 3**
Effects of seaweed extracts on flower and ornamental crops, and turf grasses.

| Crop | Seaweed extract | Effects | Reference |
|---|---|---|---|
| *Amaranthus* tricolor | *A. nodosum* extract | Increased stalk length of inflorescences, length and number of inflorescences, fresh and dry weight of inflorescences under salt stress | Aziz et al. (2011) |
| Marigold | *Ecklonia maxima* | Increased in vegetative and reproductive growth | Van Staden et al. (1994) |
| Petunia, Pansy and Cosmos | *A. nodosum* extract along with N-P-K fertilizer | Increased length of root, leaf area and development of root and shoot in response to drought stress | Neily et al. (2010) |
| Paper birch | Seaweed extract | Increased in chlorophyll and carotenoids | Richardson et al. (2004) |
| Tall fescue sod | *A. nodosum* extract in | Increased root mass, and foliar content of α | Zhang et al. (2010) |
| Turf grass | combination with humic acid | tocopherol and zeatin riboside under drought | Zhang et al. (2004) |
| Turf and forage | *E. maxima* commercial extract | stress | Zhang et al. (2003) |
| grasses | *A. nodosum* extract based | Enhanced grass color, organic components | Hunter (2004) |
| | cytokinins | Increased leaf *trans*-zeatin riboside content, | Zhang and Ervin (2008) |
| | *A. nodosum* extract in | alleviated chlorophyll content reduction in | Zhang and Schmidt (2000) |
| | combination with humic acid | response to heat stress | Allen et al. (2001) |
| | and propiconazole | Improved post transpalnt rooting, quality; | Kauffman et al. (2007) |
| | *A. nodosum* commercial extract | protected the plants against heat stress during shipment | |
| | | Enhanced ascorbic acid, ß-carotene content and increased antioxidant activity of superoxide dismutase, glutathione reductase, and ascorbate peroxidase | |

their diet (Dillehay et al., 2008). Available resources ranging from ancient scriptures and folklore to ethnographic studies reveal that seaweeds have been used by humans for multifarious purposes including food, medicine, agriculture, cosmetic products, colouring dyes, textiles. Various seaweeds have found their places in diverse cultures throughout the globe (Guiry and Blunden, 1991) Deity Ukimochi, the Goddess of food, is depicted to be associated with seaweed in Japanese mythology (Coulter and Turner, 2013). Ancient Romans were familiar with the fertilizing nature of seaweeds as Collumella, the most noted writer on agriculture of the Roman Empire, depicted that roots were to be wrapped in "seaweed" (genus not specified) in order to retain the greenness of the seedlings (Henderson, 2004). In more recent times, the use of various seaweeds as manure has been practiced in the British Isles, including Scotland and Ireland (Wells et al., 2007).

A number of seaweeds are reported to possess plant-growth promoting activity and thus they have found one of their more universal and continuing relevancies in agriculture and horticulture as organic manures and fertilizers (Craigie, 2011). Use of varied seaweeds in agriculture, as many other popular practices, has been evaluated and established by the practical experiences, and trials of farmers. However, since the 1950s the use of whole seaweeds has generally been supplanted by use of different types of extracts made from different varieties of seaweeds. Seaweed extracts have now gained much wider acceptance as "plant biostimulants". In general, seaweed extracts, even at low concentrations, are capable of inducing an array of physiological, plant responses, such as promotion of plant growth, improvement of flowering and yield, and also enhanced quality of products, improved nutritional content of edible product as well as shelf life. Furthermore, applications of different extract types have been reported to enhance plants' tolerance to a wide range of abiotic stresses, i.e. salinity, drought and temperature extremes. Extensive studies on the chemical composition of various extracts made from a diversity seaweeds revealed that the nutrient content (typically macronutrients including N, P, K) of the extracts were insufficient to elicit physiological responses at the typical concentrations that the seaweed extracts were applied in the field (Blunden, 1971, 1991; Khan et al., 2009). Thus it is has long been suggested that the physiological effect of seaweed extracts are largely mediated by growth promoting compounds and elicitors. In this review we reported the use of various seaweed extracts as plant biostimulants in horticulture and the possible modes of action including the chemical components that may be responsible for the elicitation of physiological responses in treated plants.

## 2. Origin, production process and chemical compositions of seaweed extracts

Seaweeds are a diverse assemblage with close to 10,000 species of red, brown and green seaweeds described (Khan et al., 2009). Based on abundance and distribution, brown seaweeds (Phaeophyta) are some of the most commonly used for the commercial manufacture of extracts for applications in agriculture and horticulture Amongst the brown seaweeds, *Ascophyllum nodosum*, *Ecklonia maxima*, *Macrocystis pyrifera* and *Durvillea potatorum* are the most frequently commercially used by the extract industries (Khan et al., 2009). In general, cellular matrices are bound by alginic acid comprising differing ratios of mannuronic and guluronic acid residues. The commercial seaweed extract industry employs a wide range of proprietary extraction processes in order to disrupt the cells and release beneficial components in to the extract; some of the processes include, alkali extraction, acid extraction and cell bust technology. The chemical composition of extract largely depends on the method of extraction and on the chemical products used during the production process. Therefore, the biological activity of extracts of the same seaweed raw material obtained by different extraction processes may be considerably different (Kim, 2012; Khairy and El-Shafay, 2013).

The various commercial extracts made from brown seaweeds as a raw material contain a diverse range of inorganic and organic components. The inorganic components of *A. nodosum* extract include nitrogen, phosphorous, potassium, calcium, iron, magnesium, zinc, sodium and sulphur (Rayorath et al., 2009). Besides the mineral components brown seaweed extracts also contain varying amounts of organic compounds that include osmolites (e.g. betaines). A number of betaines and betaine analogues have been identified in seaweed extracts (Blunden et al., 2009; MacKinnon et al., 2010). Blunden et al. (2009) reported that the dominant betaine in *A. nodosum* was γ-aminobutyric acid betaine (ABAB), which was present at levels of 0.02–0.07% dry weight. Recently, four betaines, viz. glycine betaine, δ-aminovaleric acid betaine, γ-aminobutyric acid betaine and laminine were reported in *A. nodosum* and its commercial extracts (MacKinnon et al., 2010). In addition to betaines extracts of brown algae are also reported to contain amino acids. However, protein fractions of brown algae possess only 3–15% of the dry weight of the brown seaweed, which is not as much as green and red algae that contain 10–47% protein in dry weights. (Fleurence, 1999; Fike et al., 2001; Nagahama et al., 2009). Brown algae also contain bioactive secondary metabolites, vitamins and vitamin precursors (Berlyn and Russo, 1990; Blunden et al., 1985). Various authors reported that these compounds interact synergistically to enhance the growth of land plants, by hitherto unknown mechanisms (Norrie and Keathley, 2006; Craigie et al., 2008; Craigie, 2011).

One of the major components of commercial extracts of all seaweeds are the polysaccharides. These may account for up to 30–40% of the extract on a dry weight basis (Rayorath et al., 2009). The common polysaccharides found in brown seaweed extracts include alginates, fucoidans, laminarans, lichenan-like glucans and fucose containing glucans (Khan et al., 2009). Fucoidans possess different structures due to their varying degrees of methylation, sulphation and branching. Depending on the chemical and physical methods employed during extraction of the raw material, the season of harvest and the algal species, the structure of the fucose containing polymers vary (Craigie, 2011). Alginates are polymers of mannuronic and guluronic acids, the viscosity of which varies depending on the seaweed species. Alginates are shown to promote plant growth (Yabur et al., 2007). Laminarins on the other hand are known and registered elicitors of plant defense responses against fungal and bacterial pathogens (Mercier et al., 2001).

Seaweeds, particularly brown seaweeds, are rich in phenolic compounds. Phenolics are secondary metabolites that are synthetized under stress which protect cells and cellular components (Nakamura et al., 1996; Wang et al., 2009). Important roles of phenolic compounds include antioxidant activity, scavenging radicals such as, single oxygen, superoxide, hydroxyl, alkoxyl and peroxy radicals (Andjelković et al., 2006). Brown seaweeds such as *Fucus vesiculosus*, *F. serratus* and *Ascophyllum nodosum* have high concentrations of total phenolics (Laetitia et al., 2010; Keyrouz et al., 2011; Balboa et al., 2013). Phenolic compounds also chelate metal ions. It has been shown that phenolic compounds with catechol (dihydroxy benzene) or galloyl (trihydroxy benzene) groups had strong chelating activities. Phlorotannins, complex polymers of phlororglucinol, such as phloroglucinol, eckol and dieckol, are phenolic compounds found in brown seaweeds, and in comparison with the other members of phenolic family, have more phenolic rings in their structure, enabling them to scavenge the radical species. Shibata et al. (2003) showed that phlorotannins, of marine algae were more efficient antioxidants compared to catechin, ascorbic acid, phlorofucofuroeckol A, dieckol, 8,8-bieckol, epigallocatechin gallate (EGCG), resveratrol and α-tocopherol.

Seaweed extracts also contain number of pytohormones including auxins, cytokinins, gibberellins, abscisic acid and brassinosteroids (Stirk et al., 2014). Phytohormone-like activity of seaweed extracts is discussed in Section 4.2.

Brown seaweeds such as *Alaria esculenta*, *Ascophyllum nodosum*, *Ectocarpus siliculosus*, *Fucus serratus*, *F. spiralis*, *F. vesiculosus*, *Halidrys siliquosa*, *Laminaria digitata*, *L. hyperborea*, *L. saccharina* and *Pilayella littoralis* contain osmolytes such as mannitol as an important protective compound in response to abiotic stressors. Mannitol is also known as a chelating agent and explains the reason that seaweed is able to release unavailable elements of the soil (Reed et al., 1985).

## 3. Modes of application of seaweeds and their extracts in horticulture

### 3.1. Seaweed biomass and seaweed meal

A number of application methods have been used to deliver seaweed products to horticultural crops. The type of application employed depends on the nature of the seaweed product (eg. meal/powder or extract). Application of whole seaweed biomass or meal is most common near coastal areas where the seaweeds are abundant. Whole seaweeds or seaweed meal are spread on the ground and are usually worked into the soil to facilitate microbial decomposition of the seaweed. Seaweeds are incorporated into the soil considerable time in advance of planting crops, because during the decomposition phase, soil bacteria deplete nitrogen in the soil resulting in a temporary nutrient deficiency that will negatively impact plant growth. The decomposed seaweed, as an organic matter, generally improved soil physico-chemical properties, water holding capacity, microbial activity and also protected plant against unfavorable environmental conditions such as extreme temperatures, water stress or excess of nutrients (Stephenson, 1972; Anderson, 2009).

### 3.2. Seaweed extracts

Seaweed extracts are the most widely used seaweed product on horticultural crops, available as liquid extracts or in a soluble powder form. Liquid extracts may be applied near the root of the plant, this can be achieved by mixing the extracts with irrigation water and applied as drip irrigation to crops. Seaweed extracts are also used as foliar sprays on a variety of flower, vegetable and tree crops including potato, tomato, plum, cherry, almonds and mango (Haider et al., 2012; Fornes et al., 2002; Rao, 1991; Selvaraj et al., 2004). Foliar application of seaweed extracts appeared to be most effective if applied in the morning when the leaf stomata are open. The efficacy of seaweed extracts also depend on the growth stage of the plant. For example, Dwelle and Hurley (1984) found that seaweed extract imparted maximum effect on the yield of potato when applied within 2-weeks following tuber initiation.

## 4. Plant biostimulant activity

### 4.1. Plant nutrient uptake

Plant absorb nutrients either through roots or from the leaf surface. Seaweed extracts alter physical, biochemical and biological properties of the soil and may also affect the architecture of plant roots facilitating efficient uptake of nutrients. Brown seaweeds contain polyuronides such as alginates and fucoidans. Alginic acid showed soil-conditioning properties and also chelated metal ions forming high molecular weight polymers (Anderson, 2009; Hegazy et al., 2009). The presence of highly cross-linked polymeric network improved water retention capacity of the soil (Verkleij, 1992; Lattner et al., 2003) and as a consequence, stimulated root growth and soil microbial activity (Chen et al., 2003). An extract of *Ecklonia maxima* improved root development in tomato and mung bean (Finnie and Van Staden, 1985; Crouch and Van Staden, 1991). One of the components of commercial seaweed extract kahydrin, a derivative of vitamin K1, altered plasma membrane proton pumps and induced the secretion of H+ ions into the apoplast leading to acidification of the rhizosphere (Luthje and Bottger, 1995). Acidification changed the redox state of soil and the solubility of metal ions, making them available to plant. Various seaweed extracts are also known to affect regulation of genes that played an important role

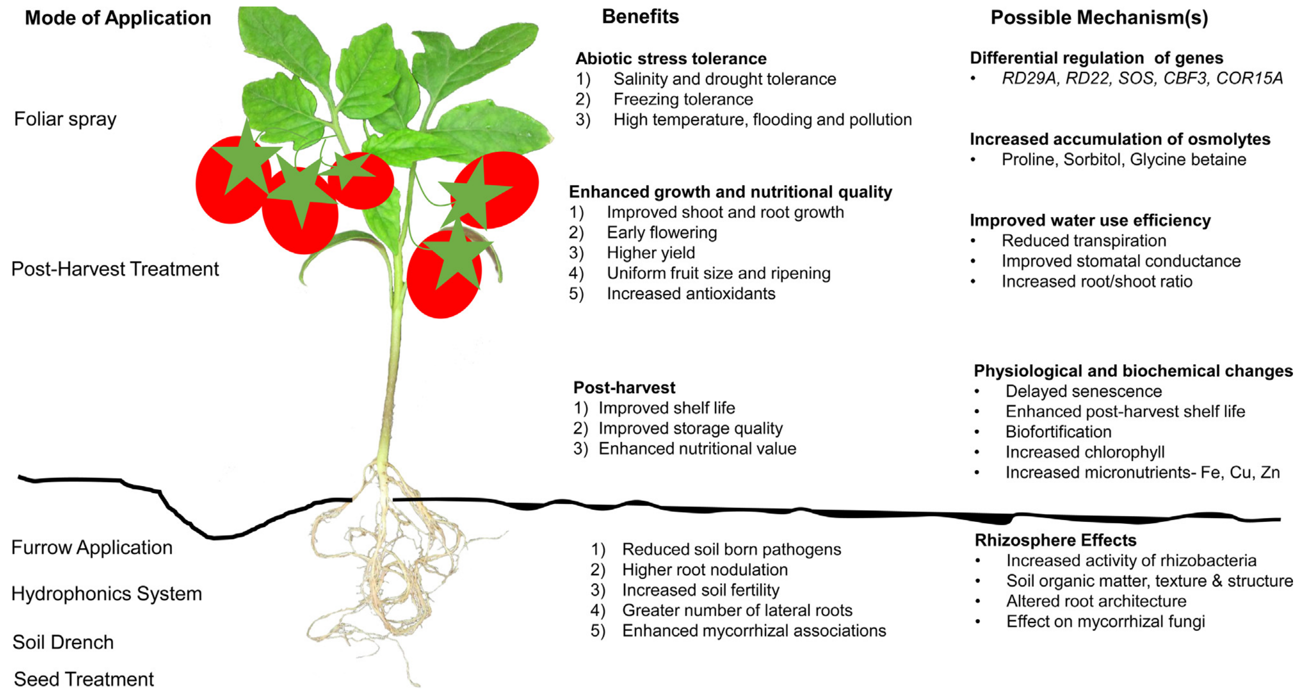


**Fig. 1.** Schematic diagram depicting methods of application of seaweed extracts, and their effects on plant and mechanisms of action.

in nutrient uptake. For example, *A. nodosum* extract upregulated the expression of a nitrate transporter gene NRT1.1. that improved nitrogen sensing and auxin transport (Krouk et al., 2010; Castaings et al., 2011), resulting in enhanced growth of lateral roots and improved nitrogen assimilation. The soil bacteria, rhizobia, form nodules on root of leguminous plants and fix atmospheric nitrogen to a form assimilated by plants (Gage, 2004). The rhizobia *Sinorhizobium melitoli* formed a greater number of N-fixing nodules in alfalfa roots in the presence of a commercial *A. nodosum* extract (ANE). ANE was found to activate the expression of NodC gene of bacteria that was known to play an important role in bacteria-to-plant signaling, by mimicking the effect of the flavonoid luteolin (Khan et al., 2012). In addition, chemical components of brown seaweed extract are known to induce growth and root colonization of beneficial soil fungi (Kuwada et al., 2000, 2006). Alginic acid, a major component of brown seaweed extracts, promoted hyphal growth and elongation of arbuscular myocorrhizal fungi (Ishi et al., 2000), such proliferation of mycorrhizal fungi lead to an improvement in phosphorus nutrition of plants. Foliar application of brown seaweed extract was reported to improve the uptake of copper in grapevine (Turan and Köse, 2004), iron in lettuce (Crouch et al., 1990) and calcium in *Brassica oleraceae* (Kotze and Joubert, 1980). More often, improvement in the uptake of these nutrients were observed when the plants were grown at sub-optimal growth conditions or under environmental stresses (Crouch and Van Staden, 1994). Moreover, alteration in the uptake of one nutrient element alters the uptake of other nutrients (De Villiers et al., 1983). Increased root and shoot growth in rapeseed treated with extract were associated with enhanced uptake and accumulation of nitrogen and sulphur (Jannin et al., 2013). Nutrients present in the seaweed extracts are readily absorbed by leaves through stomata and cuticle hydrophilic pores. The absorption of these mineral nutrients from the leaf surface are affected by environmental conditions such as temperature, humidity or light intensity that influenced opening of stomata and permeability of cuticle and cell wall. It was shown under nutrient deficient conditions, foliar application of seaweed extract products including those of a commercial *A. nodosum* extract increased the Cu uptake in grapevine, probably by increased permeability of the cell membrane. In another study, it was observed that application of a commercial extract of *E. maxima* on lettuce grown under optimal conditions improved yield and the concentration of Ca, K and Mg in the leaves (Crouch et al., 1990). Another product based on *E. maxima* when applied to nutrient stressed cucumbers as a foliar spray, or root application, enhanced root growth and accumulated higher amounts of P, but less N (Nelson and Van Staden, 1984). Application of a commercial product made with brown seaweed increased mineral nutrient (N, P, K, Ca, Zn and Fe) content of tomato (Dobromilska et al., 2008).

### 4.2. Phytohormone-like activity

The growth and development of higher plants are regulated by phytohormones. The effect of commercial seaweed extracts on growth of plant is reminiscent of activity of phytohormones, they improved growth at low concentrations and inhibited growth at high concentrations with similar physiological effects to those of phytohormones (Provasoli and Carlucci, 1974; Khan et al., 2009). For examples, in a study with a commercial extract made from *E. maxima* a lower concentration promoted the growth of tomato roots while at a higher concentration the extract strongly inhibited root growth (Finnie and Van Staden, 1985). Brown seaweed extracts are reported to contain phytohormones such as indole acetic acid (IAA), cytokinin, gibberellic acid (GA), polyamines and abscisic acid (ABA). (Provasoli and Carlucci, 1974; Stirk et al., 2003; Jacobs, 1993; Khan et al., 2009; Wally et al., 2013). According to the current body of knowledge, the growth promoting effects of seaweed extracts are related to the direct or indirect effect of phytohormones present in the extracts. The auxin-like property of seaweed extract was changed by an induction of profuse root primodia in plants such as corn, cabbage, marigold and tomato (Jeannin et al., 1991; Aldworth and Van Staden, 1987; Crouch and Van Staden, 1992, 1993). The specific phytohormone-like activity in the seaweed extract depend on the type of seaweed used for extraction and also how the seaweed was handled after harvest and how it was processed. For example, fresh extracts of E. maxima had both cytokinin and auxin-like activities, however upon extended storage, the extract lost auxin activity while there was a change in the cytokinin-like activity (Stirk et al., 2004). Commercial extracts of *E. maxima* contained different concentration of ABA, GA and brassinosteroids than unprocessed seaweed suggesting that processing of seaweed causes changes in the concentration of phytohormone-like compounds (Stirk et al., 2014). However, the phytohormone-like activity of seaweed extracts might also be caused by chemical components in the extract other than phytohormones themselves. In an extensive study, Wally et al. (2013) measured concentration of phytohormones in a number of commercial seaweed extracts using ultra-performance liquid chromatography-electrospray tandem mass spectrometry (UPLC-ESI–MS/MS) and concluded that the concentration of phytohormones present in the extracts were insufficient to invoke physiological responses in plants at the concentrations they were normally applied in the field. These authors suggested that the phytohormone-like activity of a commercial *A. nodosum* extract was due to elicitor molecules present in the extract that perturb endogenous phytohormone metabolism in the treated plants by a selective regulation of phytohormome metabolic genes. In another study, Rayorath et al. (2008) reported that chemical components of an *A. nodosum* extract induced amylase activity in barely seeds that was independent of gibberellins (GA3) further suggesting that seaweed extracts might contain compounds that were structurally different from phytohormones nonetheless induce physiological responses reminiscent of phytohormones.

### 4.3. Abiotic stress tolerance

Abiotic stresses such as drought, water logging, salinity and extreme temperatures are major factors that affect productivity and quality of horticultural crops (Kobayashi et al., 2008). There has been an increase in the incidence of abiotic stresses in the recent years, largely due to climate change that caused an unprecedented increase in extreme weather patterns and incidents. Furthermore, the impact of intensive agricultural practices is also contributing to widespread occurrence of unfavorable conditions for growth and development of crop plants. Abiotic stresses account for considerable losses in crop production around the world (Zhu, 2000; Wang et al., 2003). For instance, it has been estimated that abiotic stresses lower the production yield to less than 50 %. Among the abiotic stressors, salinity affects approximately half of all irrigated land (Flowers and Yeo, 1995; Moghadam et al., 2013). Salinity alone could significantly limit the yield of major agricultural crops for food production (Zhu, 2000). On the other hand, strategies that are currently available to mitigate the abiotic stresses that adversely affect plant productivity are limited. One of the major limitations being the genetic complexity of abiotic stress resistance in plants. Most of the abiotic stress resistance mechanisms are oligogenic, a large number of genes mediate plant response to abiotic stresses. This limits the development of plant genotypes that are resistant to abiotic stresses both via conventional breeding and by using biotechnological approach. Therefore, alternate stress mitigation technologies will play a significant role in improving crop production in the future. Seaweeds and their extracts have been shown to reduce the impact of abiotic stress in a large number of plants and offer a tantalizing opportunity.

Bioactive compounds present in the seaweed extracts enhance the performance of plants under abiotic stresses. Spray applications of extracts have been shown to improve plant tolerance to freezing temperature stress (Mancuso et al., 2006). In particular, freezing tolerance in grapes was improved with an application of an *A. nodosum* extract formulation, the extract caused a reduction in the osmotic potential of the leaves, a key indicator of osmotic tolerance. The average osmotic potential of treated plants was −1.57 MPa compared to −1.51 MPa in the untreated controls after nine days of seaweed extract treatment (Wilson, 2001).

In greenhouse studies, the treatment of vegetables, bedding plants and turf crops with a commercial extract of *A. nodosum* significantly delayed wilting, decreased water use (i.e. better water use efficiency), increased leaf water content and improved the recovery of drought- wilted plants, as compared to controls (Little and Neily, 2010; Neily et al., 2008). Root applications of a commercial *Ascophyllum* extract to almonds, at two week intervals, enhanced the negative mid-day stem-water potential in the treated plots (Little and Neily, 2010). The commercial *A. nodosum* extract was also reported to promote the performance of lettuce seedling under high temperature stress. In addition, seed germination of lettuce was influenced by priming with *A. nodosum* extract in that germination improved under high temperature conditions (Moeller and Smith, 1998).

Considerable research had been conducted on the effect of seaweed extract on turf grass. Seaweed extract significantly improved the survival of Kentucky Bluegrass (*Poa pratensis* L. cv. Plush) under salinity conditions. Seaweed extract treatment enhanced both above and below ground growth of the grass at a soil salinity of 0.15 S m$^{-1}$ (Nabati et al., 1994). One of the mechanism activated from seaweed extract was a significant reduction in the accumulation of sodium ions in the plant, grass treated with seaweed extract had less sodium in the tissue, as compared to grass that did not receive seaweed extract treatment (Yan, 1993). In addition, seaweed extracts have been reported to improve the thermal tolerance of plants. Applications of seaweed extracts imparted heat tolerance in creeping bent grass (Ervin et al., 2004; Zhang and Ervin, 2008), the authors suggested that this effect was due to the presence of "cytokinin-like" substances in the extract along with an increase in $K^+$ uptake.

### 4.4. Plant metabolism and physiology

Seaweed extracts affect physiology of the plant, a number of recent publications demonstrated that the extracts impact global transcriptome profile and also caused changes to the metabolome of treated plant (Jannin et al., 2013; Nair et al., 2012). Recent advances in seaweed extract research involving gene expression analyses are shedding light on plants' metabolic regulatory pathways that are specifically affected by seaweed extracts and chemical components of extracts. Increases in abundance of transcripts of regulatory enzymes involved in nitrogen metabolism (i.e. cytosolic glutamine synthetase), antioxidative capacity (glutathione reductase), and glycine betaine synthesis (betaine aldehyde dehydrogenase and choline monooxygenase) were associated with increased total soluble protein, antioxidant property, content of phenolics and flavonoid in spinach treated with a commercial brown algal extract (Fan et al., 2013). Flavonoids, a secondary metabolite, play an important role in plant development and interaction with the environment factors such as response to UV light and other abiotic and also biotic stresses. Chalcone isomerase (*CHI*), is a key enzyme in the biosynthesis of flavanone precursors and phenylpropanoid plant defense compounds, also increased following treatment with seaweed extract.

One of the characteristic response of seaweed extract treatment is an increase in chlorophyll content in the treated plants, this effect has been observed in a wide range of crops including grapevine and strawberry (Blunden et al., 1997; Fan et al., 2013; Jannin et al., 2013; Mancuso et al., 2006; Sivasankari et al., 2006; Spinelli et al., 2010). The study of the molecular responses in plants in response to the treatment with seaweed extract revealed that the increase in the chlorophyll content was largely due to an increase in the biogenesis of chloroplasts, a reduction in chlorophyll degradation and a delay in senescence (Jannin et al., 2013; Rayorath et al., 2009; Nair et al., 2012; Blunden et al., 1997). Senescence associated cysteine proteases were down-regulated whereas expression of genes associated with photosynthesis, cell metabolism, stress response, S and N metabolism were significantly also up-regulated in plants treated with *A. nodosum* extract (Jannin et al., 2013). Cytokinin imparts protective effects on chloroplasts (Zavaleta-Mancera et al., 2007) and enhanced chloroplast division (Okazaki et al., 2009). Seaweed extracts are known to possess cytokinin-like activity (Ervin et al., 2004; Zhang and Ervin, 2008) and also promote endogenous cytokinin synthesis in the treated plants (Wally et al., 2012).

Application of a commercial seaweed extract on apple trees (variety Fuji) alleviated the issue of alternate bearing under nutrient deprived condition but not in standard nutrient management conditions (Spinelli et al., 2009). Alternate bearing can be reduced by the application of plant growth regulators such as gibberellin, auxin and cytokinin. Thus it appears the effect of a commercial seaweed extract made from *A. nodosum* on alternate bearing, under nutrient deprived conditions might be, at least in part, due to a hormone or a signaling molecule being present in the extract. However, it is difficult to explain the reason for the reduction of alternate bearing caused by the commercial *A. nodosum* extract only under deficient nutrition condition.

### 4.5. Product quality and shelf life

Extensive studies on the effect of a commercial *A. nodosum* extract treatment on spinach showed that not only the storage quality was improved, but also flavonoid synthesis and nutritional quality of the spinach leaf was enhanced (Fan et al., 2011, 2013). Two treatments 7 and 14 days prior to harvest were sufficient to alter the concentration of health promoting flavonoids in spinach. Using the invertebrate *Caenorhabiditis elegans* model, the authors provided evidence that the spinach treated with *A. nodosum* extract imparted a greater degree of stress tolerance to the animal as compared to the untreated spinach control. Furthermore, there was a considerable difference in the accumulation of lipid and its composition in the animals that received *A. nodosum* treated spinach. *A. nodosum* extract improved the productivity, quality and nutrient status of olives (Chouliaras et al., 2009). Foliar application of *A. nodosum* extract along with root application of nitrogen and boron increased K, Fe and Cu concentrations in the leaves with a concomitant decrease of Mn. The seaweed extract treatment caused changes in the fatty acid profile of the olive oil; there was a significant increase in the concentration of linolenic and oleic acid and a considerable decrease in palmitoleic, stearic and linoleic acid. Apart from yield and quality, application of seaweed extract enhanced the shelf life of avocado and pears (Blunden et al., 1978; Kamel, 2014). Application of seaweed extract caused an increase in concentration of phenolic compounds in cabbage, potato and onion; *A. nodosum* extract was applied in the field at 3–10 L/ha, once a month and the phenolic and antioxidant composition of the product was measured. The seaweed extract treatment did not affect yield but significantly increased health promoting phenolics and flavonoids (Lola-Luz et al., 2013; Lola-Luz et al., 2014).

Seaweed extracts have also been used as post-harvest treatments. Post-harvest treatment of navel orange with seaweed extract containing a combination of *Sargassum, laminaria* and *A. nodosum* extracts significantly improved post-harvest shelf-life and quality when stored at ambient temperature or in the cold storage. The effect of seaweed extract was superior to $CaCl_2$ treatment. The 4% seaweed extract treatment caused a significant increase in total soluble solids content, total sugars and reducing sugars. However, there was no difference between $CaCl_2$ and seaweed extract in terms of fruit rot.

## 5. Conclusions and future directions

Collectively, commercial extracts from raw materials of different seaweeds have received a greater acceptance in horticulture as plant biostimulants. Extracts of various types are now being using widely and a number of the larger agrochemical companies include seaweed extract and formulations amongst their offerings. In particular, seaweed extracts made from different starting raw materials, and by different procedures are attributed with a number of beneficial effects such as increased nutrient uptake, biotic and abiotic stress tolerances, and improvement in the quality of products (Tables 1–3; Fig. 1). Therefore, seaweed extracts are suggested to be applied especially when there is a stressful condition that affect crop performance.

Considerable advancements have been made in studying the action mechanisms of seaweed extract-elicited physiological responses, thanks to the 'omics' tools available to modern researchers. However, there are a number of questions that still need to be addressed for better use of seaweed resources and their extracts in horticultural crops. These include but are not exclusive to: 1) Not all seaweeds and therefore not all seaweed extracts are the same (Craigie 2011), even the same raw material processed by different extraction methods leads to extracts with different characteristics (Craigie et al., 2009). There might be merit in combining different extracts from different seaweeds at different concentrations for synergistic effects. 2) At what stage of the crops the extracts should be applied to get the maximum benefit. What is the timing and frequency of applications required and at what particular rate for obtaining a desired outcome? This would allow for a much more precise protocol to applications especially when evaluated on a "return on investment basis" (i.e. how much is the value of the crop increased for every unit cost of the applied extract?). There have not been any systematic studies to tease out the differences in the physiological response at different stages of the crop. 3) How long the effect persists after application of seaweed extract? Establishing the longevity of the physiological effects will aid in the scheduling of the frequency of extract application. Researches in our laboratory and others demonstrated that crop species respond differently to the extracts (concentration and frequency) and therefore more crop-specific research is required to optimize the seaweed extract application and to realize the best possible outcome (i.e. return on investment). Most of the seaweed extract products currently in the market are extracts of the whole seaweeds. It would be interesting to study the physiological effects of specific chemical components in order to develop a second generation of seaweed products with specific plant biostimulant activities.

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