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

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Abstract

In order to meet increasing food demands in the future, we will need to improve the current crop productivity. Abiotic stresses like drought and salinity are major factors resulting in crop yield losses and soil degradation worldwide. Recent studies suggest that seaweed-based biostimulants could be a solution for this problem. Here we summarise the current findings of using these biostimulants and highlight current knowledge gaps. Seaweed extracts were shown to enhance nutrient uptake and improve growth performance in crops under stressed and normal conditions. Seaweed extracts contain phytohormones, polysaccharides, polyphenols, lipids, amino acids and proteins. Although it has been shown that some of these compounds are active and have growth-promoting properties on plants, their underlying molecular mechanism of action and optimal applications especially in crops exposed to abiotic stress remains understudied. Seaweed extracts were shown to also improve protein content of crops and contribute to a healthy soil by facilitating water retention, soil aeration and nutrient availability, thereby promoting plant growth. In this paper we review the role of these extracts and their bioactive compounds as plant biostimulants. The targeted application to improve crop performance and the impact of seaweed extracts for enhancing the protein content of crops are discussed.

Running title: The power of seaweeds

Review paper

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Abiotic stress, mechanism of action, protein transition, plant growth and development, seaweed biostimulants, sustainable agriculture.

Abstract

In order to meet increasing food demands in the future, we will need to improve the current crop productivity. Abiotic stresses like drought and salinity are major factors resulting in crop yield losses and soil degradation worldwide. Recent studies suggest that seaweed-based biostimulants could be a solution for this problem. Here we summarise the current findings of using these biostimulants and highlight current knowledge gaps. Seaweed extracts were shown to enhance nutrient uptake and improve growth performance in crops under stressed and normal conditions. Seaweed extracts contain phytohormones, polysaccharides, polyphenols, lipids, amino acids and proteins. Although it has been shown that some of these compounds are active and have growth-promoting properties on plants, their underlying molecular mechanism of action and optimal applications especially in crops exposed to abiotic stress remains understudied. Seaweed extracts were shown to also improve protein content of crops and contribute to a healthy soil by facilitating water retention, soil aeration and nutrient availability, thereby promoting plant growth. In this paper we review the role of these extracts and their bioactive compounds as plant biostimulants. The targeted application to improve crop performance and the impact of seaweed extracts for enhancing the protein content of crops are discussed.

1. Introduction

Closing yield gaps

In the future our world will face two major problems: climate change and a growing world population. Estimated global population is expected to reach 10 billion in 2050 (UN DESA, 2017) and with rising temperatures, more desiccation and salinisation will be observed with negative consequences on crop growth and productivity worldwide (Mueller *et al.*, 2012). The substantial increase in food demand must be met while decreasing agriculture's global environmental footprint, and at the same time when agriculture is already challenged due to climate change.

Combining this with a global shift to a more animal-based diet (Henchion *et al.*, 2014), a higher crop productivity worldwide is needed with an important focus on increased plant protein production. The global demand for animal source food is expected to increase by over 70% in 2050, not only because of the growing world population but also due to increased welfare (Alexandratos and Bruinsma, 2012). With increasing welfare the percentage of animal-based food products in the daily diets increases. For example, Western diets shifted from 40% of protein originating from animal sources in the 1960's to more than 60% today (Alexandratos and Bruinsma, 2012; Jalil, Tasoff and Bustamante, 2020). As a consequence of increasing animal-based food consumption, the demand for animal feed will increase even more. To produce 1 kg of animal protein, 3-6 kg of plant protein is needed (Alexandratos and Bruinsma, 2012). Therefore when animal-based food consumption is increasing, the need for plant-based feed is increasing even more. It is predicted that the global protein demand only for feed will reach 1500 Mton in 2050, which will be a real challenge in view of increasing food demand for the growing world population (Alexandratos and Bruinsma, 2012).

Biostimulants as alternatives to enhance crop productivity

To meet future global food demand, it is necessary to increase food production while dealing with less favourable conditions. Stresses like drought, extreme temperatures, water logging and salinity affect productivity and quality of agricultural crops. This challenge forms the basis for a new era in food production where a stable and sustainable increase of crop yield across different environments and under different conditions is key. One approach to meet these demands is to use crops that are more resilient to environmental stresses. Traditionally, breeding programs and improved cultural practices are used to increase crop resilience by producing more tolerant cultivars. However, the success rate and time required for breeding new varieties have been major challenges due to the genetic complexity of abiotic stress resilience in crops. Recently, novel alternatives to enhance crop growth such as the use of plant biostimulants have attracted researchers' attention due to their diverse applications that can enhance plant fitness. Biostimulants are 'materials other than fertilizers and pesticides' that stimulate nutritional processes independent of the crop's nutrient content with the specific aim of enhancing nutrient use efficiency, resilience to abiotic stress, quality traits, or availability of confined nutrients in the soil or rhizosphere (EU, 2019; Rouphael and Colla, 2020). These materials can

be substances and/ or microorganisms that enhance plant growth, increase tolerance to unfavourable environmental conditions, and promote efficient use of plant resources (Yakhin *et al.* , 2017; Campobenedetto *et al.* , 2021). Biostimulants are obtained from e.g., microorganisms, plant- or animal-based by-products recycled from the food industry, or seaweed extracts.

Seaweed extracts as plant biostimulants

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

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

2. Seaweed extracts increase crop productivity under abiotic stresses

Biostimulants derived from seaweed have been commercialised in recent years as substances that improve plant productivity. Under normal environmental conditions, seaweed extracts use may result in higher crop yield and productivity (Yakhin *et al.* , 2017; Roupael and Colla, 2020). Field grown crops (and even sometimes, crops grown in greenhouses) are typically exposed to various stresses during their life cycle. Abiotic stresses such as drought and salinity are responsible for exorbitant crop losses, causing up to 50% reduction in crop yield as well as reducing the productivity potential of arable land (FAO and ITPS, 2015; Gull, Lone and Wani, 2019). Estimations indicate that at least 10% of total arable land are under salinisation or drought globally, with some areas simultaneously experiencing both stresses (FAO and ITPS, 2015; Shahid, Zaman and Heng, 2018; Rojas, 2020). It is therefore important to mitigate the disastrous effects of abiotic stress on crops, while improving crop productivity under these stress conditions.

Crops treated with seaweed extracts recovered from the damaging effects of heat and frost, and showed improved growth and survival under drought and saline conditions (Shukla *et al.* , 2019). The application of seaweed extracts reduced relative water loss and encouraged plant recovery from short-term (4 to 10 days) drought stress in *Arabidopsis* , tomato, soybean and wheat (Santaniello *et al.* , 2017; Goñi, Quille and O'Connell, 2018; Shukla *et al.* , 2018; Sharma *et al.* , 2019). In these cases a reduction of leaf wilting and a significant increase in plant growth parameters were also associated with the seaweed extracts application. Chickpea plants treated with seaweed extracts prior to salinity stress exposure, showed a significant increase in vegetative growth compared to the control, saline-stressed plants not treated with seaweed extracts (Abdel Latef *et al.* , 2017). The same enhanced plant growth under saline conditions was also observed in wheat and rice given seaweed extracts (Zou *et al.* , 2018; Liu *et al.* , 2019).

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

Even though most abiotic stress experiments were performed in controlled greenhouses, positive results of seaweed extracts increasing productivity have also been translated to, and could be replicated on, farm fields (Sharma *et al.* , 2019). The results obtained in field experiments highlight the applicability and potential benefits of using seaweed extracts under more realistic farming conditions. In most cases, crop productivity under severe stress conditions after seaweed extracts treatment remained lower than yields under unstressed conditions (Murtic *et al.* , 2018; Trivedi *et al.* , 2018; Hashem *et al.* , 2019). For example, salinity stress decreased crop productivity of cherry tomatoes by ~ 50%. The use of the *Ascophyllum nodosum* -based biostimulant increased productivity by 85% of the initial crop yield under non-stressed conditions, therefore the yield gap was not fully closed (Murtic *et al.* , 2018). In few published cases, crops treated with seaweed extracts and grown under abiotic stress conditions showed no significant differences in crop yield (Di Stasio *et al.* , 2018) or even inhibitory germination responses (Masondo *et al.* , 2018). Thus, seaweed extracts are not always able to completely reverse or eliminate stress-induced damages, especially under severe abiotic stress. Therefore optimisation of seaweed extracts application rate (dosage and timing) for the crops, as well as insights on the underlying mechanisms may confer efficient use of the biostimulants.

3. Metabolite composition of seaweed-based biostimulants

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

Seaweed extracts are enriched in phytohormones, sterols like fucosterol, carbohydrates, polysaccharides, sugars, polyphenols like flavonoids, macro- and micronutrients, vitamins, lipids, amino acids and proteins, including enzymes (Khan *et al.* , 2009; Shukla *et al.* , 2019). Bioactive polysaccharides identified in seaweed extracts are: galactans (carrageenans and agarans) and floridean starch, ulvans, starch, lignin and cellulose, laminarin, fucoidan, and alginic acid (Shukla *et al.* , 2019). Most seaweed extraction methods result in

a (partial) depolymerization of the polysaccharide pool, resulting in a dominant presence of oligo- and monosaccharides in seaweed extracts (Gullón *et al.* , 2020). Fucoidan oligosaccharides function as elicitors of the local defence response and as priming agents in the systemic defence of plants (Klarzynski *et al.* , 2003). Seaweed-derived alginates and their oligo-derivatives are reported to act in the stimulation of plant growth, development and resistance (Shukla *et al.* , 2019; Mukherjee and Patel, 2020). For example, foliar application of an alginate oligosaccharide (AOS) solution in a short-term hydroponic experiment ameliorated the stress caused by polyethylene glycol-induced drought in wheat (Liu *et al.* , 2013). Moreover, this study reported that upon application of AOS, upregulation of abscisic acid (ABA)-responsive genes that are related to drought resistance was observed (Liu *et al.* , 2013). Therefore, these results suggest that AOS stimulate drought resilience via the ABA-signalling pathway (Liu *et al.* , 2013). Together with the fact that alginate comprises up to 45% of the dry weight in brown seaweed, an important role for this (depolymerized) polysaccharide in seaweed extracts' bioactivity is implied (Vera *et al.* , 2011). Another polysaccharide, laminarin, has been well described as a bio-elicitor in plant defence responses against various pathogens (Romanazzi *et al.* , 2016; Garde-Cerdán *et al.* , 2017; Pugliese *et al.* , 2018). Additionally, laminarin oligosaccharides increased transient Ca^{2+} influx in the cytosol of tobacco (*Nicotiana plumbaginifolia*) cells. Free cytosolic Ca^{2+} is known to mediate a plethora of cellular processes involved in plant growth, development and resistance (Lecourieux *et al.* , 2002). Carrageenans and oligo-carrageenans (polysaccharides abundant in red seaweeds) also enhance growth of various plants by altering key physiological and/ or biochemical processes. These processes include photosynthesis, cell division, synthesis of nucleotide bases of purines and pyrimidines, and nitrogen-, carbon- and sulphur assimilation (Castro *et al.* , 2012; González *et al.* , 2013; Ahmadi *et al.* , 2015; Shukla *et al.* , 2016).

Soluble alginates from seaweeds and protein hydrolysates have been reported to facilitate aggregation of soil particles, which improves the nutrient availability, aeration and water holding capacity in the soil (Khan *et al.* , 2009; Colla *et al.* , 2017). Apart from the direct benefits for the plant, seaweed extracts positively affects the soil microbiome, promoting increase of endophytes. Microbes are reported to absorb free amino acids to a higher extent than plants. In various crops it was observed that only 6% to 25% of the flagged amino acids was absorbed by the roots, while the rest was taken up by the soil microbiome (Moe, 2013). However, another study indicated that microbes excrete a substantial part of the amino acid-derived nitrogen back into the soil as ammonium, where it can be captured by the plant (Jones *et al.* , 2005; Jones, Nguyen and Finlay, 2009). Interestingly, Rouphael *et al.* , 2017 showed a synergistic effect in lettuce between a microbe-based biostimulant and a plant-based protein hydrolysate-rich extract. Crop performance was improved in the combined treatment, compared to the treatment with solely the microbe-based product. This performance was characterised by a higher total root length and surface, enhanced chlorophyll levels and an increase in nitrogen assimilation. Together this represents a strategy to ameliorate salt stress (Rouphael *et al.* , 2017), suggesting that general crop performance can be induced by supplementing the plant's microbiome with protein hydrolysates derived from seaweed extracts.

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

plant. Depolymerization and the degree of sulfation is associated with bioactivity of polysaccharides, thus is regarded to be of importance for the perception of these compounds (Battacharyya *et al.* , 2015; Shukla *et al.* , 2016).

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

4. Mechanism of action in response to biostimulant application

Seaweed extracts efficacy and its mode of action in crops have not yet been fully characterised. Seaweed extracts are thought to have specific modes of action, and mechanisms on how they may increase crop productivity and stress resilience have been proposed (Fig. 1), but linking and validating specific underlying mechanisms to crop responses due to seaweed extracts application still remains unanswered. Chemical analyses of seaweed extracts depicted bioactive components that can be linked to plant metabolic and hormone pathways. This are usually first indications, providing insight into the (possible) underlying mechanisms employed by the seaweed extracts.

Compounds in seaweed extracts may act as signaling molecules regulating key pathways at the transcriptional and/ or post-translational levels (microRNAs), causing differential expression of essential genes in crops (Fig. 1) that all together contribute to increased plant growth and abiotic stress resilience. Genes involved in cell metabolism, including lipid-, amino acid-, nucleotide- metabolism, glycolysis and transport; cell- and cell wall development were specifically modulated upon exposure to seaweed extracts in non-stress conditions (Goñi *et al.* , 2016). An upregulation of stress responsive genes e.g., ABA signaling regulators, Na⁺/ K⁺ transporters, late embryogenesis abundant (LEA) proteins, dehydrins and aquaporins occurred in crops under abiotic stress and treated with seaweed extracts (Muñoz-Mayor *et al.* , 2012; Goñi, Quille and O'Connell, 2018; Pushp S. Shukla *et al.* , 2018; Zou *et al.* , 2018; Sharma *et al.* , 2019). Application of an *Ascophyllum* -derived seaweed extracts in the presence of salinisation, stimulated expression of the microRNAs (miR) miR169g-5p, miR399, miR827 and miR2111b which results in altered expression of target genes, by this means inducing phosphate uptake and salinity resilience of *Arabidopsis* plants (Shukla *et al.* , 2018). Growth stimulation due to the application of seaweed extracts may also be linked to higher photosynthetic rates and corresponding increased levels of chlorophyll pigments (chlorophyll a, b and carotenoids) in such crops, relative to their non-treated and abiotic stressed counterparts (Abdel Latef *et al.* , 2017; Murtic *et al.* , 2018; Trivedi *et al.* , 2018; Hussein *et al.* , 2021). Mediating the activity of enzymes and genes involved in efficient nutrient assimilation (Fig. 1b, d) is another proposed mode of action that contributes to overall increased growth (Goñi *et al.* , 2016; Yakhin *et al.* , 2017; Shukla *et al.* , 2019). Crops treated with seaweed extracts accumulate more macro- and micro-elements, as well as carbohydrates, proteins and vitamins independent of the presence or absence of stress (Di Stasio *et al.* , 2018; Trivedi *et al.* , 2018; Hussein *et al.* , 2021). Furthermore, higher production of phenolic acids such as flavonoids e.g., naringenin and rutin in tomato, are stimulated by seaweed extracts treatment (Fig. 1b, d) leading to enhanced fruit colouring and flavour profile of the crops (Murtic *et al.* , 2018; Shukla *et al.* , 2019).

Modulation of hormone pathways due to seaweed extract application promote plant growth and develop-

ment under both stress and unstressed conditions (Fig. 1d). Derivatives of the phytohormones ABA, auxin e.g., indole-3-acetic acid (IAA) and indole-3-butyric acid (IBA), CK e.g., benzyl adenine (BA) and zeatin, gibberellin e.g., gibberellic acid (GA3), and jasmonic acid were further induced in rapeseed plants treated with certain seaweed extracts and exposed to salinity stress (Hashem *et al.* , 2019). Additionally, seaweed extracts alleviate abiotic stresses by increasing antioxidant activity of reactive oxygen species (ROS) scavenging enzymes e.g., superoxide dismutase, peroxidases, catalases and phenolic antioxidants (Abdel Latef *et al.* , 2017; El Boukhari *et al.* , 2020; Hussein *et al.* , 2021). This leads to a reduction in ROS accumulation (Fig. 1d), observed as decreased H₂O₂ levels and reduced accumulation of lipid peroxidation, measured as the malondialdehyde content (Abdel Latef *et al.* , 2017; Goñi, Quille and O'Connell, 2018; Trivedi *et al.* , 2018). The accumulation of osmo-protectants such as proline, sugars and organic acids also occur due to the application of seaweed extracts (Fig. 1d). Drought and salt-exposed plants treated with seaweed extracts show increased proline and sugar (glucose, fructose and sucrose) levels (Goñi, Quille and O'Connell, 2018) that serve as osmolytes essential for maintaining osmotic balance during the stress (Singh *et al.* , 2015).

Of importance is that small differences in the components of extracts derived from the same seaweed species may still lead to much bigger variation at the molecular or cellular level and in overall crop responses, in crops where these seaweed extracts are applied (Goñi *et al.* , 2016; Ertani *et al.* , 2018). Thus, generalisations on the mode of action (and resulting benefits) of the seaweed extracts should not be made, rather independent experiments must be performed to confirm hypotheses. Most of the strategies discussed in the paragraphs above are typically employed by plants during their life cycle, including the activation of specific pathways to cope with abiotic stress (Zhu, 2016, Fig. 1c). Moreover, a lot of cross-talk occurs between signaling pathways, therefore application of seaweed extracts may induce and/ or repress multiple pathways or metabolic processes simultaneously. Hence, this presents one of the difficulties in deciphering and characterising specific underlying mechanisms employed by seaweed extracts. Although the presence of phycocolloids e.g., alginates and carrageenans in seaweed extracts, that are otherwise absent in land plants, support the argument that these extracts have a unique mode of action, it is still possible that the application of a single seaweed-based extract may have broad spectrum additive impact on crops, modulating several response mechanisms to stimulate growth and survival of plants in both stressed and unstressed conditions. Overall, further research in this direction is still needed to make concrete inferences. Understanding exactly how the underlying mechanisms function is key for increasing seaweed extracts effectivity and efficiency, to improve crop performance under abiotic stress in the field.

5. Effect of seaweed extracts on protein production in crops

Global seaweed production has risen exponentially in recent decades to 30 Mton annually. Moreover, apart from their potential as a direct food source for humans and animals, seaweed extracts were not only shown to boost abiotic stress resistance in crops but also to increase its nutritional value (Shukla *et al.* , 2019). Overall crop yield could be increased by application of seaweed extracts as biostimulants under normal and stress conditions. Here we summarise (Table 1) that seaweed extracts can also increase protein productivity in crops. Several reports showed that seaweed extracts increased the crude protein content in plant families like *Fabaceae* and *Poaceae* . The highest increase in protein content by two-fold (~ 200%) was reported in *Vigna sinensis* (Table 1). Considerable protein increase was shown as well in *Triticum aestivum* , *Musa spp.* and *Allium cepa* (Table 1). An explanation for the increased protein content is the amplified plant uptake of more essential nutrients for protein production, that may be due to enhanced root systems because of the seaweed extracts application as reported in Sivasankari *et al.* (Sivasankari *et al.* , 2006). Alteration of the root system and increased nutrient assimilation in crops have also been reported during abiotic stress (Shukla *et al.* , 2019; El Boukhari *et al.* , 2020; Campobenedetto *et al.* , 2021), so there is a potential of increased protein productivity during abiotic stress. However, whether seaweed extracts improve root system and therefore crop protein productivity under adverse conditions remains unanswered, since all the experiments (Table 1) were only performed under non-stressed conditions.

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

6. Perspective

Today there are many commercial seaweed biostimulants available for agricultural use (Khan *et al.* , 2009; Shukla *et al.* , 2019), so the basis for a broad use of seaweed extracts is already created. Although the effectiveness of many of these extracts have been proven, especially under experimentally controlled conditions, not all mechanisms of action have been revealed (Shukla *et al.* , 2019). In addition, more field trials testing the optimal concentrations of extracts for different crops and under varied soil conditions should be carried out. Future field experiments should also address the business case i.e., how many seaweed extracts applications are needed and what is the return on investment. Also, these experiments may, in combination with seaweed extracts factory production data, give insight in which direction large-scale commercial seaweed production should evolve. Further elaboration on the question whether ‘seaweeds should be cultivated to stimulate productivity of arable crops under normal and unstressed conditions, or are they more beneficial as direct food source for humans?’ remains of interest. We advocate that less seaweed cultivation surface area is needed to finally produce similar or more protein productivity in arable crops after seaweed extracts application, compared to direct seaweed (protein) consumption.

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

Overall, seaweed biostimulants have numerous positive effects on plant growth and thus have the potential to solve some of the problems agriculture will face in the future. Our findings suggest that future agricultural practices can make use of seaweed-based biostimulants to increase crop yield, nutritional value and protein content per acre, including in crops grown on marginal lands currently subject to severe drought and salinity. In this way seaweed extracts can contribute to an increased annual global protein productivity, without increasing arable land use at the cost of precious natural habitat and biodiversity. The application of seaweed extracts to improve soil quality (Shukla *et al.* , 2019) may be further explored as a potential solution for soil recovery or to facilitate bioremediation.

Author Contributions

A.O.D.-A., I.M.vdM., R.K. collected the data and wrote the original manuscript. A.O.D.-A., I.M.vdM., A.vdW., R.K. reviewed and edited the manuscript. All authors have read and agreed to the published version of the manuscript.

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Conflicts of Interest

There is no conflict of interest.

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Figure 1. Underlying mechanism of action under (a) normal conditions and (b) normal conditions with the application of seaweed extracts (SE). Under normal (unstressed) conditions, seaweed extracts stimulate a number of processes resulting in improved crop growth and productivity. Seaweed extracts facilitate assimilation of both macro- and micronutrients e.g., N (nitrogen), K (potassium), Ca (calcium), Mg (magnesium) and Fe (iron). Alginates present in seaweed extracts improve soil quality and structure by boosting water retention, air circularity and promoting endophyte activity. Seaweed extracts induce genes/ enzymes involved in cell wall biosynthesis and photosynthesis. Induction of other genes/ enzymes of important metabolic pathways by seaweed extracts result in higher crop protein, amino acid, lipid, carbohydrate, vitamin, flavonoid, chlorophyll and carotene content. Proposed mechanism of action in response to (c) abiotic stress conditions and (d) abiotic stress conditions with seaweed extracts' application. Under abiotic stresses like salinity, drought and freezing, seaweed extracts mediate certain metabolic processes resulting in improved crop resilience and growth under the stress. Seaweed extracts cause up/ down-regulation of transcription factors (TFs), microRNAs and genes involved in maintaining N and P (phosphorus) homeostasis. The application of seaweed extracts to crops increase the levels of the phytohormone ABA (abscisic acid) and hormonal derivatives IAA (indole-3-acetic acid), IBA (indole-3-butyric acid), zeatin, GA3 (gibberellic acid) and JA (jasmonic acid). Stress responsive dehydration responsive element binding (DREB) TFs, late embryogenesis abundant (LEA) proteins and aquaporins are further induced in the presence of seaweed extracts. Osmotic balance is maintained by further accumulation of osmo-protectants like proline and sugars, by the seaweed extracts. The extracts have a positive effect on chlorophyll pigment and flavonoid accumulation. Reactive oxygen species (ROS) production is inhibited upon treatment with seaweed extracts.

Table 1. Seaweed extracts increase protein content in crops.

Source	Seaweed specie	Crop	Concentration of seaweed
(Hidangmayum and Sharma, 2017)	<i>Ascophyllum nodosum</i>	<i>Allium cepa</i>	0,55%
(Kocira <i>et al.</i> , 2018)	<i>Ascophyllum nodosum</i>	<i>Glycine max</i> L. (Annushka)	0,70%
(Kocira <i>et al.</i> , 2018)	<i>Ascophyllum nodosum</i>	<i>Glycine max</i> L. (Atlanta)	0,70%
(Kocira <i>et al.</i> , 2018)	<i>Ascophyllum nodosum</i>	<i>Glycine max</i> L. (Mavka)	1,00%
(Kulkarni <i>et al.</i> , 2019)	<i>Ecklonia maxima</i>	<i>Spinacea oleracea</i> L	0,40%
(Rengasamy <i>et al.</i> , 2016)	<i>Ecklonia maxima</i>	<i>Brassica oleracea</i>	0,40%
(Sivasankari <i>et al.</i> , 2006)	<i>Caulerpa chemnitzia</i>	<i>Vigna sinensis</i>	20,00%
(Sivasankari <i>et al.</i> , 2006)	<i>Sargassum wightii</i>	<i>Vigna sinensis</i>	20,00%
(Jothinayagi and Anbazhagan, 2009)	<i>Sargassum wightii</i>	<i>Abelmoschus esculentus</i>	20,00%
(Shah <i>et al.</i> , 2013)	<i>Kapaphycus alvarezii</i>	<i>Triticum aestivum</i>	7,50%
(Shah <i>et al.</i> , 2013)	<i>Gracilaria edulis</i>	<i>Triticum aestivum</i>	7,50%

Source	Seaweed specie	Crop	Concentration of seaweed
(Layek <i>et al.</i> , 2018)	<i>Gracilaria edulis</i>	<i>Oryza sativa</i>	15,00%
(Layek <i>et al.</i> , 2018)	<i>Kapaphycus alvarezii</i>	<i>Oryza sativa</i>	15,00%
(Karthikeyan and Shanmugam, 2016)	<i>Kapaphycus alvarezii</i>	<i>Musa spp.</i> (Robusta)	5,00%
(Karthikeyan and Shanmugam, 2016)	<i>Kapaphycus alvarezii</i>	<i>Musa spp.</i> (Njali poovan)	5,00%
(Karthikeyan and Shanmugam, 2016)	<i>Kapaphycus alvarezii</i>	<i>Musa spp.</i> (Red banana)	5,00%
(Karthikeyan and Shanmugam, 2016)	<i>Kapaphycus alvarezii</i>	<i>Musa spp.</i> (Nendran)	5,00%
(Zodape <i>et al.</i> , 2011)	<i>Kapaphycus alvarezii</i>	<i>Vigna radiata</i>	10,00%

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Figure1.pdf available at <https://authorea.com/users/437344/articles/539045-the-power-of-seaweeds-as-plant-biostimulants-to-boost-crop-production-under-abiotic-stress>