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Mini-Review: brown macroalgae as a promising raw material to produce biostimulants for the agriculture sector

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The worldwide growing food demand and the excessive use of synthetic and chemical inputs compel the agricultural sector to find innovative and sustainable solutions to enhance or at least maintain crop yields in times of increased abiotic stresses levels linked to global change. Currently, great research efforts are carried out on brown seaweeds as their environment lead them to produce a broad range of compounds, with osmoregulatory, antioxidant, pro-bacterial, and plant-growth promoting activities. Indeed, numerous studies are looking at different combinations of algal species, extraction processes, plant species and environments of plant culture to highlight the various effects of algal extracts on plant growth and development, and resistance to abiotic stresses. Consequently, a wide variety of novel commercial products are emerging, presenting diversified chemical compositions, formulations and means of application. Such products allow the biostimulation of plants and soil by alleviating abiotic stresses such as drought, frost, and salt. The action of brown macroalgal extracts on plant and soil health has been repeatedly demonstrated, yet the precise relation between the extract chemical composition and its subsequent effect is still to be elucidated, as molecular synergy is suspected to play an important role. In this review, we present the interest of using brown macroalgal extracts to produce biostimulants with beneficial action on soil health, plant growth and development, as well as resistance against abiotic stresses, in relation to the molecular changes occurring.

KEYWORDS

Phaeophyceae, seaweeds extracts, primary and secondary metabolites, plant physiology, agricultural biostimulants, commercial products, abiotic stress tolerance, mechanisms of action

1 Introduction

The upcoming years will see the agriculture sector facing several threats that could hinder its capacity to ensure global food safety. Indeed, world population is estimated to reach 9.7 billion by 2050 (UN DESA, 2017), considerably increasing crop production need for direct human consumption and livestock farming. Meanwhile, global change is altering biotic and abiotic factors (Shrivastava and Kumar, 2015; Raza et al., 2019), negatively impacting crop development and yield (European Environment Agency, 2017; FAO, 2021). Hence, the crop production demand will rise in an increasingly hostile environment for agricultural cultivation, which calls for a modification of current agricultural practices. Additionally, as ecological awareness is gaining momentum, being durable and safe is one of the leading challenges of modern agriculture (Sujeeth et al., 2022). During the last decades, intensive agriculture has rendered the once-fertile arable soils into impoverished lands, both in terms of nutrients and physical structure (Patle et al., 2019; Mandal et al., 2020). Non-degradable synthetic inputs have tenacious persistence in the environment and are responsible for eutrophication from run-offs and water pollution. These chemicals also have harmful consequences on human and animal health, stemming from their strong toxicity (Ali et al., 2021a). Consequently, more and more legislations are being passed to manage nutrient excess and reduce the range of harmful synthetic agricultural products, which have resulted in an increase in fertiliser prices (European Commission, 2021; Baffes and Chian Koh, 2022). As a result, the agricultural industry attempts to reduce synthetic inputs in crops and is pressured to look for efficient natural alternatives.

Biostimulants are currently gaining attention in this regard. According to the last European regulation on fertilisers EU2019/1009, a biostimulant is a product of natural origin, that “stimulates plant nutrition processes independently of the product’s nutrient content with the sole aim of improving one or more of the following characteristics of the plant or the plant rhizosphere: (a) nutrient use efficiency, (b) tolerance to abiotic stress, (c) quality traits, (d) availability of confined nutrients in soil or rhizosphere” (European Parliament and Council, 2019). Overall, the use of biostimulants on crops lead to an increase of the parameters sought by the agri-food sector, *i.e.* food product yield, quality, and shelf-life (EBIC, 2021). Their utilization, in synergy with organic and inorganic fertilisers, enhances the effects of the latter, and confers abiotic stress resilience (Rouphael and Colla, 2018). It allows the reduction of synthetic inputs, and indirectly their impact on the environment by limiting leachates. The biostimulant market is ever-growing, with a worldwide double-digit growth, showing a will of the agricultural sector to shift their practices (Smiglak-Krajewska and Wojciechowska-Solis, 2021; Moolla, 2022). This rapid growth is also linked to numerous actors and products already present on the market, sometimes creating confusion on terminologies and claimed product effects (Caradonia et al., 2019; Moolla, 2022). To harmonize the European market, a new regulation frames the registration of biostimulants and the authorization to commercialize under this nomenclature. It encompasses several criteria, including evidences of biostimulant effects by independent studies, and microbiological and chemical safety, notably regarding heavy metals contamination (European Parliament and Council, 2019).

Biostimulants are categorized according to their raw material source, their principal bioactive compound, or their mode of action (du Jardin, 2015). Among them, one of the most promising classes is brown macroalgal extracts (BME). They do not naturally possess enough fertilizing power to be classified as fertilisers, but they can stimulate plant internal responses for growth and defense, thus having tremendous potential for the agricultural sector (Samuels et al., 2022). Overall, BME application results in increases in production levels, health and quality of crops (Nanda et al., 2022), and is considered harmless for humans, animals and the environment (Renaut et al., 2019). Finally, as brown macroalgae are growing at sea, they do not enter in land competition with crop production (Deolu-Ajayi et al., 2021) and do not require water nor fertilisers supply to grow. Therefore, BME are rapidly developing in the biostimulant market, with the emergence of numerous commercial products (El Boukhari et al., 2020; Critchley et al., 2021; EBIC, 2021). Brown macroalgae, or Phaeophyceae (Chromista, Ochrophyta), are the second largest group of macroscopic algae, with ~2,100 identified species (Guiry and Guiry, 2023). They all contain a specific xanthophyll pigment, fucoxanthin, responsible for their characteristic brown-yellow color (Lee, 1999). They also produce a broad range of bioactive compounds, of which a large number have positive effects on plant growth and development, and stress alleviation (Sujeeth et al., 2022).

The present review aims to highlight the potential of BME as biostimulants for agrochemical alternatives. Various brown macroalgal compounds displaying plant promotion and stress alleviation activities are first presented. Then, biostimulant activities are displayed in respect to macroalgal species, plant species and potential compounds involved. Though biocontrol-like activities have sometimes been reported for biostimulant products, this review only focuses on biostimulant effects *i.e.*, under abiotic stresses. Finally, the potential molecular mechanisms implicated in the various activities are presented. The conceptual diagram in Figure 1 summarizes the full potential of BME regarding plant global health.

2 Brown macroalgal metabolites beneficial to plant health and growth

Brown macroalgae biochemical composition is modulated by their stressful living environment, which involves both biotic and abiotic parameters. In response, they produce a wide range of bioactive metabolites that modulate their resilience to stress factors (Connan and Stengel, 2011; Stengel et al., 2011; Lalegerie et al., 2020). These metabolites, *i.e.* minerals, carbohydrates, proteins, lipids, phlorotannins, pigments, vitamins, have applications in numerous sectors, including plant health and growth (Sujeeth et al., 2022).

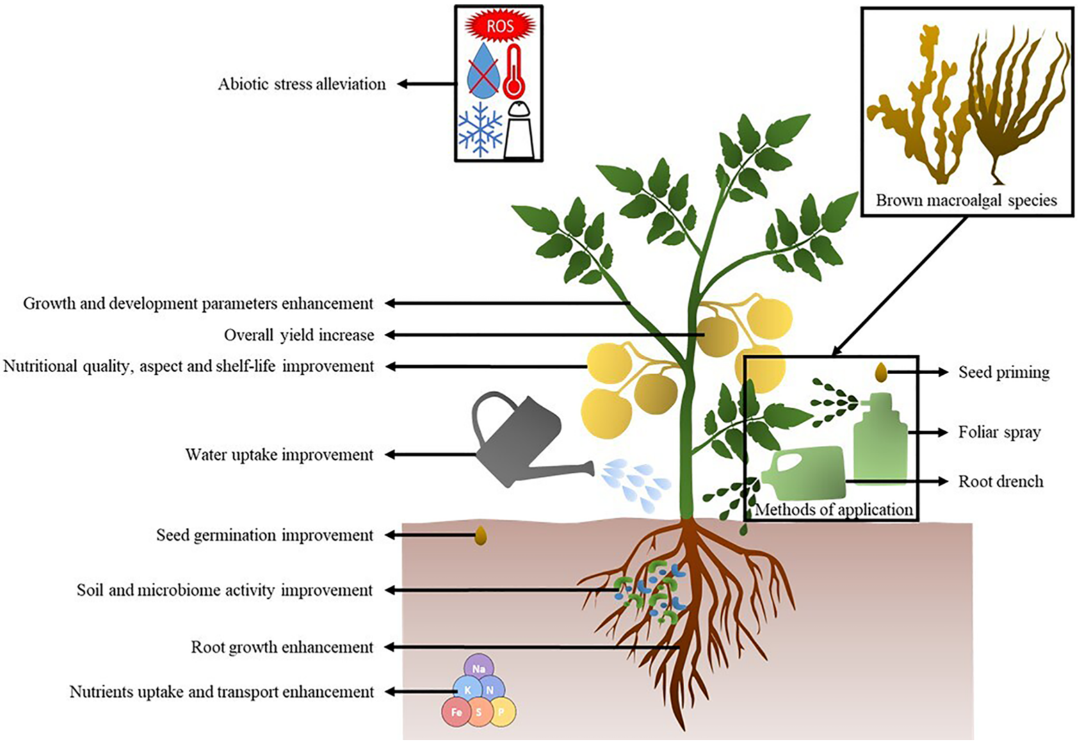

FIGURE 1
Conceptual diagram of the beneficiary effects of brown macroalgal extracts on plants.

Brown macroalgae have strong absorption and accumulation capacities of surrounding salts and minerals. As a result, they usually have a high mineral content, between 9 and 44% of the algal dry weight (DW). This content varies depending on species, seasonality, and surrounding seawater mineral concentration (Circuncisão et al., 2018). Minerals are involved in various plant cellular metabolism pathways and can trigger and/or directly enhance plant growth and defense mechanisms, leading to enhanced crop yields and quality (Kolbert et al., 2022; Lešková et al., 2022). Indeed, metal elements such as copper (Van Nguyen et al., 2022), iron (Rout and Sahoo, 2015; Murgia et al., 2022), manganese (Alejandro et al., 2020), molybdenum (Huang et al., 2022), nickel (Tanveer, 2020), and zinc (Thiébaut and Hanikenne, 2022) are essential plant micronutrients, involved in energy metabolism, photosynthesis, respiration, reproduction, gene expression regulation, and stress tolerance (D'Oria et al., 2021). Conversely, mineral deficiencies can reduce nutrient uptake and metabolism, which in turn negatively affect growth, yield and quality of the harvested product (Courbet et al., 2019; Thiébaut and Hanikenne, 2022).

Brown macroalgae are especially rich in carbohydrates, *i.e.* alginates, fucoidans, laminarans, mannitol and cellulose (Percival and McDowell, 1967; Stiger-Pouvreau et al., 2016), reaching up to 80% DW in some species; this proportion varying greatly according to species, geographical location, maturation degree and seasonality (Stiger-Pouvreau et al., 2016; Mohd Fauziee et al., 2021). Carbohydrates have several functions in soil health and crop enhancement, notably as metabolic triggers signals for physiological defense responses such as the production of phytochemical compounds (Laporte et al., 2007; Briceño-Domínguez et al., 2014). These effects were notably observed in cabbage (Di Stasio et al., 2017b), tobacco (Chandía and Matsuhiro, 2008), tomato (Mzibra et al., 2021), and wheat (Chandía et al., 2004; Zou et al., 2019; Zou et al., 2021).

Proteins are not usually abundant in brown macroalgae, ranging from 3 to 15% DW, owing to species, seasonality and environmental conditions such as temperature variations (Fleurence, 1999). Brown macroalgae are rich in aspartic and glutamic acids (Pangestuti and Kim, 2015), which are involved in the biosynthesis of nitrogen-containing compounds such as proline (El-Metwally et al., 2022), improve nitrogen uptake (Colla et al., 2015; El-Metwally et al., 2022), have a positive effect on photosynthetic activity (El-Metwally et al., 2022), and reduce physiological damages induced by oxidative stress (Rizwan et al., 2017; El-Metwally et al., 2022).

Brown macroalgae have a low lipid content, ranging from 0.3 to 6% DW (Nugroho Jati et al., 2019; Alghazeer et al., 2022). Lipophilic compounds play roles in plant growth and stress resilience processes, regulating cell membrane permeability and increasing the tolerance to freezing stress (Rayorath et al., 2008b; Muthuramalingam et al., 2022).

Phlorotannins, specific phenolic compounds of brown macroalgae (Stengel et al., 2011; Stiger-Pouvreau et al., 2014), range from 0.1 to 18% DW (Connan et al., 2004; Stiger-Pouvreau et al., 2014) depending on localization, season, light, and algal species and age (Stiger-Pouvreau et al., 2014). They have a broad range of bioactivities, including antioxidant, antibacterial, antifungal, anthelmintic and nematicide to alleviate biotic and abiotic stresses in plants (Zubia et al., 2015), and enhance the nutritional quality of food products (Teklić et al., 2021).

Finally, pigments or vitamins could have biostimulant properties, but few studies have been made to evaluate their effects on plants (Khan et al., 2009; Ali et al., 2021a; Teklić et al., 2021).

3 Beneficiary effects of BME on plants

BME have multiple beneficiary effects on plants (Figure 1; Table 1). Several parameters influence the ability to obtain these desired outcomes. Indeed, various combinations of BME (species, methods of extraction, qualitative composition…), plant species and methods of application (dose rate, foliar or root drench application…) induce a wide variability of end results (Caradonia et al., 2022).

3.1 Soil structure and quality

A healthy soil is essential for plant productivity. BME can improve soil physical, chemical, and biological properties (Samuels et al., 2022). Indeed, they contain several chelating agents, such as alginates, that can combine with metallic ions to form high molecular weight aggregates (Kholssi et al., 2022). These aggregates promote water absorption and retention, as well as soil stability and aeration through improved pores capillary activity (Illera-Vives et al., 2015; Shukla et al., 2019). Furthermore, BME improve nutrients availability by stimulating soil microbial activity for nutrient mineralization (Renaut et al., 2019), and as a direct source of organic matter and trace elements (Di Filippo-Herrera et al., 2019). BME can also function as biosorption agents for polluted soils bioremediation. Their polyanionic abilities allow the entrapment of pollutants, notably heavy metals, to eliminate them from the environment (Amador-Castro et al., 2021).

3.2 Root growth and nutrients uptake

BME can stimulate plant roots growth and development, in particular when applied on early growth stages (Samuels et al., 2022). Growth and elongation stimulatory activity on tomato roots was reported for the commercial *Ecklonia maxima* extract at lower concentrations (0.038-0.057g/L), while a more concentrated extract (0.230g/L) inhibited root growth (Finnie and van Staden, 1985). The authors related the activity to endogenous plant hormones and found an equivalent activity with 0.1 nM cytokinin zeatin. Root growth and development parameters enhancement were also assessed both in lettuce treated by a *Durvillaea* commercial mixture (Yusuf et al., 2019), and strawberry treated by *Ascophyllum nodosum* (AN), *Sargassum* sp. and *Laminaria* sp. extracts under nutrient stress (El-Miniawy et al., 2016). Improvements in the root system allow a better nutrients and water absorption and use, by acting on genes involved in nutrient root uptake. Indeed, nitrogen, phosphorus, potassium and sulphur uptakes were enhanced after the application of the commercial AN extract, following the improvement of rapeseed root growth (Billard et al., 2014). Similarly, a *Laminaria* sp. acid extract improved boron, calcium, copper, iron, manganese, magnesium, molybdenum, sulphur and zinc uptake in nutrient-stressed maize (Ertani et al., 2018). The root stimulatory effect was lost when the extract was reduced to ash, suggesting an organic origin of the bioactive compounds (Zhang and Ervin, 2004).

3.3 Soil and plant microbiome

Leaves, roots and surrounding soil are fully colonized by microorganisms, allowing active microbe-plant interactions. These surfaces secrete soluble compounds such as carbohydrates, amino and organic acids, that can be used as an carbon source by a wide range of beneficial microorganisms for their proliferation (Haichar et al., 2008). Microorganisms have an important role in soil health and healthy plant growth and development, through biofilm formation for particles aggregation, water retention, nutrient cycling and transport, degradation of toxic substances, and control of plant illnesses (Renaut et al., 2019).

The action mechanism of BME on rhizosphere and phyllosphere microbiota and the precise interactions between microbiota and plants are still unknown. Extracts characterization, observations of their impacts on microbial communities and resulting plant-microbe interactions can help to understand the links between algal extract composition, microbial structure and plant growth enhancement (Renaut et al., 2019). The modification of the plant and soil secretions by BME can influence the structure and activity of the microbial population, which in turn impact the plant growth and development process (Shukla et al., 2019). In this sense, an increase in root and soil microbial α-diversities and a low but significant positive impact on microbial β-diversity following the application of an AN commercial extract on pepper and tomato were observed (Renaut et al., 2019). The rhizosphere microbial α-diversity of strawberry was also increased after the application of another AN commercial extract rich in betaine, alginic acid and caidrine (Spinelli et al., 2010). Both studies suggest at least a partial implication of the extracts on the structure of the microbial communities. BME can also prompt beneficial soil microbial growth and activity, as well as soil conditioning compounds production by these microorganisms (Deolu-Ajayi et al., 2021).

3.4 Seed priming

Plant seedlings can be subjected to various abiotic stresses, including drought and salinity, threatening their germination and establishment. These stresses can trigger a physiological dormant state that prevents germination under unfavorable conditions. Application of BME can induce a “primed” physiological state of seedlings by inducing various biochemical changes that lead to dormancy break and trigger germination under stressful conditions

TABLE 1 Brown macroalgal species, bioactive compounds and associated biostimulant commercial products, regarding their activities on various plants.

Algal species (Order)	Bioactive compound	Commercial product	Plant species	Benefits	References
***Ascophyllum nodosum* (Fucales)**	Plant growth regulators-like (gibberellins, betaines, cytokinins)	Acadian® Actiwave® AlgaeGreen™ Algal30® Algamare® ALGEA® Algifert® Algifol™ Algreen® AZAL5® Bio-algeen® Ekologik® Goëmar® Maxicrop® Seasol® Stella Maris® Stimplex® SuperFifty® Tasco® Wokozim® WUXAL®	Apple (*Malus domestica*) Asparagus (*Asparagus aethiopicus*) Barley (*Hordeum vulgare*) Bell pepper (*Capsicum annuum*) Blueberries (*Vaccinium corymbosum*) Broccoli (*Brassica oleracea*) Carrot (*Daucus carota*) Cauliflower (*Brassica oleracea*) Cherry tomato (*Solanum lycopersicum* var. *cerasiforme*) Creeping bentgrass (*Agrostis stolonifera*) Cucumber (*Cucumis sativus*) Cyclamen (*Cyclamen persicum*) French bean (*Phaseolus* sp.) Grapevine (*Vitis vinifera*) Kiwi (*Actinidia* sp.) Lettuce (*Lactuca sativa*) Lily (*Lilium* sp.) Maize (*Zea mays*) Olive (*Olea europaea*) Onion (*Allium cepa*) Orange (*Citrus* spp.) Pine (*Pinus* sp.) Poplar (*Populus* sp.) Potato (*Solanum tuberosum*) Rapeseed (*Brassica napus*) Rice (*Oryza sativa*) Soybean (*Glycine max*) Spinach (*Solanum oleracea*) Strawberry (*Fragaria x ananassa*) Sugarcane (*Saccharum officinarum*) Thale cress (*Arabidopsis thaliana*) Tobacco (*Nicotiana tabacum*) Tomato (*Solanum lycopersicum*) Turfgrass (*Festuca arundinacea*) Watermelon (*Citrullus lantus*) Wheat (*Triticum aestivum*)	- Nutrient uptake and transport enhancement - Water uptake improvement - Root growth enhancement - Soil and plant microbiome structure and activity improvement - Seed germination improvement - Growth and development parameters increase - Overall yield increase - Nutritional quality (total soluble sugars carotenoids, lycopene, flavonoids, phenolics, proteins, anthocyanins, vitamin C, quercetin), aspect and shelf-life improvement - Abiotic stress (drought, heat, frost, salinity, oxidative) alleviation	Abetz and Young, 1983; Blunden et al., 1986; Steveni et al., 1992; Whapham et al., 1993; Fornes et al., 1995; Chouliaras et al., 1997; Möller and Smith, 1999; Fike et al., 2001; Fornes et al., 2002; Zhang and Ervin, 2004; Colapietra and Alexander, 2006; Norrie and Keathley, 2006; Basak, 2008; Rayorath et al., 2008a; Rayorath et al., 2008b; Zhang and Ervin, 2008; Chouliaras et al., 2009; Loyola and Muñoz, 2009; Spinelli et al., 2009; Abdel-Mawgoud et al., 2010; Neily et al., 2010; Spann and Little, 2010; Spinelli et al., 2010; Zhang et al., 2010; Fan et al., 2011; Khan et al., 2011; Spann and Little, 2011; De Lucia and Vecchietti, 2012; Gajc-Wolska et al., 2012; Khan et al., 2012; Lola-Luz et al., 2012; MacDonald et al., 2012; Muñoz-Mayor et al., 2012; Nair et al., 2012; Alam et al., 2013; Fan et al., 2013; Jannin et al., 2013; Wally et al., 2013; Alam et al., 2014; Amaral Carvalho et al., 2014; Billard et al., 2014; Fan et al., 2014; Lola-Luz et al., 2014a; Lola-Luz et al., 2014b; da Silveira et al., 2015; Xu and Leskovar, 2015; El-Miniawy et al., 2016; Goñi et al., 2016; Martynenko et al., 2016; Di Stasio et al., 2017a; Fei et al., 2017; Gomathi et al., 2017; Hidangmayum and Sharma, 2017; Santaniello et al., 2017; Al-Ghamdi and Elansary, 2018; Ali et al., 2018; Di Stasio et al., 2018; Ertani et al., 2018; Goñi et al., 2018; Mattner et al., 2018; Murtic et al., 2018; Shukla et al., 2018a; Shukla et al., 2018b; Valencia et al., 2018; Chen et al., 2019; Dalal et al., 2019; de Sousa et al., 2019; Renaut et al., 2019; Silva et al., 2019; Yusuf et al., 2019; Zamani-Babgohari et al., 2019; Abbas et al., 2020; Di Stasio et al., 2020; Dziugieł and Wadas, 2020; Omidbakhshfard et al., 2020; Dell'Aversana et al., 2021; Dookie et al., 2021; Goñi et al., 2021; Rasul et al., 2021; Staykov et al., 2021
***Bifurcaria bifurcata*(Fucales)**			Tomato (*Solanum lycopersicum*)	- Seed germination improvement	Mzibra et al., 2021
Cystoseira* sp.** ***C. compressa ***C. foeniculacea* (Fucales)**			Maize (*Zea mays*) Rapeseed (*Brassica napus*) Tomato (*Solanum lycopersicum*)	- Seed germination improvement - Growth and development parameters increase - Overall yield increase - Nutritional quality improvement - Abiotic stress (salinity) alleviation	Hashem et al., 2019; Hussein et al., 2021; Mzibra et al., 2021

(Continued)

TABLE 1 Continued

Algal species (Order)	Bioactive compound	Commercial product	Plant species	Benefits	References
Durvillaea antarctica ***D. potatorum* (Fucales)**		Seasol®	Broccoli (*Brassica oleracea*) Lettuce (*Lactuca sativa*) Strawberry (*Fragaria x ananassa*) Tomato (*Solanum lycopersicum*)	- Root growth enhancement - Growth and development parameters increase - Overall yield increase - Abiotic stress (nutrient) alleviation	Carrasco-Gil et al., 2018; Mattner et al., 2018; Yusuf et al., 2019
Ecklonia arborea ***E. maxima* (Laminariales)**	Plant growth regulators-like (cytokinins)	Kelpak®	Apple (*Malus domestica*) Barley (*Hordeum vulgare*) Bean (*Phaseolus* sp., *Vigna* sp.) Bell pepper (*Capsicum annuum*) Cabbage (*Brassica oleracea*, *B. rapa*) Carrot (*Daucus carota*) Cascading geranium (*Pelargonium peltatum*) Wild foxlove (*Ceratotheca triloba*) Lettuce (*Lactuca sativa*) Maize (*Zea mays*) Marigold (*Tagetes patula*) Peanut (*Arachis* hypogaea) Pine (*Pinus pinea*) Potato (*Solanum tuberosum*) Spinach (*Solanum oleracea*) Swish chard (*Beta vulgaris*) Tomato (*Solanum lycopersicum*) Wheat (*Triticum aestivum*)	- Nutrient uptake and transport enhancement - Root growth enhancement - Growth and development parameters increase - Overall yield increase - Nutritional quality (vitamin C, phenolics) improvement	Featonby-Smith and van Staden, 1983; Nelson and van Staden, 1984; Finnie and van Staden, 1985; Nelson and van Staden, 1986; Aldworth and van Staden, 1987; Featonby-Smith and van Staden, 1987a; Featonby-Smith and van Staden, 1987b; Beckett and van Staden, 1989; Temple et al., 1989; Beckett and van Staden, 1990; Crouch et al., 1990; Crouch and van Staden, 1991; Crouch and van Staden, 1992; Atzmon and Van Staden, 1994; Beckett et al., 1994; van Staden et al., 1994; Kowalski et al., 1999; Arthur et al., 2003; Basak, 2008; Matysiak et al., 2011; Urbanek Krajnc et al., 2012; Di Stasio et al., 2017b; Masondo et al., 2018; Rouphael et al., 2018; Di Filippo-Herrera et al., 2019; Kulkarni et al., 2019; Mola et al., 2019; Dziugieł and Wadas, 2020; Poberezny et al., 2020; Wadas and Dziugieł, 2020
***Fucus* sp.** ***F. spiralis* (Fucales)**		Algafect®	Apple (*Malus domestica*) Bean (*Phaseolus vulgaris*) Maize (*Zea mays*) Tomato (*Solanum lycopersicum*)	- Overall yield increase - Nutritional quality improvement	Malaguti et al., 2002; Mansori et al., 2015; Bradáčová et al., 2016; Mzibra et al., 2021
***Gongolaria barbata* (Fucales)**			Aubergine (*Solanum melongena*) Bell pepper (*Capsicum annuum*) Tomato (*Lycopersicon esculentum*)	- Seed germination improvement - Abiotic stress (freezing) alleviation	Demir et al., 2006
***Hydroclathrus* sp. (Ectocarpales)**			Rice (*Oryza sativa*)	- Seed germination improvement - Nutrient uptake and transport enhancement - Growth and development parameters increase - Overall yield increase	Sunarpi et al., 2011
***Laminaria* sp.** ***L. hyperborea* (Laminariales)**		Algafect® Algreen®	Barley (*Hordeum vulgare*) Maize (*Zea mays*) Strawberry (*Fragaria x ananassa*)	- Seed germination improvement - Nutrient uptake and transport enhancement - Growth and development parameters increase - Overall yield increase - Nutritional quality improvement - Abiotic stress (drought) alleviation	Möller and Smith, 1999; Bradáčová et al., 2016; El-Miniawy et al., 2016; Ertani et al., 2018

(Continued)

TABLE 1 Continued

Algal species (Order)	Bioactive compound	Commercial product	Plant species	Benefits	References
Lessonia flavicans ***L. nigrescens*** ***L. vadosa* (Laminariales)**	Alginic acids Fucoidans		Apple (*Malus hupehensis*) Wheat (*Triticum aestivum*)	- Soil and plant microbiome structure and activity improvement - Abiotic stress alleviation	Wang et al., 2016; Wang et al., 2017; Zou et al., 2019
Macrocystis pyrifera ***M. integrifolia* (Laminariales)**	Plant growth regulators-like (cytokinins)	GaiaAT®	Bean (*Phaseolus* sp., *Vigna* sp.) Cucumber (*Cucumis sativus*)	- Overall yield increase - Nutritional quality (phenolics, vitamin C) improvement - Abiotic stress (drought) alleviation	Temple et al., 1989; Valencia et al., 2018; Di Filippo-Herrera et al., 2019; Zou et al., 2021
***Saccharina japonica* (Laminariales)**	Oligoalginates Mannitol		Trifoliate orange (*Citrus trifoliata*)	- Soil and plant microbiome structure and activity improvement	Ishii et al., 2000; Kuwada et al., 2005
Sargassum* sp.** ***S. horneri ***S. latifolium*** ***S. muticum*** ***S. myriocystum*** ***S. polycystum*** ***S. vulgare*** ***S. wightii* (Fucales)**		AlgaminoPlant® Algreen®	Black lentil (*Vigna mungo*) Chickpea (*Cicer arietinum*) Grapevine (*Vigna sinensis*) Lettuce (*Lactuca sativa*) Maize (*Zea mays*) Bean (*Vigna radiata*) Red radish (*Raphanus raphanistrum* subsp. *sativus*) Rice (*Oryza sativa*) Strawberry (*Fragaria x ananassa*) Tomato (*Solanum lycopersicum*) Wheat (*Triticum aestivum*)	- Seed germination improvement - Root growth enhancement - Growth and development parameters increase - Overall yield increase - Nutritional quality (protein, amino acid, sugars, vitamin C) improvement - Abiotic stress (salinity, oxidative, drought) alleviation	Jeannin et al., 1991; Sivasankari et al., 2006; Kumar and Sahoo, 2011; Matysiak et al., 2011; Sunarpi et al., 2011; Kalaivanan and Venkatesalu, 2012; Kasim et al., 2015; El-Miniawy et al., 2016; Abdel Latef et al., 2017; Di Filippo-Herrera et al., 2019; Mahmoud et al., 2019; Silva et al., 2019; Yao et al., 2020; Dookie et al., 2021
***Stoechospermum polypodioides* (Dictyotales)**			Cluster bean (*Cyamopsis tetragonoloba*)	- Growth and development parameters increase - Overall yield increase - Nutritional quality (protein, sugars) improvement	Ramya et al., 2011
Turbinaria murayana ***T. ornata* (Fucales)**			Rice (*Oryza sativa*)	- Seed germination improvement - Abiotic stress (nutrient) alleviation	Sunarpi et al., 2011

(Masondo et al., 2018). Furthermore, seed priming also provides seedlings with additional sources of minerals, amino acids and soluble sugars to enhance germination and improve vigor (Silva et al., 2019). As a result, BME induce early seed germination and increase germination rate and establishment in many crops, for many algal species (Kumar and Sahoo, 2011; Lola-Luz et al., 2012; Masondo et al., 2018; Mzibra et al., 2021). For example, seedlings of aubergine, pepper and tomato subjected to cold temperatures, treated with a *Gongolaria barbata* extract had enhanced germination rates linked to improved vigour (Demir et al., 2006). Additionally, tomato seedlings treated with *Cystoseira foeniculacea*, *Fucus spiralis* and *Bifurcaria bifurcata* extracts increased germination rate and percentage (Mzibra et al., 2021). Seed priming also grants the grown plant faster and/or stronger responses to abiotic stresses (Sujeeth et al., 2022). Extract drenching is the main method of application for seed priming, with caution paid to extract composition and concentration, as high concentrations of extracts can lead to a germination inhibition, due to the presence of several growth regulators compounds (Silva et al., 2019).

3.5 Plant growth and development

BME have a positive impact on overall plant growth and development, demonstrated by an increase in root and shoot length, surface area and volume, stem size, and overall fresh and dry weight. For example, improvements in all physical and biochemical growth parameters of bean were observed after the application of a low concentrated *Stoechospermum polypodioides* extract (Ramya et al., 2011). Meanwhile, higher concentrations application resulted in growth inhibition. In addition, growth stimulatory activities of commercial AN and *Durvillaea* extracts were tested on nutrient-stressed lettuce, leading to root biomass increase (Yusuf et al., 2019). The impact of an AN commercial extract on lettuce, melon, pepper and tomato was studied under drought stress (Neily et al., 2010). In each case, the treatment allowed an improvement of growth parameters, as well as an early development of root and shoot. BME can be applied directly to soil and roots or as a foliar spray, and effects on plant growth are concentration-dependent (El Boukhari et al., 2020). The growth-promoting properties of the extracts could be attributed to the presence of oligosaccharides, amino acids and vitamins (Briceño-Domínguez et al., 2014; Renaut et al., 2019).

BME can increase the chlorophyll content of treated plant leaves for an improved photosynthesis. Indeed, a higher leaf chlorophyll content in nutrient-stressed lettuce was measured after AN commercial alkali extract application (Yusuf et al., 2019). The extract reduced chlorophyll degradation in chloroplasts, linked to plant endogenous betaines synthesis enhancement induced by BME (Blunden et al., 1996). Furthermore, antioxidant compounds, like phlorotannins and carotenoids, can protect the photosynthetic apparatus against photooxidative damages occurring during abiotic stress by scavenging reactive oxygen species (ROS) thus preventing chlorophyll degradation and increasing leaf chlorophyll content (Mansori et al., 2015). Extracts can also trigger early flowering and fruiting in bean (El-Yazied et al., 2012), pepper (Ali et al., 2021b), marigold (van Staden et al., 1994), strawberry (El-Miniawy et al., 2016) and tomato (Crouch and van Staden, 1992; Ali et al., 2021b). It is suspected that BME trigger the biosynthesis of endogenous cytokinins, which influence flowering (Samuels et al., 2022).

3.6 Crop yield and quality

Improvements of the above-mentioned parameters by BME result into enhanced crops yields, as observed in barley (Blunden et al., 1996), bean (El-Yazied et al., 2012), broccoli (Gajc-Wolska et al., 2012), cabbage (Di Stasio et al., 2017b), grapevine (Taskos et al., 2019), lettuce (Mola et al., 2019), maize (Hussein et al., 2021), onion (Hidangmayum and Sharma, 2017), pepper (Arthur et al., 2003), potato (Dziugieł and Wadas, 2020), rapeseed (Jannin et al., 2013), spinach (Rouphael et al., 2018), tomato (Yao et al., 2020), watermelon (Abdel-Mawgoud et al., 2010) and wheat (Amaral Carvalho et al., 2014). Additionally, an AN commercial extract had a positive impact on apple's fruit set, number, size and weight, when applied at low concentrations (de Sousa et al., 2019). An increase was measured in maize ear weight of 37-42% and 48-50% after *E. maxima* and *Sargassum* sp. commercial extracts application, respectively (Matysiak et al., 2011). Increases in fruit size and harvest volume of blueberry (Loyola and Muñoz, 2009), grapevine (Norrie and Keathley, 2006; Khan et al., 2012), kiwi (Chouliaras et al., 1997), pepper (Arthur et al., 2003), potato (Dziugieł and Wadas, 2020) and tomato (Dookie et al., 2021) were also observed. Nevertheless, as commercial biostimulants are sometimes supplemented with growth enhancers including synthetic plant hormones to boost biostimulation effects, increases in yield cannot be solely attributed to BME.

3.7 Biofortification

The application of BME enhances the nutritional value of the crops. Indeed, the nutritional qualities of broccoli (Lola-Luz et al., 2014b), carrot (Poberezny et al., 2020), cucumber (Valencia et al., 2018), grapevine (Frioni et al., 2018), onion (Lola-Luz et al., 2014a), potato (Lola-Luz et al., 2014a), spinach (Fan et al., 2011) and strawberry (Kapur et al., 2018) were improved upon the addition of BME, such as AN or *Macrocystis* sp. In the same way, after BME application, the fruits accumulate higher amounts of healthy and taste-beneficial compounds, such as soluble carbohydrates (fructose and sucrose), phenols, flavonoids, anthocyanins, quercetin and vitamin C (Di Stasio et al., 2018; Frioni et al., 2018; Kapur et al., 2018; Valencia et al., 2018). Shelf-life seems to be extended by AN commercial extracts treatment on grapes (Norrie and Keathley, 2006) and spinach (Fan et al., 2014). On the contrary, AN and *E. maxima* commercial extracts application decreased preservation duration of apple fruits (Basak, 2008).

3.8 Resilience to abiotic stresses

Field-cultivated crops are regularly exposed to multiple abiotic stresses usually occurring simultaneously. They originate from environmental conditions variation, and usually encompass oxidative, hydric, frost, heat, and saline stresses (Samuels et al., 2022). BME contain compounds that can elicit several defense systems in plants by triggering stress signals involved in transduction pathways, and heighten resistance and resilience to these stresses to a certain extent (Larsen et al., 2003). Indeed, an AN commercial extract applied on cherry tomato under saline and drought stresses limited yield loss to 15% (Murtic et al., 2018).

Oxidative stress induces damaging free radicals and ROS production in the plant. In *Arabidospis*, pepper and tomato under oxidative stress, AN extract application induced the accumulation of cytokinins and phenolic compounds, which have ROS-scavenging capabilities (Omidbakhshfard et al., 2020; Staykov et al., 2021). Salinity and drought stresses can be similarly mitigated by a reduction of osmotic potential to avoid excessive water loss. This involves osmoprotectants accumulation, such as proline, carbohydrates, organic acids and proteins, and stimulation of stomatal closure, which can be enhanced by BME, such as AN extracts on asparagus (Al-Ghamdi and Elansary, 2018) and spinach (Xu and Leskovar, 2015), or *Cystoseira* sp. extract on rapeseed (Hashem et al., 2019). For example, long-term dehydration effect prevention consecutive to the application of AN extracts on drought-stressed *Arabidopsis* was observed (Santaniello et al., 2017; Rasul et al., 2021). Conversely, heat stress is mitigated by an increase in transpiration to improve thermoregulation (Franzoni et al., 2022). Freezing stress protection is enhanced by the accumulation of proline, soluble sugars and lipophilic compounds such as unsaturated fatty acids, as observed in freezing-stressed *Arabidopsis* treated by an AN lipophilic extract (Nair et al., 2012). Stress mitigation can also be enhanced by the application of several extracts from different macroalgal species at once, to handle a wider variety of stresses (Deolu-Ajayi et al., 2021).

4 Molecular modes of action of BME in crops

Currently, the precise mechanisms activated and regulated by BME application are still not fully understood, as the intricate molecular processes responsible for plant growth responses and stress alleviation induced by BME are complex. Extensive composition analysis of BME and improved genomic techniques to oversee resulting effects on plant physiology are key elements to unveil the processes in which the extracts constituents improve plant growth, health and vigour (Sujeeth et al., 2022). It is suspected that these compounds act as signaling mechanisms for specific metabolic and hormonal pathways, to modulate gene expression and induce metabolic changes in the plant (Nanda et al., 2022; EBIC, 2023; Table 2). Under stress conditions, these pathways can be amplified to improve plant adaptation and survival, or delay stress effects. Furthermore, some of these compounds present antioxidant activities, which directly reduce the deteriorating effects of free radicals produced by plants under stress conditions (Franzoni et al., 2022). Small variations in extract composition can lead to different molecular and cellular end-results, which suggest the activation of distinct underlying pathways. Furthermore, a single extract can concurrently trigger and/or restrain several metabolic or hormonal pathways. Thus, no generalities can be made on the mode of action and the subsequent benefits solely based on extract composition (Deolu-Ajayi et al., 2021).

4.1 Nutrient and water uptake and transport enhancement

Nutrients uptake and transport are stimulated through the upregulation of several genes responsible for transcription of nutrient transporters in the plant membrane, which can be induced by BME application. For example, AN extracts application on *Arabidopsis* and barley upregulated calcium, copper, nitrate, sulphate, amino acids, peptides, nucleotides, sugar, nucleotide-sugar derivatives transporters genes (Goñi et al., 2016; Goñi et al., 2021). Meanwhile, AN commercial extracts on spinach upregulate the glutamine synthetase gene that catalyses the inorganic nitrogen form, ammonium, into the organic form, glutamine, and the nitrate reductase gene responsible for the nitrate-to-nitrite reduction towards the assimilation of nitrate (Fan et al., 2013). BME application can also trigger the synthesis of membrane proteins aquaporins to facilitate water transmembrane exchanges (Santaniello et al., 2017; Al-Ghamdi and Elansary, 2018; Rasul et al., 2021).

4.2 Soil and plant microbiome structure and activity improvement

BME differentially trigger several enzyme genes involved in compounds degradation into assimilable nutrients for the microbial community development. Depending on the extract composition, microorganism genes expression varies differently, impacting encoded enzyme activity, such as cellulase, invertase, nitrite reductase, phosphatase, proteinase, and urease, for cellulose, carbohydrates, nitrite, phosphate, proteins, and urea degradation respectively (Eyras et al., 1998). Assimilable nutrients availability is thus altered, and differentially favors microbial communities. This positive modification of the microbiome structure was observed in apple cultivars following the application of a *Lessonia* extract (Wang et al., 2016).

4.3 Seed priming and germination improvement

The priming action of BME to enhance the seed resistance to stresses is modulated through epigenetic and chromatin pathways (Lämke and Bäurle, 2017). The acquired resistance is then retained by the plant from a few days to several weeks (Liu et al., 2022). Beside

TABLE 2 Benefits induced by brown macroalgal extracts on plants, and their suspected molecular mode of action in plants.

Benefits	Molecular mode of action	References
Nutrient uptake and transport enhancement	- Upregulation of calcium (CAX3, CAX7, ACA1), copper (COPT2), iron (NRAMP3), potassium (HKT2;1), sodium (NHX2), nitrate (NRT1.1, NRT2.1, NRT1.5), sulphate (SULTR1, SULTR3, AST56), amino acids (LHT1, AAP5), peptides (ATOPT3), nucleotides (ATPUP10), nucleotides-sugars derivatives (UTR2, UTR3), sugars (MSS1) transporter genes - Upregulation of glutamine synthetase (GS1) gene - Upregulation of nitrite reductase (NR) gene	Fan et al., 2013; Jannin et al., 2013; Billard et al., 2014; Goñi et al., 2016; Goñi et al., 2018; Shukla et al., 2018a; Dell'Aversana et al., 2021; Goñi et al., 2021
Water uptake improvement	- Upregulation of transmembrane protein aquaporins (PIP1;2, PIP2;2, PIP2;3) genes	Santaniello et al., 2017; Al-Ghamdi and Elansary, 2018; Rasul et al., 2021
Soil and plant microbiome structure and activity improvement	- Upregulation of cellulase, dehydrogenase, inverterase, nitrite reductase, phosphatase, proteinase and urease genes	Eyras et al., 1998; Wang et al., 2016
Seed germination improvement	- Upregulation of α-amylase enzyme genes by gibberellin A3 signalling	Akazawa and Hara-Nishimura, 1985; Beck and Ziegler, 1989; Sun and Gubler, 2004; Rayorath et al., 2008b
Growth and development parameters enhancement	- Modulation of the phenylpropanoid and flavonoid pathways - Upregulation of cellulose synthase-like E1 (CSLE1), UDP-glucose 4-epimerase 1 (UGE1), pectin acetylesterase 8 (PAE8) genes - Upregulation of growth hormones auxin (IAA), cytokinin (IPT), gibberellin (GA2Ox) biosynthesis genes - Upregulation of FLOWERING TIME (FT), CLAVATA (CLV), SQUAMOSA PROMOTER BINDING-LIKE (SPL) genes - Upregulation of Single Flower Truss (SFT), Self-Pruning (SP), Jointless (J), Anantha (AN), Falsiflora (FA) and Constans-1 (CO) genes	Wally et al., 2013; Goñi et al., 2016; Ali et al., 2019; Ali et al., 2021b; Dookie et al., 2021; Baghdadi et al., 2022
Photosynthesis enhancement	- Upregulation of betaine aldehyde dehydrogenase and choline monooxygenase genes - Upregulation of glycine betaine biosynthesis genes - Downregulation of chlorophyll degradation (AtCLH1 and AtCLH2) genes	Genard et al., 1991; Nair et al., 2012; Fan et al., 2013; Xu and Leskovar, 2015
Nutritional quality enhancement	- Upregulation of thylakoid-bound ascorbate peroxidase (APX) and monodehydroascorbate reductase genes	Fan et al., 2014; Xu and Leskovar, 2015
Abiotic stress alleviation	- Modulation of ABA, RCAR and RBOHD signalling-dependant compounds - Modulation of signalling compounds mediated by cytokinin, cytokinin response regulator2 (ARR2) and apoplastic peroxidase (PRX34) - Upregulation of ABA-signalling and biosynthesis (NCED3, PP2CA, PP2C52, PYL8, ABI1, ABI2, SnRK2,8, DREB1A, DREB3) genes - Upregulation of proline synthesis (P5CS1 and P5CS2) genes - Downregulation of proline degradation (ProDH) gene - Upregulation of polysaccharide degradation (9SEX1, SEX4) genes - Upregulation of carbohydrate biosynthesis (GOLS2, GOLS3) genes - Downregulation of sucrose degradation genes - Upregulation of cell cycle marker (HISTONE H4) gene - Downregulation of programmed cell death associated (WRKY33, ATG) gene - Upregulation of glutathione (GSH) gene - Upregulation of drought-responsive (LEA4-5, LEA7, LEA46) and dehydrine (TAS14) genes - Downregulation of negative growth regulator stress responsive (RESPONSIVE TO DESICCATION 26) gene - Upregulation of freezing-tolerance (DGD1, COR15A, RD29A, CBF3) genes - Upregulation of stomatal chloroplast proteins cryoprotection transcription factor (DREB1A, COR78/RD29A) genes - Upregulation of freezing tolerance (galactinol synthase2, pyroline 5-carboxylate synthetase, acetyl-CoA carboxylase) genes - Upregulation of ascorbate-glutathione antioxidant system (APX1, AO) genes - Upregulation of ROS-scavenging enzyme (superoxide dismutase, peroxide dismutase, catalase, ascorbate peroxidase) genes - Downregulation of oxidative stress-induced cell death lipids (TAGS and GABA) genes	Pharr et al., 1995; Stoop et al., 1996; Burchett, 2000; Zhang and Ervin, 2004 ; Zhang and Ervin, 2008; Muñoz-Mayor et al., 2012; Nair et al., 2012; Santaniello et al., 2017; Goñi et al., 2018; Hashem et al., 2019; Zamani-Babgohari et al., 2019; Di Stasio et al., 2020; Omidbakhshfard et al., 2020; Rasul et al., 2021; Staykov et al., 2021

seed resistance improvement, BME compounds, found for example in AN, can trigger the biosynthesis of the hormone gibberellin A3 that functions as a signal for α-amylase enzyme gene activation. The enzyme then participates in starch hydrolysis into carbohydrates, which is used as an energy source by the seed for germination (Akazawa and Hara-Nishimura, 1985; Beck and Ziegler, 1989; Sun and Gubler, 2004; Rayorath et al., 2008b). Other compounds can also be responsible for α-amylase enzyme activation, as it was also elicited by a GA3-deprived AN extract (Rayorath et al., 2008b).

4.4 Growth, photosynthesis, and nutritional quality enhancement

The stimulation of plant growth by BME is modulated through several plant hormonal pathways, namely phenylpropanoid and flavonoid (Sujeeth et al., 2022). BME compounds are able to act as signals for the endogenous plant growth hormones auxin, cytokinin and gibberellin biosynthesis through the upregulation of their respective genes (Wally et al., 2013; Ali et al., 2019; Shukla et al., 2019; Ali et al., 2021b; Baghdadi et al., 2022). Moreover, accumulation of plant growth hormones was correlated with growth parameters improvement of tomato and bell pepper, as well as on *Arabidopsis* consecutive to the application of AN and *Sargassum vulgare* extracts (Wally et al., 2013; Ali et al., 2019; Ali et al., 2021b; Baghdadi et al., 2022). AN and *Sargassum* extracts applied on tomato upregulated the genes responsible for flowering, which is regarded as an index of yield (Dookie et al., 2021; Baghdadi et al., 2022). BME also elicit the upregulation of cellulose synthase-like E1, UDP-glucose 4-epimerase 1 and pectin acetylesterase 8 genes, responsible for the development and strengthening of plant cell walls (Goñi et al., 2016).

BME can improve the plant photosynthetic system by upregulating betaine aldehyde dehydrogenase and choline monooxygenase genes involved in the photosynthetic process (Xu and Leskovar, 2015). They also trigger the upregulation of glycine betaine biosynthesis genes that prevent chlorophyll degradation and delay photosynthetic activity loss, and the downregulation of chlorophyll degradation genes (Genard et al., 1991; Nair et al., 2012). Both processes resulted in increased leaf chlorophyll content and enhanced photosynthetic activity, as observed after AN extract application on spinach (Fan et al., 2013; Xu and Leskovar, 2015).

Quality and shelf-life of post-harvest food products are improved upon BME applications. Indeed, an AN commercial alkali extract elicited the upregulation of thylakoid-bound ascorbate peroxidase and monodehydroascorbate reductase genes involved in the accumulation of carotenoids, flavonoids, phenols in spinach (Fan et al., 2014; Xu and Leskovar, 2015).

4.5 Abiotic stress alleviation

Plants cultivated in open fields are frequently subjected to oxidative, hydric, saline, heat, and frost stresses. Those stresses and their impact on plant health and yield can be alleviated by BME through several metabolic pathways. For example, alginates of AN can act as signals for the accumulation of abscisic acid through the activation of its biosynthesis and signaling genes (Santaniello et al., 2017; Rasul et al., 2021). Accumulation of abscisic acid in plants is one key factor in multiple stress resilience. Furthermore, osmotic balance maintenance is a crucial parameter to ensure the plant survival, as it allows efficient water and ion exchange through cell membranes. When a plant is subjected to saline, hydric or frost stress, application of an AN lipophilic extract can trigger the accumulation of proline, an osmoprotectant, through the upregulation of proline synthesis and the downregulation of proline degradation genes (Nair et al., 2012). Similarly, the accumulation of mannitol is induced by the upregulation of genes encoding for mannitol-1-P-dehydrogenase and mannose-6-P-reductase enzymes, responsible for the reduction of fructose-6-P and mannose-6-P into mannitol-1-P, respectively, while the gene encoding for mannitol dehydrogenase, responsible for the oxidation of mannitol into carbohydrate monomers, is downregulated (Pharr et al., 1995; Stoop et al., 1996).

Oxidative stress generates ROS responsible for several damages in plants. BME application on crops under oxidative stress can upregulate the ROS-scavenging enzymes genes to inhibit ROS production and prevent harm (Fike et al., 2001; Abdel Latef et al., 2017; Goñi et al., 2018; Hussein et al., 2021). Indeed, AN extract application on oxidative-stressed *Arabidopsis* upregulated genes associated to ROS detoxification ascorbate-glutathione antioxidant system, and downregulated programmed cell death-associated and lipid cell death-associated genes, which suggest a reduction of damages caused by oxidative stress (Omidbakhshfard et al., 2020; Rasul et al., 2021; Staykov et al., 2021). Saline and hydric stresses are both mainly mitigated through osmotic pathways, including the accumulation of osmoprotectants. Stressed *Arabidopsis* treated with an AN commercial alkali extract modulated cytokinin response regulator2 and apoplastic peroxidase activities, both involved in stomatal closure (Rasul et al., 2021). Stomatal closure enhancement allows for a reduction of transpiration and an increase of water retention. AN extracts also elicited the upregulation of drought-responsive and dehydrin genes (Muñoz-Mayor et al., 2012; Goñi et al., 2018; Rasul et al., 2021), and downregulated the negative growth regulator stress responsive gene in *Arabidopsis* (Rasul et al., 2021). Frost stress is alleviated through the upregulation of freezing-tolerance genes, the upregulation of stomatal chloroplast proteins cryoprotection transcription factor genes and the upregulation of genes coding for enzymes involved in the synthesis of freezing tolerance compounds (Nair et al., 2012; Zamani-Babgohari et al., 2019). Protection against frost is also improved through the accumulation of several compounds, including proline and unsaturated fatty acids, involved in cell protection against freezing-induced damages, as well as carbohydrates, to increase the energy stock for continued metabolism performance. Carbohydrates accumulation is mediated through the upregulation of polysaccharide degradation genes, carbohydrate biosynthesis genes and the downregulation of sucrose degradation genes (Nair et al., 2012).

5 Conclusion and future directions

As the agricultural sector is actively looking for agrochemical alternatives to enhance crop yield and prevent abiotic stress threats, brown macroalgal biostimulants are gaining momentum. The wide range of bioactive compounds of brown macroalgae make them prime candidates for such applications. Encouraging results have already been highlighted regarding soil structure and stability, seed priming, nutrient and water uptake, root and plant growth and development, overall yield and nutritional quality, and abiotic stress alleviation. Nevertheless, the precise mode of action of extracts are still unclear, as several metabolic pathways are involved, and the extracts complex composition associated with compounds' synergy do not allow a clear understanding of the mechanisms involved. Improvements in genomic techniques and extensive characterization of BME could allow, in the future, for a better comprehension of plant mechanisms, which in turn would allow for extract optimization to further enhance the activities. In addition, these findings will allow commercial BME producers to develop and standardize more systematically their extracts which will guarantee more homogeneous products with sufficient bioactivity to meet targeted results. Currently, brown macroalgae are still considered an underexploited resource, but are gaining more interest from scientists and industries. Indeed, their application fields are numerous, and their offshore growth neither requires water and fertilisers supply nor competes with crop production for arable lands. Brown macroalgae are a renewable resource, thanks to their high recovery rate, but harvest from wild populations must be tightly regulated to avoid biomass overexploitation and surrounding marine ecosystem disruption. In this regard, cultivation could ensure a continuous supply of algal biomass without threatening wild communities.

Author contributions

Conceptualization: NK, VS-P, SC, FH, and JB. Methodology and investigation: NK, VS-P, SC, FH, and JB. Bibliographic research and writing of the original draft: NK. Supervision: VS-P, SC, FH, and JB. Reviewing and editing: NK, VS-P, SC, FH and JB. Funding acquisition: VS-P, FH, and JB. All authors contributed to the article and approved the submitted version.

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Conflict of interest

Authors NK, FH, JB were employed by company ALGAIA.

The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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