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Seaweed and microalgae as major actors of blue biotechnology to achieve plant stimulation and pest and pathogen biocontrol – a review of the latest advances and future prospects

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Abstract

Modern agriculture needs proper solutions to face the current trend of pesticides and fertilizers reduction. One of the available leverages to support this transition is the use of bioproducts that are more environmentally friendly and less hazardous for human health. Among them, blue biotechnology and more precisely seaweed and microalgae gain interest every year in the scientific community. In agriculture, seaweeds (Macroalgae) have been used in the production of plant biostimulants while microalgae still remain unexploited. Microalgae are widely described as renewable sources of biofuels, bioingredients and biologically active compounds, such as polyunsaturated fatty acids (PUFAs), carotenoids, phycobiliproteins, sterols, vitamins and polysaccharides, which attract considerable interest in both scientific and industrial communities. They affect agricultural crops for enhancement of plant growth, seedling growth. They can also improve nutrient incorporation, fruit setting, resistance properties against pests and diseases, improving stress management (drought, salinity and temperature). The present review aimed at the interest of blue biotechnology in agronomy, with a specific focus on microalgae, their biological activities and their possible application in agriculture as a potentially sustainable alternative for enhanced crop performance, nutrient uptake and resilience to environmental stress. This review does not only present a comprehensive study of microalgae as plant biostimulants but also as biofertilizers, with a particular emphasis on future challenges these solutions will have to deal with, microalgae being able to synthesize secondary metabolites with potential biopesticidal action.

Introduction

In a world of rapid changes, the use of biotechnology offers a solution to meet the challenges in medicine and those related to agriculture, food and renewable energies. Among the different biotechnology, blue biotechnology that focuses on the exploration and exploitation of marine organisms in order to develop new products (turning aquatic biomass into novel foods, feed, energy, packaging…) is booming. One major field of application is the use of seaweed and microalgae in agriculture. They can elicit defensive responses resulting in protection against pathogen or insect damage, and can be used as biofertilizers (Chatzissavvidis and Therios, 2014). Biofertilizers are gaining significance in sustainable agriculture as a means of enhancing crop productivity, in an environmentally friendly and economically viable manner, and reducing the polluting effects of synthetic fertilizers (Renuka *et al.*, 2018; Nosheen *et al.*, 2021). Among the various types of biofertilizers, formulations based on photosynthetic organisms, including eukaryotic microalgae and cyanobacteria, are gaining importance because of their significant contributions, particularly to the maintenance of soil fertility and enhancing crop yield (Li *et al.*, 2017; Guo *et al.*, 2020).

The loss of yield from agricultural production due to the presence of pests has been treated over the years with synthetic pesticides, but the use of these substances negatively affects the environment and presents health risks for consumers and animals. Natural compounds derived from plants such as *Rhus muelleri, Aquilegia vulgaris* (commonly called European crowfoot and granny's bonnet) can treat fungal infections. Phytopathogens, which remain current as one of the most common plant diseases, also represent one of the most significant issues for agricultural companies (Jimenez-Reyes *et al.*, 2019). *P. sarmentosum* (wild pepper) extract bioformulations can for example potentially be applied as bio-pesticides for the management of rice diseases (Syed-Ab-Rahman and Omar, 2018).

Researchers are also focusing on potential biological control microbes as viable alternatives for the management of pests and plant pathogens. In fact, there is a growing body of evidence that notes the potential of leaf and root-associated microbiomes to increase plant efficiency and yield in cropping systems (Syed Ab Rahman *et al*., 2018). A variety of endophytic bacteria and free-living rhizobacteria on the root surface and rhizosphere utilize the nutrients released from the host, as well as secrete metabolite substances to the soil that aid in controlling plant diseases caused by fungi or bacteria. Besides, microalgae, especially cyanobacteria, are able to biosynthesize a number of secondary metabolites with potential biopesticidal action and can be considered potential biological agents for the control of harmful organisms to soils and plants (Costa *et al*., 2019; Gonçalves, 2021). These activities are attributed to phenolic compounds, polyphenols, tocopherols, saponins, nitrogen-rich peptides and sesquiterpenes.

Plant pathogens are forming a huge problem on the economic and life stability. They cause diseases for leaf, stem, root, vascular system and fruit indeed. They comprise viruses, bacteria, fungi, nematodes and parasitic plants, and induce diseases for leaf, stem, root, vascular system and fruit. The plant pathogen attacks the plant by using some mechanisms that are responsible for increasing the disease and appearance of the symptoms. New strategies not only directly protect plants against pathogens but can also induce enhanced immunity that permanently protects against pathogenic strains. For example, *Chlorella fusca* protects the host plant against pathogenic fungi *Colletotrichum orbiculare* (anthracnose) and *Botrytis squamosa* (leaf blight of onion) in cucumber and Chinese chive (Kim *et al*., 2018).

Agriculture is also dealing with major issues to ensure food production quantities and constant evolution of quality standards (pesticide residues, GMOs-free, organoleptic properties). This is the goal of the current European Green Deal project: becoming climate neutral by 2050 by turning the political commitment into a legal obligation and a trigger for investment (European Commission, 2019). As a turning point in this project, concrete changes are observed in regulations in order to reduce our reliance on hazardous chemicals and invest in environmentally friendly technologies. Careful consideration of all available methods to ensure the success of cultures and their integration to discourage the development of populations of harmful organisms is of prime importance (Barzman *et al*., 2015). Seaweed and microalgae are one of the solutions to overcome this challenge along with plant and microbial extracts (Jamiołkowska, 2020; Morales-Cedeño *et al*., 2021). One of the best historical examples of an algal product to protect crops is the use of purified laminarin extracted from *Laminaria digitata*, as an elicitor of plant defences (Klarzynski *et al*., 2000). Currently, many other algal bioproducts have reached the market, exploiting the enormous diversity of potential modes of action they offer (Ronga *et al*., 2019).

The present review aimed at the interest of blue biotechnology in agronomy, with a specific focus on microalgae, their biological activities and their possible application in agriculture as a potentially sustainable alternative for enhanced crop performance, nutrient uptake and resilience to environmental stress.

Biotechnology

Biotechnology is defined as the application of science and technology related to living organisms, in order to modify living or non-living materials for the production of knowledge, goods and services (Organisation for Economic co-operation and Development, 2005). This includes microorganisms (microalgae, bacteria and fungi), algae and invertebrates. For more than three decades the field of biotechnology has had an extraordinary impact on science, law, regulatory environment and business. Since 2010, progress for biotechnology has increased quickly, with a focus in the pharma industry for science and health care (Niosi and McKelvey, 2018).

Historically, blue technology is linked to the health domain. For example, in the 1950's antiviral drug development was based on the identification of nucleosides in *Tectitethya crypta* (Demospongiae) by Bergman and Feeney (1951). Zidovudine (AZT) and Acyclovir drugs stem directly from this development. These authors also studied marine products against microbes. A few years later, in the 1960's, the first marine antibiotic (pentabromopseudilin) was described from the marine bacterium *Pseudomonas bromoutilis* (Uzair *et al*., 2011).

Currently, marine biotechnology contributes to several applications. Among them, a sustainable blue economy, the core idea of which is to draw economic benefit from marine and freshwater environments without sacrificing their ecological resilience, has emerged (Similä *et al*., 2020).

Focusing on algae, they can produce biodiesel, bioethanol through fermentation, biomethane by anaerobic digestion and biohydrogen (Jayaseelan *et al*., 2021). Biodiesel is made from algal biomass including oil extraction, knowing that microalgae oil contains more free fatty acids compared to the oil from terrestrial plants.

Microalgae and seaweeds have also been used for various purposes that range from food sources to drug development . They, in fact, represent an abundant unexplored source of highly diverse phytochemicals that possess various biological functions. Thousands of novel compounds and their metabolites, with diverse biological activities ranging from anticancer to antiviral, have been isolated since the 1990s (Yasuhara-Bell and Lu 2010). These compounds are rich in metabolites such as carotenoids, polysaccharides, terpenes, phenol derivatives, nitrogen-containing compounds and alkaloids which have huge potential for the cure of diseases (Abd El-Hack *et al*., 2019). Because of their healthy and bioactive compounds such as carotenoids, phycobilins, fatty acids, polysaccharides, vitamins and sterols, microalgae have been widely used in the health food market. Microalgal fat is also a vegetarian source of n-3 fatty acids [eicosapentaenoic acid (EPA), docosahexaenoic acid (DHA), γ-linolenic acid (GLA)], and show a high protein content. Multiple nutritional evaluations demonstrated the suitability of algae biomass as a valuable feed supplement or substitute for conventional protein sources (soybean meal, fish meal, rice bran, etc.). Besides the use of algae animal feed as a protein source for livestock, many of the health benefits also apply to animals (improved immune response, improved fertility, better weight control) (Remize *et al*., 2021). However, the technology to produce microalgae is still immature, even innovation has been done and continues on cultivation systems (Kratzer and Murkovic 2021).

Microalgae have also received interest among agrochemical industries, through their capabilities to increase seed germination, seedling growth, crop productivity, as well as tolerance to abiotic

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stressors. However, compared to green biotechnology related to agricultural (Barkha *et al.*, 2016), the field for blue biotechnology can still be considered underdeveloped and future prospects will contribute significantly to tomorrow's agriculture (Barre and Bates, 2018; Rizwan *et al.*, 2018). It appears that this domain is currently offering the best possibilities for future developments (Rizwan *et al.*, 2018). The phylogenetic diversity is significantly more important in water than on land. Life appeared in the water around 4 billion years ago and many phyla are present only in the marine environment. By linking all these features, it is easy to consider the potential of research dealing with marine organisms, the fruits of lengthy evolutionary processes and potentially full of unique metabolic specificities. It is also interesting to note that marine environments present highly contrasting conditions of life (deep seas, hydrothermal sources, streams…), increasing the possibility of encountering novelties and revealing new marine biotechnology applications (Costello and Chaudhary, 2017).

The agronomical use of blue biotechnology

The potential of seaweed or microalgae in agricultural applications is used since antiquity (Nabti *et al.*, 2017). They have been used since ancient times directly or in composted form as a soil amendment to improve the productivity of crops in coastal regions (Craigie, 2011). It is also reported that in the second half of the first century, seaweed manure had widely been used (Metting *et al.*, 1990).

Out of more than 800 000 species of algae that exist in nature, only 5000 have been characterized to date. Out of 5000 species, only a small number of the algae species have been selected to determine their potential applications in plant growth under defined growth conditions (Nabti *et al.*, 2017; Lee and Ryu 2021). It is important to note the real growing interest in this field over the past 20 years, studies having almost doubled in the last 5 years (Lee and Ryu, 2021). This is mainly due to the fact that the current trend for agricultural practices is to reduce pesticides and fertilizers for the benefit of alternatives with a lower impact on human and environmental health. The use of genetically selected plants for their aptitude to resist biotic and abiotic stresses, mechanical weeding, physical barriers to avoid pest problems, cultural practices, adjustments and the use of chemical (as a last alternative) or biological solutions (Barzman *et al.*, 2015; Lamichhane *et al.*, 2015).

The use of plants genetically selected for their ability to resist biotic and abiotic stresses, mechanical weeding, physical barriers to avoid pest problems, and the use of biological solutions were means to reduce the use of chemical solutions (Barzman *et al.*, 2015; Lamichhane *et al.*, 2015). In this respect, blue biotechnology and more precisely the use of seaweed and microalgae enter the last category: biological solutions. They are a source of diverse natural substances and microorganisms, able to achieve plant stimulation and/or pest and pathogen biocontrol effects (Nabti *et al.*, 2017; Righini *et al.*, 2019; Ronga *et al.*, 2019; Stirk *et al.*, 2020). For example, cyanobacteria are regarded as the main biological pest control agents that control the various diseases in the plants, by producing various bioactive compounds against fungi, nematodes and other diseases (Thirumurthy and Mol, 2020). The algal polysaccharide has biostimulant activities of plant growth, nutrients uptake and biotic and abiotic stresses tolerance (Zou *et al.*, 2019). Microalgae act also against phytopathogens. A general summary of the involvement of blue biotechnology in agricultural practices is presented in Fig. 1. More details on the latest advances and further prospects are discussed later on in the present paper.

A plant biostimulant is 'any substance or micro-organism, in the form in which it is supplied to be user, applied to plants, seeds or the root environment with the intention to stimulate natural processes of plants benefiting nutrient use efficiency and/or tolerance to abiotic stress, regardless of its nutrients content, or any combination of such substances and/or microorganisms intended for this use' (European Commission, 2014). Starting in 2022, the EU market will open the single market for fertilizing products and aye down common rules on safety, quality and labelling requirements for fertilizing products.

Biological control is a strategy that was proposed half a century ago (Alabouvette *et al.*, 2006). Biocontrol solutions protect plants against biotic stresses (diseases, insects and other harmful organisms, weeds). They use natural mechanisms and interactions. According to the International Biocontrol Manufacturers Association (IBMA), the principle of biocontrol is based on the management of stresses and natural balances of the populations of aggressors rather than on their suppression. Biocontrol solutions are regulated in Europe the same way as chemical pesticides under the regulation EC 1107/2009 (Anonymous, 2009). In order to be competitive on these aspects of plant protection (against abiotic and/or biotic stresses), seaweed and microalgae offer a large range of features (Chanda *et al.*, 2019).

Known products and attributes of seaweed and microalgae in agriculture

Plant stimulation compounds

Plant growth is marked by its adaptability to continuous changes in the environment and led by the distribution of growth substances in the whole organism. These substances are produced by the plant, but they may also be brought exogenously by other organisms. They have been investigated in order to elucidate their mode of action in microalgae and higher plants (Lu and Xu 2015). Phytohormones, including auxin (IAA), abscisic acid (ABA), cytokinin (CK), ethylene (ET) and gibberellins (GAs) are therefore described for their beneficial actions on major traits in phototrophic organisms. The presence and role of active hormones have been long speculated in algae, but the first proof of the bioactive forms of auxin, cytokinin, Gibberellic Acid (GA), brassinosteroid, Abscisic Acid (ABA), Jasmonic Acid (JA) and polyamines came from the work of Tarakhovskaya *et al.* (2007).

Auxins are a class of plant hormones, essential for plant growth. They were the first class of plant hormones to be discovered. Indole-3-acetic acid (IAA) is the most abundant and the basic auxin natively occurring and functioning in plants. Auxin content in plant parts is variable depending on its needs and the associated development of the plant from the single cell to the whole organism (Li *et al.*, 2016). They act quickly on gene expression and regulation, and a large set of candidate genes that are potentially regulated by auxins have been identified in the last three decades (Di *et al.*, 2016). Environmental conditions are linked to the pattern of auxin distribution within the plant, modifying the development of plant organs. Thus, plants react to external factors and adapt their needs through the active transport of auxin molecules.

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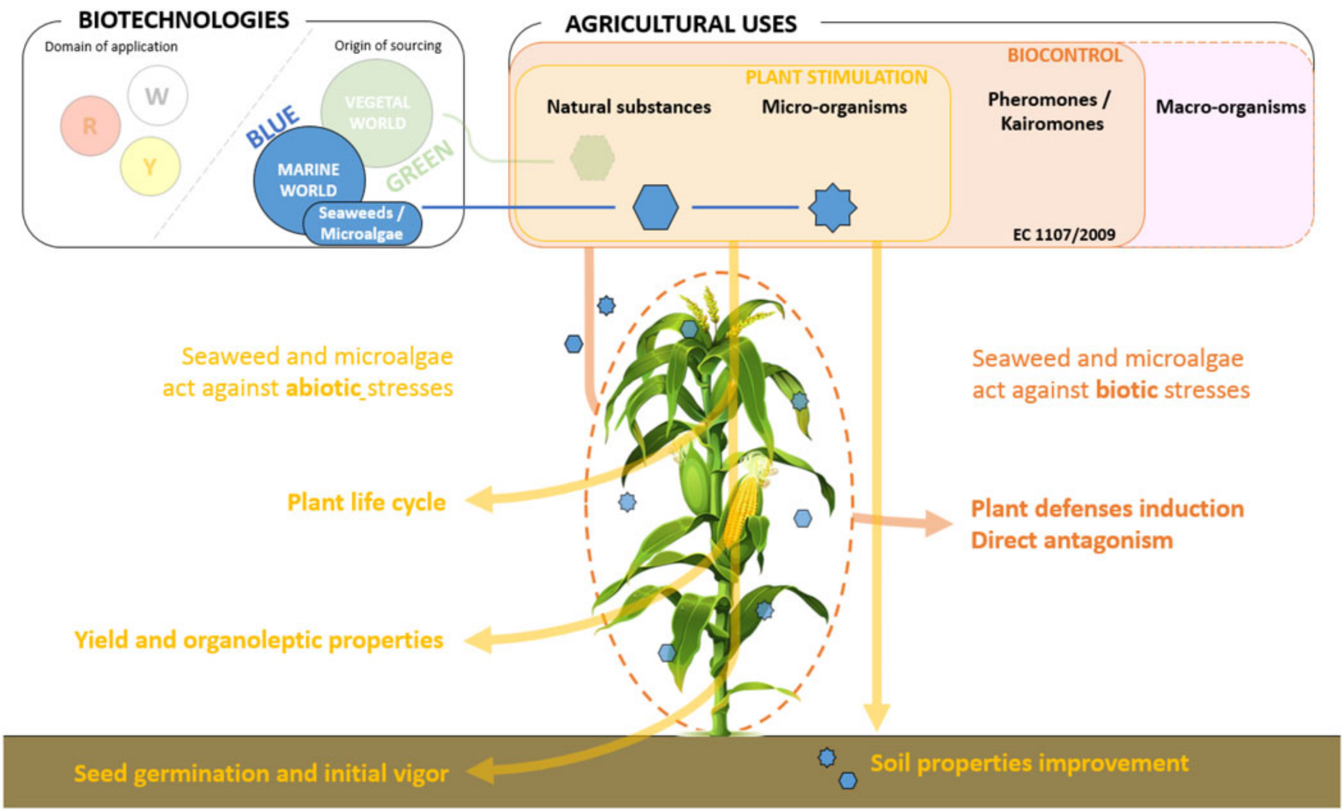

Fig. 1. Colour online. Action of blue technology on agricultural uses, seaweed and microalgae represent natural substances and micro-organisms both involved in plant stimulation and pest and pathologies biocontrol.

The presence and/or functions of auxins (i.e. indole-3-acetic acid, IAA; indole-3-butyric acid, IBA; phenylacetic acid, PAA) were confirmed in different microalgal species from *Chlorella*, *Scenedesmus* and *Acutodesmus* genus (Žižková *et al.*, 2017; Piotrowska-Niczyporuk *et al.*, 2018). *Nannochloropsis oculata, Nannochloropsis oceanica* and *Dunaliella salina* also present bioactive forms of auxins (Han *et al.*, 2018).

These phytohormones are the most essential endogenous molecules for modifying physiological and molecular reactions and are critically required by the plant for its survival under heavy metal stress. They act as chemical messengers and, under a complex regulation, allow plants to sustain abiotic stresses such as excess heavy metal ions (Piotrowska-Niczyporuk *et al.*, 2020). Recent sequencing efforts have shown that the indole-3-pyruvic acid pathway, one of the primary biosynthetic pathways in land plants, is also found in the red, brown and green algae (Morffy and Strader, 2020). Generally speaking, various concentrations of IAA or its derivatives are identified in microalgae extracts and supernatants, implementing both stimulatory and inhibitory effects on the growth and metabolism of higher plants and microalgae (Han *et al.*, 2018).

Cytokinins are a class of plant hormones with many physiological processes, including stimulation of cell division, differentiation and growth, regulation of seed dormancy and germination, and inhibition of the root apical meristem (Wybouw and De Rybel, 2019). There are two types of cytokinins: adenine-type and phenylurea-type cytokinins, with the first being the only one retrieved in plants (Mok, 2019). In microalgae, it had been speculated that the levels of active cytokinins are controlled by *de novo* biosynthesis (Sakakibara, 2006). For instance, Nayar (2021) showed that the direct activation of cytokinins is functional in *Chlorella variabilis*. Cytokinins are also present in *Acutodesmus obliquus, Chlorella protothecoides, Dunaliella salina, Chlorella vulgaris and Gracilaria caudata* (Han *et al.*, 2018).

Occurrence in brown algae is well described and cytokinins can be found in several genus, such as *Ascophyllum, Cystoseira, Ecklonia, Fucus, Macrocystis* and *Sargassum* (Nabti *et al.*, 2017), *Ascophyllum nodosum* extracts being used as biostimulant to promote growth and productivity in a number of agricultural production systems. *Ecklonia maxima* extracts present a high potential for application in agriculture due to its high content of several plant hormones (Nabti *et al.*, 2017).

Gibberellins (Gas) are a class of plant hormones, essential for plant development, including stem elongation, dormancy, flowering and senescence (Hedden and Sponsel, 2015). They induce seed germination by breaking the seed's dormancy and acting as a chemical messenger. Hundreds of gibberellins have been discovered, however, only a few of them are recognized as bioactive (GA1, GA3, GA4 and GA7). GAs are be found in microalgae, such as *Nannochloropsis oceanica* (Lu and Xu 2015) and Chlorella Sorokiniana. Recently, Do *et al.* (2020) determined that auxins (IAA and IPA) and gibberellins (GA4 and GA7) were endogenous phytohormones produced by *C. sorokiniana* TH01 under both phototrophic and mixotrophic cultivation modes (Dumale *et al.*, 2018). Green algae such as *Trebouxiophyceae, Ulvophyceae* and *Charophycea* also possess functional phytohormone metabolic pathways (Žižková *et al.*, 2017).

Abscisic acids (ABA) are a class of plant hormones, involved in plant development including dormancy, cell size and stomatal

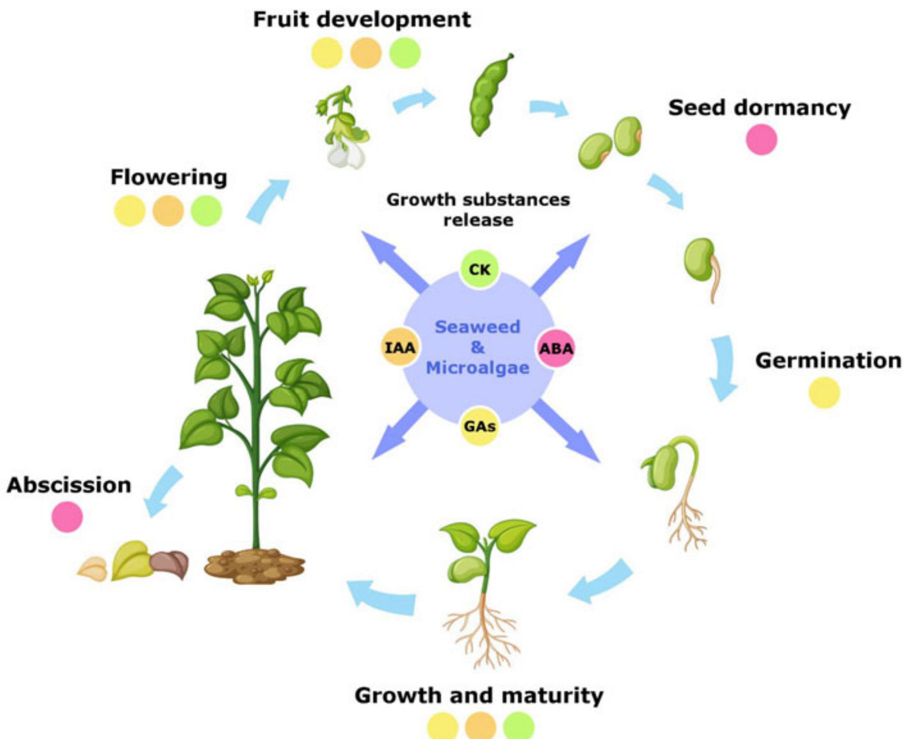

Fig. 2. Colour online. Known phytohormones produced by seaweed and microalgae and their potential impact on the life cycle of a crop. IAA, Auxins; CK, Cytokinins; GAS, Gibberellins and ABA, Abscisic Acid.

closure. Abscisic acids are also linked to plant responses against environmental stresses like heavy metal stress, drought, thermal or heat stress, high level of salinity, low temperature and radiation stress (Vishwakarma *et al*., 2017). A comprehensive review of abscisic acids on plants from Chen *et al*. (2020) highlighted the importance of their role for plant growth and development, while leaving many unanswered questions on the associated mechanisms.

The presence of ABA in seaweed has been identified in *Chlorophyta* species such as *Chara foetida*, *Draparnaldia mutabilis*, *Dunaliella parva*, *Ulva lactuca*, *Stigeoclonium tenuen* (green algae) and in *Phaeophyta* species such as *A. nodosum* and three *Laminaria* species (brown algae). It is also important to note that when it comes to algae, ABA has been reported to mitigate stresses for cyanobacteria (salt stress) and algae (salt, osmotic, oxidative, drought and nutrient stresses) (Lu *et al*., 2014). Therefore, it has been proposed that the cultivation of microalgae can lead to more high-valued bioproducts with the combination of exogenous ABA and stress.

In summary, this overview on plant growth substances potential highlights that both seaweed and microalgae represent excellent candidates for plant biostimulation purposes, based on their confirmed content in phytohormones. Their use can therefore be considered at a different time of the plant's development cycle (Fig. 2).

Complex molecules, macronutrients and micronutrients contribution

Seaweed and microalgae are naturally composed of a wide diversity of compounds which, once applied to soil and/or plants, may contribute to crop development. As for other living organisms, they contain variable amounts of proteins, carbohydrates, lipids, macronutrients (i.e. Na, Ca, K, P, Mn…) and micronutrients (B, Cl, Cu, Fe, Mn, Mo, Zn) essential for crop growth and health. Moreover, it is now observed that microalgae by-products (i.e. culture 'juice' after production, cell walls…), are also used as bioproducts for agriculture, because of their richness in a large diversity of elements (Daneshvar *et al*., 2020).

Proteins, carbohydrates and lipids represent a pool of organic matter, easily assimilable by other organisms including plants, when released by dead organisms. As many seaweed and microalgae bioproducts contain dead cells with grinded biomass and/or atomised cells, they are, therefore, a direct source of nutrition when used, leading to direct stimulation of plants. Moreover, these compounds often reach more than 50% (and up to 70%) of the fresh weight under optimal growth conditions (Barre and Bates, 2018). As an example, a detailed representation of the composition of the microalgae *Nannochloropsis occulata* summarized from the available literature, is given in Fig. 3.

Carbohydrates also act as plant biostimulants. Polysaccharides found in seaweed extracts (i.e. ulvans, alginates, fucoidans, laminarans, lichenan like glucans and fucose containing glucans), neutral sugars and sulphates, showed a positive correlation between the sulphate content of polysaccharide enriched extracts and shoot dry weight as well as chlorophyll content in tomato plants (Arioli *et al*., 2015; Mzibra *et al*., 2018). Different environmental/abiotic stresses are known to induce overproduction of oxygen radicals and their derivatives, so-called reactive oxygen species (ROS), which are able to oxidatively injure cells. Microalgae polysaccharides can mitigate ROS toxicity by stimulating the antioxidant defence system. More precisely, Chanda *et al*. (2019) suggested that algal polysaccharides are perceived by membrane receptors as microbial associated molecular patterns (MAMPs) and thereby inducing the MAMPs-dependent signalling pathways which involves the activation of ROS scavenging enzymes.

Finally, the application of polysaccharide enriched extracts on soil proved to be more effective in improving plant growth parameters than direct foliar application (Mzibra *et al*., 2021).

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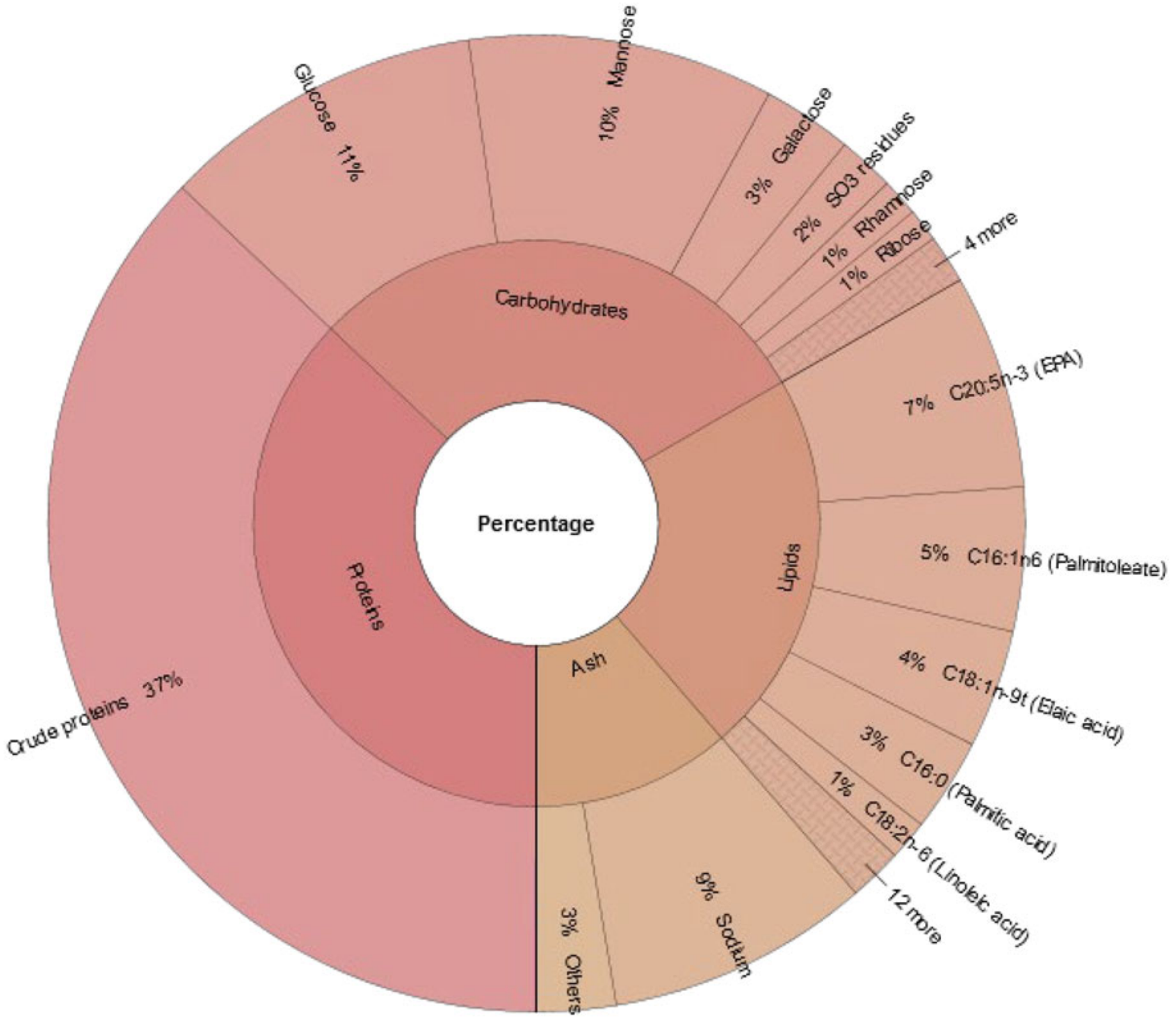

Fig. 3. Colour online. Detailed composition of the microalgae *Nannochloropsis occulata*. Mean of the available literature set proteins content to 37%, carbohydrate content to 30% and lipid content to 22% of total biomass. Ashes are mainly composed of sodium and chlorine.

Soil properties improvement

Seaweed and microalgae may also act indirectly on plant stimulation because of their beneficial effect on soil properties.

Nitrogen fixation

Arable soils are amended with organic and inorganic fertilizers yearly, to offset the losses due to crop rotation. According to the FAO forecast, global nutrient consumption exceeds 200 million tonnes in 2020 (FAO, 2020). Among microalgae, cyanobacteria can synthesize the enzyme nitrogenase and present the capacity to fix nitrogen. These microalgae develop non-dividing cells called heterocysts which contain the enzyme nitrogenase (Chen *et al*., 2014). This capacity is of major importance to agriculture because it represents the only way to add nitrogen to the soil without organic or mineral amendment. There is currently a trend to improve the use of nitrogen fertilizer as an agricultural management practice in order to avoid economic loss and environmental pollution (Martínez-Dalmau *et al*., 2021). Therefore, this capacity to directly fix inorganic nitrogen from the air and to convert it into an organic and usable form in the soil has been estimated to save around 25–40% of chemical N fertilizers (Nabti *et al*., 2017; Renuka *et al*., 2018; Martínez-Dalmau *et al*., 2021). This natural fixation, due to the capacity of microalgae to immobilize N through the formation of biological soil crusts, limits the impact of nitrogen on the environment (i.e. runoff and leaching) (Veluci *et al*., 2006).

Organic matter in the soil

One of the key factors for the establishment and the development of plants in soils, is their content of organic matter. Manure and slurry are commonly used to enrich soils with organic matter, resulting in a cost for farmers. One way to minimize this economic issue is the use of seaweed and microalgae as they are autotrophic communities, able for plants to fix atmospheric carbon dioxide through photosynthesis (Singh and Ahluwalia, 2013). Their contribution to the total soil carbon content is significant and thus, soils treated with algal biofertilizers are in better condition for plant development (Yilmaz and Sönmez, 2017; Gonçalves, 2021).

Nutrient availability

As for microbial organisms, microalgae possess a set of enzymatic features (i.e. siderophores, organic acids), able to directly contribute to the global soil biomineralization process (Rizwan *et al*., 2018). Moreover, recent studies highlighted that these processes can also occur indirectly, with microalgae inoculation modulating the rhizosphere microbiome and changing the diversity and abundance of microorganisms involved in the nutrients availability (Manjunath *et al*., 2016; Prasana *et al*., 2016).

Pest and pathogen biocontrol modes of action

Two modes of action are recognized for pest and pathogen biocontrol achieved by seaweed and microalgae products, depending if they act directly against pathogens by direct antagonism or indirectly after being detected by plants resulting in the induction of their natural defences (Righini *et al*., 2019; Gonçalves, 2021).

Direct antagonism

Microalgae can be considered one of the major biocontrol agents for fungi and soil-borne plant diseases issues (Lee and Ryu, 2021). This is mainly due to their capacity for secondary metabolites production expressing a wide range of actions i.e. antifungal, antibiotic, nematicide… (Gonçalves, 2021). The set of involved molecules is large, including carbohydrates, proteins, peptides, polyphenols, tocopherols, oils, saponins and sesquiterpenes (Gonçalves, 2021). They act directly on cell membrane with functional and structural modifications, disruption, enzyme inactivation, inhibition of protein synthesis (Lee and Ryu, 2021). Additionally, seaweed is a good source of bioactive compounds (i.e. fatty acids esters, phenolic compounds…) with a direct antagonistic effect against known pathogens, responsible for important crop diseases (Mukherjee and Patel, 2020).

Plant defence induction

Seaweed is used for its capacity to induce plant defences. Plants have developed a complete innate immunity to fight against plant diseases, with defence systems activated after the recognition of microbial components called pathogen-associated molecular patterns (PAMPs) (flagellin, lipopolysaccharides, chitin) (Choi and Klessig, 2016). A large set of seaweed polysaccharides and derived polysaccharides trigger plant defence induction against a range of pathogens by activating salicylic acid, jasmonic acid and/or ethylene signalling pathways at a systemic level (Sharma *et al*., 2014; Gonçalves, 2021).

The immune system of a plant is also stimulated by microalgae. Polysaccharides produced by microalgae are perceived by a plant's membrane receptors as elicitors, and trigger a series of defence mechanisms (Chanda *et al*., 2019). In a study by Farid *et al*. (2019), polysaccharides extracted from *Chlorella vulgaris* and *C. sorokiniana* exhibited a significant increase in β-1,3-glucanase activity, that break down the cell wall components of pathogens.

Focus of studies realized since 2018 on algae and microalgae recorded on plants

Seed germination and initial vigour

As the first step in a plant's life, a good start in seed germination often leads to a vigorous plant with a better chance to achieve its complete life cycle. This includes the establishment of the plant's autotrophic functioning mode after the use of reserve resources contained in the seed, essential to the plant's emergence. Compounds such as minerals, nutrients, amino acids, vitamins, pigments and polysaccharides present in the seaweed may refine seed germination, growth and development by providing them as biofertilizers or biostimulants (Chanda *et al*., 2019). The plant tolerance towards extreme environments like high heat and drought conditions becomes better. It also appears that seaweed liquid fertilizer can influence cellular metabolism and improve its yield (Rajan *et al*., 2020). It contains plant growth regulators like cytokinin, auxin and gibberellins, abscisic acids, cytokinins and ethylene, and is also the supreme source of nitrogen, phosphorous, potassium, calcium and magnesium required for the normal growth of plants (Han *et al*., 2018).

Recent research focused on the tomato plant model highlighted that several seaweed extracts were able to promote seed germination. This is the case of neutral and alkaline seaweed extracts of *U. lactuca* and *Padina gymnospora* when used at 0.2% extracts were able to enhance germination parameters (Hernández-Herrera *et al*., 2019). Similarly, Mzibra *et al*. (2021) observed a significant increase of germination and speed in tomatoes associated with a significant reduction of mean germination time of seeds treated with 0.02 mg/ml of seaweed polysaccharide enriched extracts obtained from *Gigartina sp., Gigartina pistillata, Chondracanthus acicularis, Gelidium crinale, Schizymenia dubyi, Cystoseira foeniculacea* and *Fucus spiralis*. Similar results were also obtained by application of higher polysaccharide enriched extracts concentration (0.1 mg/ml) extracted from *Ulva rigida, Codium tomentosum, Codium decorticatum* and *Bifurcaria bifurcate* (Mzibra *et al*., 2018). Garcia-Gonzalez and Sommerfeld (2016) tested cellular extracts and dry biomass of the green algae *Acutodesmus dimorphus* on tomato seeds of Roma tomato plants. Treated seeds with extract concentrations at 750 mg/ml triggered faster seed germination, occurring 2 days earlier than the control group.

Comparable effects were recorded for an *A. nodosum* seaweed-based biostimulant on seed germination and seedling growth of sunflower, at a dosage of 15 mg/l (dos Santos *et al*., 2019) and of onion, at a dosage of 5500 ppm (Hidangmayum and Sharma, 2017). Besides, *A. nodosum* used in the early stages of plant growth and germination offer protection against salt stresses for avocado (*Persea americana* Mill.) and on the fruit yield (Bonomelli *et al*., 2018; Yildiztekin *et al*., 2018).

Puglisi *et al*. (2020) showed that low concentrations of *Chlorella vulgaris* and *Scenedesmus quadricauda* (the equivalent of 1–2 mg of organic carbon contained in the extracts) were able to significantly enhance sugar beet seed germination. Moreover, individual application of *Chlorella vulgaris* and *Spirulina platensis* (3 g/kg of soil) increased the rate of germination and seedling length of maize crops (Dineshkumar *et al*., 2019).

Plant development

The most common and generalized use of seaweed and microalgae products for biostimulation purposes is the application during vegetative stages of plant development. Foliar application of seaweed extracts enhance nutrient uptake, growth promotion and root development in different agricultural crops, such as maize, tomato, grape and broccoli (Mukherjee and Patel, 2020). Castellanos-Barriga *et al*. (2017) reported that low concentrations (0.2%) of acid-extracts obtained from *U. lactuca* can enhance growth parameters in mung bean (plumule and radicle length,

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shoot and root length as well as fresh and dry weight). Similarly, 3% extract of the brown seaweed *Sargassum swartzii* enables improvement in the shoot length and the number of leaves in *Vigna inguiculata* plants (Vasantharaja *et al.*, 2019). During the onion life cycle, the application of a 0.55% extract of *A. nodosum* proved to increase leaf number, plant height, crop growth height bulb diameter and pigment content (Hidangmayum and Sharma, 2017). Mahmoud *et al.* (2019) studied the effect of the commercial product ACTION® containing the seaweed *Sargassum vulgare* on red radish plants. The most effective treatment was found to be seaweed-soaked seeds before sowing and foliar sprayed seaweed extract at 3 mg/l once 20 days after sowing, with a greater number of roots and aerial parts compared to non-treated seeds and plants.

Garcia-Gonzalez and Sommerfeld (2016) tested cellular extracts and dry biomass of the green algae *A. dimorphus* as a foliar spray to evaluate plant growth and fruit production in Roma tomato plants. Aqueous extracts applied as foliar fertilizers at 3.75 g/ml resulted in increased plant height and greater numbers of flowers and branches per plant.

Yield and nutritional quality

Yield and nutritional quality are of major concern for farmers. The environmental factors affecting crop yield can be classified into abiotic and biotic constraints. Actually, these factors are more intensified with global warming which leads to climate change (Food and Agriculture Organization of the United Nations, 2017). Abiotic stresses adversely affect growth, productivity and trigger a series of morphological, physiological, biochemical and molecular changes in plants. A direct link between seaweed/microalgae and these parameters can be done, ensuring real interest in the use of these bioproducts in order to stabilize potential financial losses (Gonçalves, 2021). The effects of germination parameters (percentage index, mean time) and growth parameters (shoot and root length) of mung bean (*Vigna radiata*) treated with acid seaweed liquid of *Ulva latucta* extracts at 0.2% were evaluated by Castellanos-Barriga *et al.* (2017). Results showed that these extracts can significantly enhance seed germination rates. Production (fresh and dry weight) of mung bean was also significantly higher compared to the control treatments. *Ascophyllum nodosum* applied at a dosage of 0.5% is efficient to increase bulb diameter and fresh weight, in addition to sulphur and protein content of onion crops (Hidangmayum and Sharma, 2017). Concerning this nutritional quality, treatments with *Ulva latucta* extracts at 0.2% also significantly increased total chlorophyll concentration and protein contents (Castellanos-Barriga *et al.*, 2017). Treatment of *Sargassum swartzii* extract at 3% on Cowpea (*Vigna unguiculata)* increased not only total phenolic content, protein and flavonoids but also yield (Vasantharaja *et al.*, 2019).

Seaweed and microalgae are thus interesting candidates as biostimulation solutions. However, many studies have highlighted the importance to clearly establish dosage for optimal efficiency (Chanda *et al.*, 2019; Mukherjee and Patel, 2020). An excessive concentration of seaweed and microalgae extracts may lead to unwanted effects or decreasing trends in the measured parameters, such as toxic effects on shoots or impaired growth (Hidangmayum and Sharma, 2017).

Pest and pathogen biocontrol

Antimicrobial activity

The use of seaweed and microalgae as biocontrol agents of microbial plant pathogens is well known and described, and their use in commercial formulations already occurs on the market (Righini *et al.*, 2019). De Corato *et al.* (2017) found that some crude extracts from brown (*Laminaria digitata* and *Undaria pinnatifida*) and red (*Porphyra umbilicalis, Eucheuma denticulatum* and *Gelidium pusillum*) seaweed achieved control of grey mould and brown rot on strawberry, peaches and lemons. The identified action was mainly due to direct pest control with the importance of fatty acids, supported by an induction of resistance elicited by carbohydrates.

From a more *in vitro* point of view, Mohy El-Din and Mohyeldin (2018) explored the capacities of four brown seaweed extracts (*Colpomenia sinuosa, Padina pavonia, Cystoseira barbata* and *S. vulgare*) for their antifungal activities against *Aspergillus niger, A. flavus, Penicillium parasiticus, Candida utilis* and *Fusarium solani*. The originality of this study was to compare extracts prepared from seaweed harvested during different seasons with multiple extractants. Methanol extracts were the most efficient, and *Cystoseira barbata* was the best seaweed to achieve maximum biocontrol effects. This difference in the type of extracts, moreover with methanol, was also highlighted by Khan *et al.* (2017) in their study using 32 seaweed extracts against *Fusarium oxysporum.* This inhibition effect was also observed for a 15% extract of the seaweed *Tubinaria conoides*, with 100% inhibition against the same pathogen (Ameer Junaithal Begum *et al.*, 2016). *Sargassum wightii* presented high levels of antioxidants with free radical scavenging ability, resulting in an inhibition of Gram-negative bacterial pathogen (Suganya *et al.*, 2016).

Spirulina sp. and *Nannochloropsis sp*. extracts were able to be very efficient against *Fusarium graminearum species complex* because they have a high content in chlorogenic acid (Scaglioni *et al.*, 2019). The advantages conferred by these microalgae extracts had led some companies to patent them, as the extracts obtained from the *Amphidinium* genus and their use as fungicidal and/or bactericidal activity on fungi, oomycetes and/or pathogenic bacteria of plants and crops seeds (Immunerise biocontrol patent, de la Crouee and Thomas, 2019).

Microalgae may also trigger a better biocontrol effect of some microbial strains. This is the case of *Trichoderma*, a well-known biocontrol genus, whose efficiency is enhanced in the presence of *Chlorella vulgaris* extracts, to control the late wilt disease caused by *Cephalosporium maydis* in maize (Elshahawy and El-Sayed, 2018).

Inhibition of other plant pests

Seaweed and microalgae also have potential roles in the control of insects or nematode populations involved in plant problematics (Renuka *et al.*, 2018). In their study, Suganya *et al.* (2016) evaluated the efficacy of two types of seaweed for their potential as an insecticide. Their ethanol extract of *Sargassum wightii* presented larvicidal activity against *Aedes aegypti* (dengue and Zika virus vector). Another insect problem, the Asian citrus psyllid *Diaphorina citri*, has been controlled by repellent and insecticidal effects of ethanolic extracts obtained from *Caulerpa sertularioides, Laurencia johnstonii and Sargassum horridum* seaweeds (González-Castro *et al.*, 2019). A recent example of success against nematodes is the use of three microalgae (*Scenedesmus*

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obliquus, Chlorella vulgaris and *Anabaena oryzae*), alone or in combination, to control the root-knot nematode *Meloidogyne incognita*. All treatments significantly reduced the number of juveniles in soil and the triple mixture was the best at increasing total phenolic content and antioxidant amounts in plants (Hamouda, 2017). The same observations occurred from the use of commercial seaweed products *A. nodosum* and *Ecklonia maxima*, which adversely affect hatching and sensory perception of the root-knot nematodes, *Meloidogyne chitwoodi* and *Meloidogyne hapla*, in *in vitro* assays on tomato (Ngala *et al.*, 2016).

Future challenges

Currently, one of the most important challenges is crop production. As the global population increases, agricultural production must also keep pace with it (Frona *et al.*, 2019). In the process to increase crop production, fungicides, nematicides, fertilizers, mainly synthetic chemicals, are being used. However, it is now well established that chemical products may be linked to environmental disasters and severe health issues. One way to reduce our reliance on synthetic chemicals is the use of solutions of natural origin. Among them, seaweed and microalgae extracts show high levels of promise, with a low or complete absence of harmful effects for the environment and human health and their first plan role to develop sustainable agriculture (Hamed *et al.*, 2018). This is also in line with the European Regulation EC 1107/2009, concerning the placing of plant protection products on the market and repealing Council Directives 79/117/EEC and 91/414/EEC-[2009, which recommends that priority should be given to non-chemical and natural alternatives wherever possible (Regulation (ec) no 1107/2009 of the European Parliament and of the Council, 2009)].

The democratization of biosolutions for agriculture and furthermore of seaweed and microalgae, remains marginal. Some limits can be identified to explain that:

(1) *Characterization of the mode of action and the correct use of these products*: Seaweed and microalgae present beneficial properties for agriculture, but only if they are correctly used. It is not always the highest concentration of the extracts that present the best results for plant simulation or biocontrol activity. Moreover, sometimes a wrong dosage leads to adverse or unwanted effects on plants (i.e. delay in its life cycle, toxic effect, death) (Hidangmayum and Sharma, 2017).

(2) *Surpass current standards*: The current use of seaweed and microalgae products often propose the same genus of organisms or by-products (*A. nodosum* and *Ecklonia maxima* as major biostimulant and laminarin as biocontrol product). However, the potential of these organisms is broad, and the diversity is not exploited. Moreover, the use of seaweed or microalgae is currently based on the direct use of biomass or enriched fractions. As our world becomes more sensitive to the sustainability of our production systems and the limitation of waste, it becomes interesting to re-think the global process of this industry and to increase the value of all its chain of production. One of the possibilities is the use of culture supernatant as a part of the formulation of the bioproduct. For microalgae production, these juices are usually thrown away after cultivation, despite their high content in nutrients and other molecules of interest such as IAA (Prieto *et al.*, 2011). An example of success for implementing this concept is the product Naneos (Greencell), a liquid including a base of *A. nodosum* and *Nannochloropsis occulata* extract.

(3) *Beyond the laboratory*: Even if there is a great potential offered by seaweed and microalgae to become tomorrow's phytosanitary product, the number of products exploiting these organisms on the market is still limited. One of the major challenges for the production of algal biopesticides is clearly to increase the number of studies in order to identify the substances with potential pesticidal activity and their mode of action (Costa *et al.*, 2019). Many compounds with 'cide' activity (the meaning of this prefix is cutting or killing) have been discovered and some of them, patented, but still not released onto the market. We can also see that most studies relating to algae are mainly conducted on biofuel and other bioproducts that they produce. Global programmes are therefore of prime importance to accompany this essential transition in our future agricultural practices.

(4) *Regulation of these products*: Regulation on biofertilizers and biostimulants is not harmonized between countries. This will soon be the case in Europe with the EU 2019/1009 regulation entering in force in 2022. This regulation will open the algae market, as organic fertilizers will not require marketing authorization anymore, thus having a strong and positive impact on blue biotechnology development for the agronomical field.

Conclusions

Research on seaweed and microalgae are one of the keys for future agriculture development. Presently, the world possesses a large number of industrial sites with plant production capacities able to provide the quantities required to supply the market. Studies are increasing in number yearly and mechanisms behind each species and/or extracts are increasingly detailed. However, a gap still needs to be overcome in order to transform scientific research on seaweed and microalgae into concrete solutions for professional users, even if the biosolutions gain momentum every year in terms of total market share.

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References

Abd El-Hack ME, Abdelnour S, Alagawany M, Abdo M, Sakr MA, Khafaga AF, Mahgoub SA, Elnesr SS and Gebriel MG (2019) Microalgae in modern cancer therapy: current knowledge. *Biomedicine & Pharmacotherapy* **111**, 42–50.

Alabouvette C, Olivain C and Steinberg C (2006) Biological control of plant diseases: the European situation. *European Journal of Plant Pathology* **114**, 329–341.

Ameer Junaithal Begum M, Selvaraju P and Vijayakumar A (2016) Evaluation of antifungal activity of seaweed extract (*Turbinaria conoides*) against Fusarium oxysporum. *Journal of Applied and Natural Science* **8**, 60–62.

Anonymous (2009) Regulation (EC) No 1107/2009 of the European Parliament and of the Council of 21 October 2009 concerning the placing of plant protection products on the market and repealing Council Directives 79/117/EEC and 91/414/EEC. *Official Journal Europe Union* **309**, 1–50.

https://doi.org/10.1017/S0021859621000885

Arioli T, Mattner SW and Winberg PC (2015) Applications of seaweed extracts in Australian agriculture: past, present and future. *Journal of Applied Phycology* **27**, 2007–2015.

Barkha S, Barthi SK and Anita S (2016) Green biotechnology and scope of genetically modified crops: facts and prejudices. *Indian Journal of Agriculture Business* **1**, 63–71.

Barre SL and Bates SS (2018) *Blue Biotechnology: Production and Use of Marine Molecules*. Weinheim, Germany: John Wiley & Sons.

Barzman M, Bàrberi P, Birch ANE, Boonekamp P, Dachbrodt-Saaydeh S, Graf B, Hommel B, Jensen JE, Kiss J, Kudsk P, Lamichhane JR, Messéan A, Moonen A-C, Ratnadass A, Ricci P, Sarah J-L and Sattin M (2015) Eight principles of integrated pest management. *Agronomy for Sustainable Development* **35**, 1199–1215.

Bergman W and Feeney RJ (1951) Nucleosides of sponges. *Journal of Organic Chemistry* **16**, 981–987.

Bonomelli C, Celis V, Lombardi G and Mártiz J (2018) Salt stress effects on avocado (*Persea americana* Mill.) plants with and without seaweed extract (*Ascophyllum nodosum*) application. *Agronomy* **8**, 64.

Castellanos-Barriga LG, Santacruz-Ruvalcaba F, Hernández-Carmona G, Ramírez-Briones E and Hernández-Herrera RM (2017) Effect of seaweed liquid extracts from *Ulva lactuca* on seedling growth of mung bean (*Vigna radiata*). *Journal of Applied Phycology* **29**, 2479–2488.

Chanda M, Merghoub N and Arroussi H EL (2019) Microalgae polysaccharides: the new sustainable bioactive products for the development of plant bio-stimulants? *World Journal of Microbiology and Biotechnology* **35**, 177.

Chatzissavvidis C and Therios I (2014) Role in algae in agriculture. In Seawweds, Ponnin VH (Eds). *Agricultutal uses, biological and antioxidant agents*. Nova Science, New York, pp. 1–37.

Chen M, Li J, Zhang L, Chang S, Liu C, Wang J and Li S (2014) Auto-flotation of heterocyst enables the efficient production of renewable energy in cyanobacteria. *Science Reports* **4**, 3998.

Chen K, Li G-J, Bressan RA, Song C-P, Zhu J-K and Zhao Y (2020) Abscisic acid dynamics, signaling, and functions in plants. *Journal of Integrative Plant Biology* **62**, 25–54.

Choi HW and Klessig DF (2016) DAMPs, MAMPs, and NAMPs in plant innate immunity. *BMC Plant Biology* **16**, 232.

Costa JAV, Freitas BCB, Cruz CG, Silveira J and Morais MG (2019) Potential of microalgae as biopesticides to contribute to sustainable agriculture and environmental development. *Journal of Environmental Science and Health. Part. B, Pesticides, Food Contaminants, and Agricultural Wastes* **54**, 366–375.

Costello MJ and Chaudhary C (2017) Marine biodiversity, biogeography, deep-sea gradients, and conservation. *Current Biology* **27**, R511–R527.

Craigie JS (2011) Seaweed extract stimuli in plant science and agriculture. *Journal Applied Phycology* **23**, 371–393.

Daneshvar E, Zarrinmehr MJ, Kousha M and Bhatnagar A (2020) Performance evaluation of different harvesting methods and cultivation media on the harvesting efficiency of microalga and their fatty acids profile. *Fuel* **280**, 118592.

De Corato U, Salimbeni R, De Pretis A, Avella N and Patruno G (2017) Antifungal activity of crude extracts from brown and red seaweeds by a supercritical carbon dioxide technique against fruit postharvest fungal diseases. *Postharvest Biology and Technology* **131**, 16–30.

de la Crouee OT and Thomas Y (2019) Use of a cellular extract of one or more microalgae of the *Amphidinium* genus, for its fungicidal and/or bactericidal activity on fungi, oomycetes and/or pathogenic bacteria of plants and culture seeds. Patent application US20190174768A1. United States.

Di D-W, Zhang C, Luo P, An C-W and Guo G-Q (2016) The biosynthesis of auxin: how many paths truly lead to IAA? *Plant Growth Regulation* **78**, 275–285.

Dineshkumar R, Subramanian J, Gopalsamy J, Jayasingam P, Arumugam A, Kannadasan S and Sampathkumar P (2019) The impact of using microalgae as biofertilizer in maize (*Zea mays* L.). *Waste and Biomass Valorization* **10**, 1101–1110.

Do TCV, Tran DT, Le TG and Nguyen QT (2020) Characterization of Endogenous Auxins and Gibberellins Produced by Chlorella sorokiniana TH01 under Phototrophic and Mixtrophic Cultivation Modes toward Applications in Microalgal Biorefinery and Crop Research. *Journal of Chemistry* **4**, 1–11.

dos Santos PLF, Zabotto AR, Jordão HWC, Boas RLV, Broetto F and Tavares AR (2019) Use of seaweed-based biostimulant (*Ascophyllum nodosum*) on ornamental sunflower seed germination and seedling growth. *Ornamental Horticulture* **25**, 231–237.

Dumale J, Gamoso GR, Manangkil JM and Divina CC (2018) Detection and quantification of auxin and gibberellic acid in *Caulerpa racemosa*. *International Journal of Agricultural Technology* **14**, 653–660.

Elshahawy IE and El-Sayed AE-KB (2018) Maximizing the efficacy of Trichoderma to control *Cephalosporium maydis*, causing maize late wilt disease, using freshwater microalgae extracts. *Egyptian Journal of Biological Pest Control* **28**, 48.

European Commission (2014) A Legal Framework for Plant Biostimulants and Agronomic Fertiliser Additives in the EU. *Ares* 1712793.

European Commission (2019) Un pacte vert pour l'Europe. https://ec.europa.eu/info/strategy/priorities-2019-2024/european-green-deal_fr.

FAO (2020) Etat de la sécurité alimentaire et de la nutrition dans le monde.. Https://www.fao.org/publications/sofi/2020/fr.

Farid R, Mutale-Joan C, Redouane B, Mernissi Najib EL, Abderahime A, Laila S and Arroussi Hicham EL (2019) Effect of microalgae polysaccharides on biochemical and metabolomics pathways related to plant defence in *Solanum lycopersicum*. *Applied Biochemistry and Biotechnology* **188**, 225–240.

Food and Agriculture Organization of the United Nations (2017) *The Future of Food and Agriculture: Trends and Challenges*. ISNN 2522-7211, Roma, Italy.

Frona D, Szenderak J and Harangi-Rakos M (2019) The challenge of feeding the world. *Sustainability* **11**, 5816.

Garcia-Gonzalez J and Sommerfeld M (2016) Biofertilizer and biostimulant properties of the microalga *Acutodesmus dimorphus*. *Journal of Applied Phycology* **28**, 1051–1061.

Gonçalves AL (2021) The use of microalgae and Cyanobacteria in the improvement of agricultural practices: a review on their biofertilising, biostimulating and biopesticide roles. *Applied Sciences* **11**, 871.

González-Castro AL, Muñoz-Ochoa M, Hernández-Carmona G and López-Vivas JM (2019) Evaluation of seaweed extracts for the control of the Asian citrus psyllid *Diaphorina citri*. *Journal of Applied Phycology* **31**, 3815–3821.

Guo S, Wang P, Wang X, Zou M, Liu C and Hao J (2020) Microalgae as Biofertilizer in Modern Agriculture. In Alam MD, XU JL and Wang Z (eds). *Microalgae Biotechnology for Food, Health, and High Value Products*. Springer, Singapour, pp. 397–411.

Hamed SM, Abd El-Rhman AA, Abdel-Raouf N and Ibraheem IBM (2018) Role of marine macroalgae in plant protection & improvement for sustainable agriculture technology. *Beni-Suef University Journal of Basic and Applied Sciences* **7**, 104–110.

Hamouda R (2017) Potential of plant-parasitic nematode control in banana plants by microalgae as a new approach towards resistance. *Egyptian Journal of Biological Pest Control* **27**, 165–172.

Han X, Zeng H, Bartocci P, Fantozzi F and Yan Y (2018) Phytohormones and effects on growth and metabolites of microalgae: a review. *Fermentation* **4**, 25.

Hedden P and Sponsel V (2015) A century of gibberellin research. *Journal of Plant Growth Regulation* **34**, 740–760.

Hernández-Herrera RM, Santacruz-Ruvalcaba F and Hernández-Carmona G (2019) Germination and seedling growth responses of tomato (*Solanum lycopersicum* L.) to seaweed extracts applied on seeds | REVISTA LATINOAMERICANA DE BIOTECNOLOGIA AMBIENTAL Y ALGAL.

Hidangmayum A and Sharma R (2017) Effect of different concentrations of commercial seaweed liquid extract of *Ascophyllum nodosum* as a plant bio stimulant on growth, yield and biochemical constituents of onion (*Allium cepa* L.). *Journal of Pharmacognosy and Phytochemistry* **6**, 658–663.

Jamiołkowska A (2020) Natural compounds as elicitors of plant resistance against diseases and new biocontrol strategies. *Agronomy* **10**, 173.

https://doi.org/10.1017/S0021859621000885

Jayaseelan M, Usman M, Somanathan A, Palani S, Muniappan G and Jeyakumar RB (2021) Microalgal production of biofuels integrated with wastewater treatment. *Sustainability* **13**, 8797.

Jimenez-Reyes MF, Carrasco H, Olea A and Silva-Moreno E (2019) Natural compounds: a sustainable alternative for controlling phytopathogens. *Journal of the Chilean Chemical Society* **64**, 2.

Khan S, Abid M and Hussain F (2017) Antifungal activity of aqueous and methanolic extracts of some seaweeds against common soil-borne plant pathogenic fungi. *Pakistan Journal of Botany* **49**, 1211–1216.

Kim MJ, Shim CK, Kim YK, Ko BG, Park JH, Hwang SG, *et al.* (2018) Effect of biostimulator *Chlorella fusca* on improving growth and qualities of Chinese chives and spinach in organic farm. *Plant Pathology Journal* **34**, 567.

Klarzynski O, Plesse B, Joubert J-M, Yvin J-C, Kopp M, Kloareg B and Fritig B (2000) Linear β-1,3 Glucans are elicitors of defence responses in tobacco. *Plant Physiology* **124**, 1027–1038.

Kratzer R and Murkovic M (2021) Food ingredients and nutraceuticals from microalgae: main product classes and biotechnological production. *Foods (Basel, Switzerland)* **10**, 1626.

Lamichhane JR, Dachbrodt-Saaydeh S, Kudsk P and Messéan A (2015) Toward a reduced reliance on conventional pesticides in European agriculture. *Plant Disease* **100**, 10–24.

Lee SM and Ryu CM (2021) Algae as new kids in the beneficial plant microbiome. *Frontiers in Plant Science* **12**, 599742.

Li S-B, Xie Z-Z, Hu C-G and Zhang J-Z (2016) A review of auxin response factors (ARFs) in plants. *Frontiers in Plant Science* **7**, 47.

Li R, Tao R, Ling N and Chu G (2017) Chemical, organic and bio-fertilizer management practices effect on soil physicochemical property and antagonistic bacteria abundance of cotton field: implications for soil biological quality. *Soil Tilage Research* **167**, 30–38.

Lu Y and Xu J (2015) Phytohormones in microalgae: a new opportunity for microalgal biotechnology? *Trends in Plant Science* **20**, 273–282.

Lu Y, Tarkowská D, Turecková V, Luo T, Xin Y, Li J, Wang Q, Jiao N, Strnad M and Xu J (2014) Antagonistic roles of abscisic acid and cytokinin during response to nitrogen depletion in oleaginous microalga *Nannochloropsis oceanica* expand the evolutionary breadth of phytohormone function. *Plant Journal* **80**, 52–68.

Mahmoud SH, Salama DM, El-Tanahy AMM and Abd El-Samad EH (2019) Utilization of seaweed (*Sargassum vulgare*) extract to enhance growth, yield and nutritional quality of red radish plants. *Annals of Agricultural Sciences* **64**, 167–175.

Manjunath M, Kanchan A, Ranjan K, Venkatachalam S, Prasanna R, Ramakrishnan B, Hossain F, Nain L, Shivay YS, Rai AB and Singh B (2016) Beneficial cyanobacteria and eubacteria synergistically enhance bioavailability of soil nutrients and yield of okra. *Heliyon* **2**, e00066.

Martínez-Dalmau J, Berbel J and Ordóñez-Fernández R (2021) Nitrogen fertilization. A review of the risks associated with the inefficiency of its use and policy responses. *Sustainability* **13**, 5625.

Metting B, Zimmerman WJ, Crouch I and Van Staden J (1990) Agronomic uses of seaweed and microalgae. In Akatsuka I (ed.), *Introduction to Applied Phycology*. The Hague: SPB, pp. 589–628.

Mohy El-Din SM and Mohyeldin MM (2018) Component analysis and antifungal activity of the compounds extracted from four brown seaweeds with different solvents at different seasons. *Journal of Ocean University of China* **17**, 1178–1188.

Mok DWS (2019) *Cytokinins: Chemistry, Activity, and Functions.Inc.*, Boca Raton, USA: CRC Press.

Morales-Cedeño LR, Orozco-Mosqueda MdC, Loeza-Lara PD, Parra-Cota FI, de los Santos-Villalobos S and Santoyo G (2021) Plant growth-promoting bacterial endophytes as biocontrol agents of pre- and post-harvest diseases: fundamentals, methods of application and future perspectives. *Microbiological Research* **242**, 126612.

Morffy N and Strader LC (2020) Old town roads: routes of auxin biosynthesis across kingdoms. *Current Opinion in Plant Biology* **55**, 21–27.

Mukherjee A and Patel JS (2020) Seaweed extract: biostimulator of plant defence and plant productivity. *International Journal of Environmental Science and Technology* **17**, 553–558.

Mzibra A, Aasfar A, El Arroussi H, Khouloud M, Dhiba D, Kadmiri IM and Bamouh A (2018) Polysaccharides extracted from Moroccan seaweed: a promising source of tomato plant growth promoters. *Journal of Applied Phycology* **30**, 2953–2962.

Mzibra A, Aasfar A, Benhima R, Khouloud M, Boulif R, Douira A, Bamoud A and Kadmiri IM (2021) Biostimulants derived from Moroccan Seaweeds: Seed germination metabolomics and growth promotion of tomato plant. *Journal of Plant Growth Regulation* **40**, 353–370.

Nabti E, Jha B and Hartmann A (2017) Impact of seaweeds on agricultural crop production as biofertilizer. *International Journal Environmental Science and Technology* **14**, 1119–1134.

Nayar S (2021) Exploring the Role of a Cytokinin-Activating Enzyme LONELY GUY in Unicellular Microalga Chlorella variabilis. *Frontiers Plant Sciences* **29**, 611871.

Ngala BM, Valdes Y, dos Santos G, Perry RN and Wesemael WML (2016) Seaweed-based products from Ecklonia maxima and *Ascophyllum nodosum* as control agents for the root-knot nematodes *Meloidogyne chitwoodi* and *Meloidogyne hapla* on tomato plants. *Journal of Applied Phycology* **28**, 2073–2082.

Niosi J and McKelvey M (2018) Relating business model innovations and innovation cascades: the case of biotechnology. *Journal of Evolutionary Economics* **28**, 1081–1109.

Nosheen S, Ajmal L and Song Y (2021) Microbes as biofertilizers, a potential approach for sustainable crop production. *Sustainability* **13**, 1868.

Organisation for Economic Co-operation and Development (2005) *A Framework for Biotechnology Statistics*. Paris, France, p. 52

Piotrowska-Niczyporuk A, Bajguz A, Kotowska U, Bralska M and Talarek-Karwel M (2018) Growth, metabolite profile, oxidative status and phytohormone levels in the green alga *Acutodesmus obliquus* exposed to exogenous auxins and cytokinins. *Journal of Plant Growth Regulation* **37**, 1159–1174.

Piotrowska-Niczyporuk A, Bajguz A, Kotowska U, Kotowska U and Zambrzycka-Szelewa SA (2020) Auxins and cytokinins regulate phytohormone homeostasis and thiol-mediated detoxification in the green alga *Acutodesmus obliquus* exposed to lead stress. *Scientific Reports* **10**, 10193.

Prasanna R, Kanchan A, Ramakrishnan B, Ranjan K, Venkatachalam S, Hossain F, Shivay YS, Krishnan P and Nain L (2016) Cyanobacteria-based bioinoculants influence growth and yields by modulating the microbial communities favourably in the rhizospheres of maize hybrids. *European Journal of Soil Biology* **75**, 15–23.

Prieto CRE, Cordoba CNM, Montenegro JAM and González-Mariño GE (2011) Assessment of caratenoid production by Dunaliella salina in different culture systems and operation regimes. Journal of Biotechnology 151: 180-185.

Puglisi I, Barone V, Fragalà F, Stevanato P, Baglieri A and Vitale A (2020) Effect of microalgal extracts from *Chlorella vulgaris* and *Scenedesmus quadricauda* on germination of *Beta vulgaris* seeds. *Plants* **9**, 675.

Rajan MSA, Thriunavukkarasu R, Joseph J and Aruni W (2020) Effect of seaweed on seed germination and biochemical constituents of *Capsicum annuum*. *Biocatalysis and Agricultural Biotechnology* **29**, 101761.

Regulation (ec) no 1107/2009 of the European Parliament and of the Council (2009) Placing of plant protection products on the market and repealing Council Directives 79/117/EEC and 91/414/EEC. *Official Journal of the European Union*.

Remize M, Brunel Y, Silva JL, Berthon JY and Filaire E (2021) Microalgae n-3 PUFAs production and use in food and feed industries. *Marine Drugs* **19**, 113.

Renuka N, Guldhe A, Prasanna R, Singh P and Bux F (2018) Microalgae as multi-functional options in modern agriculture: current trends, prospects and challenges. *Biotechnology Advances* **36**, 1255–1273.

Righini H, Roberti R, Varma A, Tripathi S and Prasad R (2019) Algae and Cyanobacteria as biocontrol agents of fungal plant pathogens. *Plant Microbe Interface*. Cham: Springer International Publishing, pp. 219–238.

Rizwan M, Mujtaba G, Memon SA, Lee K and Rashid N (2018) Exploring the potential of microalgae for new biotechnology applications and beyond: a review. *Renewable and Sustainable Energy Reviews* **92**, 394–404.

Ronga D, Biazzi E, Parati K, Carminati D, Carminati E and Tava A (2019) Microalgal biostimulants and biofertilisers in crop productions. *Agronomy* **9**, 192.

https://doi.org/10.1017/S0021859621000885

Sakakibara H (2006) Cytokinins: activity, biosynthesis, and translocation. *Annual Review of Plant Biology* **57**, 431–449.

Scaglioni PT, Pagnussatt FA, Lemos AC, Nicolli CP, Del Ponte EM and Badiale-Furlong E (2019) *Nannochloropsis* sp. and *Spirulina* sp. as a source of antifungal compounds to mitigate contamination by *Fusarium graminearum* species complex. *Current Microbiology* **76**, 930–938.

Sharma HSS, Fleming C, Selby C, Rao JR and Martin T (2014) Plant biostimulants: a review on the processing of macroalgae and use of extracts for crop management to reduce abiotic and biotic stresses. *Journal of Applied Phycology* **26**, 465–490.

Similä J, Soininen N and Paukk E (2020) Towards sustainable blue energy production: an analysis of legal transformative and adaptive capacity. *Journal of Energy and Natural Resources Law*. https://doi.org/10.1080/02646811.2021.1875687.

Singh UB and Ahluwalia AS (2013) Microalgae: a promising tool for carbon sequestration. *Mitigation and Adaptation Strategies for Global Change* **18**, 1.

Stirk WA, Rengasamy KRR, Kulkarni MG and van Staden J (2020) Plant biostimulants from seaweed. In Geelen D, Xu L, Stevens CV (eds), *The Chemical Biology of Plant Biostimulants*. Belgium: John Wiley 1 sons, Ltd., pp. 31–55.

Suganya T, Varman M, Masjuki HH and Renganathan S (2016) Macroalgae and microalgae as a potential source for commercial applications along with biofuels production: a biorefinery approach. *Renewable and Sustainable Energy Reviews* **55**, 909–941.

Syed-Ab-Rahman SF and Omar D (2018) Development of bio-formulations of *Piper sarmentosum* extracts against bacterial rice diseases. *Current Biotechnology* **7**, 6.

Syed Ab Rahman SF, Singh E, Pieterse CMJ and Schenk PM (2018) Emerging microbial biocontrol strategies for plant pathogens. *Plant Science* **267**, 102–111.

Tarakhovskaya ER, YuI M and Shishova MF (2007) Phytohormones in algae. *Russian Journal of Plant Physiology* **54**, 163–170.

Thirumurthy P and Mol I (2020) Microalgae as bio-pesticides for the development of sustainable agriculture. *Wide Spectrum* **6**, 5–22.

Uzair B, Mahmood Z and Tabassum S (2011) Antiviral activity of natural products extracted from marine organisms. *BioImpacts: BI* **1**, 203–211.

Vasantharaja R, Abraham LS, Inbakandan D, Thirugnanasambandam R, Senthilvelan T, Jabeen SKA and Prakash P (2019) Influence of seaweed extracts on growth, phytochemical contents and antioxidant capacity of cowpea (*Vigna unguiculata* L. Walp). *Biocatalysis and Agricultural Biotechnology* **17**, 589–594.

Veluci RM, Neher DA and Weicht TR (2006) Nitrogen fixation and leaching of biological crust communities in mesic temperate soils. *Microbiology Ecology* **189**, 189–196.

Vishwakarma K, Upadhyay N, Kumar N, Yadav G, Singh J, Mishra RK, Kumar V, Verma R, Upadhyay RG, Pandey M and Sharma S (2017) Abscisic Acid Signaling and Abiotic Stress Tolerance in Plants: A Review on Current Knowledge and Future Prospects. *Frontiers in Plant Science* **20**, 161.

Wybouw B and De Rybel B (2019) Cytokinin – a developing story. *Trends in Plant Science* **24**, 177–185.

Yasuhara-Bell J and Lu Y (2010) Marine compounds and their antiviral activities. *Antiviral Research* **86**, 231–240.

Yildiztekin M, Tuna AL and Kaya C (2018) Physiological effects of the brown seaweed (*Ascophyllum nodosum*) and humic substances on plant growth, enzyme activities of certain pepper plants grown under salt stress. *Acta Biologica Hungarica* **69**, 325–335.

Yilmaz E and Sönmez M (2017) The role of organic/bio–fertilizer amendment on aggregate stability and organic carbon content in different aggregate scales. *Soil and Tillage Research* **168**, 118–124.

Žižková E, Kubes M, Dobrec PI, Pribyl P, Simura J, Zahajska L, Drabkova LZ, Novak O and Motyka V (2017) Control of cytokinin and auxin homeostasis in cyanobacteria and alga. *Annals of Botany* **119**, 151–166.

Zou P, Lu X, Zhao H, Yuan Y, Meng L, Zhang C and Li Y (2019) Polysaccharides derived from the brown algae *Lessonia nigrescens* enhance salt stress tolerance to wheat seedlings by enhancing the antioxidant system and modulating intracellular ion concentration. *Frontiers in Plant Science* **10**, 48.