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Review

The Use of Microalgae and Cyanobacteria in the Improvement of Agricultural Practices: A Review on Their Biofertilising, Biostimulating and Biopesticide Roles

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Abstract: The increase in worldwide population observed in the last decades has contributed to an increased demand for food supplies, which can only be attained through an improvement in agricultural productivities. Moreover, agricultural practices should become more sustainable, as the use of chemically-based fertilisers, pesticides and growth stimulants can pose serious environmental problems and lead to the scarcity of finite resources, such as phosphorus and potassium, thus increasing the fertilisers' costs. One possible alternative for the development of a more sustainable and highly effective agriculture is the use of biologically-based compounds with known activity in crops' nutrition, protection and growth stimulation. Among these products, microalgal and cyanobacterial biomass (or their extracts) are gaining particular attention, due to their undeniable potential as a source of essential nutrients and metabolites with different bioactivities, which can significantly improve crops' yields. This manuscript highlights the potential of microalgae and cyanobacteria in the improvement of agricultural practices, presenting: (i) how these photosynthetic microorganisms interact with higher plants; (ii) the main bioactive compounds that can be isolated from microalgae and cyanobacteria; and (iii) how microalgae and cyanobacteria can influence plants' growth at different levels (nutrition, protection and growth stimulation).

Keywords: bioactive compounds; crops' yield; cyanobacteria; growth stimulation; microalgae; plants' nutrition; plants' protection; sustainable agriculture

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1. Introduction

Worldwide population is increasing. According to different studies, this number has raised from six to seven billion between 1999 and 2011, and it is expected to further increase to nine billion by 2050 [1,2]. This increasing trend has resulted in an increased demand for food supplies, with a strong impact on agricultural practices. On the one hand, the increase in the global population results in a higher demand for food products, requiring higher agricultural productivities [1–4]. On the other hand, the social and economic activities developed by this increasing population have contributed to [1]: (i) a reduction in the area available for the production of food crops; (ii) water resources degradation and scarcity; (iii) accumulation of xenobiotic compounds in the soils; and (iv) degradation of soils' quality and fertility. To overcome the challenges related to the increase in global population and anthropogenic activities and meet the requirements for food supplies, an improvement in the productivity and sustainability of agricultural practices is required [1,5]. Higher productivities can be achieved in different ways: (i) increasing crops' yields; or (ii) preventing culture losses under stress conditions (both biotic and abiotic).

Chemically-based products have been widely used in agriculture, either as plant-growth promotors (improving crops' yields), or as plant protection agents (protecting plants from different stress conditions) [5–8]. However, most of these agents are toxic and their accumulation in the plants and in the soil can be a threat to humans and to the environment. Moreover, their accumulation has been associated with the development of microbial resistance to several drugs [3,5,7,8]. Considering the negative impacts of these products, current regulations are limiting the use of mineral fertilisers and chemical products in agriculture [5,7]. In the search for more sustainable and environmentally-friendly solutions to improve agricultural productivities, researchers have focused their attentions on biologically-based products, with microalgae and cyanobacteria emerging as a valuable resource for crops' production and protection due to their biofertilising and biostimulating potential [1–3,5,7,9].

The use of algae in agriculture dates from thousands of years ago [5,9]: for example, in coastal areas of Europe, farmers used to apply algae harvested near the shore in their cultures, both directly or after composting, observing positive effects in soil fertilisation. Since this period, algal biomass has been extensively used in agriculture, but in the 20th century, products obtained from algal extracts have attracted the attention of farmers worldwide [5]. In fact, a wide variety of biologically-active compounds extracted from algae and cyanobacteria (e.g., phenols, terpenoids, free fatty acids—FFAs, polysaccharides, and carotenoids) has demonstrated to have promising effects in crops' production [2,7]. According to the literature, algal metabolites can play an important role in [4,9]: (i) soil decontamination and fertilisation; (ii) plant protection against biotic and abiotic stress factors; and (iii) plant development. In addition, microalgae and cyanobacteria also present phytohormones, which are known for their activity as plant-growth promotors [7,10,11]. Taking into account their potential benefits for the development of a sustainable agriculture, both biomass and extracts from microalgae and cyanobacteria are commercially available [9].

This manuscript presents an overview of how algal biomass and extracts can improve crops' production, presenting the most recent applications of these microorganisms in the agricultural sector.

2. Microalgae as a Source of Biofertilisers, Biostimulants and Biopesticides

Microalgae and cyanobacteria are an important source of biologically-active compounds, such as phenolic compounds, polysaccharides, hormone-like substances and proteins, known for their benefits as antioxidant agents, plant-growth promotors, among others. Moreover, living organisms, both prokaryotes (e.g., nitrogen-fixing cyanobacteria) and eukaryotes (e.g., microalgae and macroalgae/seaweeds), are broadly recognised for their role in soils' fertilisation and plant growth stimulation [3]. Besides these important characteristics, the production of microalgal/cyanobacterial biomass can be quite advantageous, when compared to the production of other biological resources [3,4]: (i) production of these photosynthetic organisms can be performed in non-arable areas, thus not competing with the areas intended for food production; (ii) microalgae and cyanobacteria can be grown in low-quality waters, such as wastewaters, thus reducing the requirements for freshwater and nutrients (mainly nitrogen and phosphorus); (iii) the wealth composition of microalgal/cyanobacterial biomass can be fully exploited towards the induction of multiple responses in the same crop; and (iv) when growing autotrophically, microalgae and cyanobacteria uptake CO_2 from the atmosphere, thus reducing the carbon footprint of agricultural practices. Although several products can be used in the improvement of crops' productivities, it is important to understand that different biological compounds may improve the agricultural productivities through different modes of action: (i) soils' improvement; (ii) crops' protection against biotic and abiotic stress factors; and (iii) direct growth stimulation. Considering these roles, microalgal/cyanobacterial products and biomass can be classified as biofertilisers, biostimulants and biopesticides. Figure 1 summarises the main activities associated to these biologically-based products in the development of agricultural practices, highlighting their action mode and effect on crops' production.

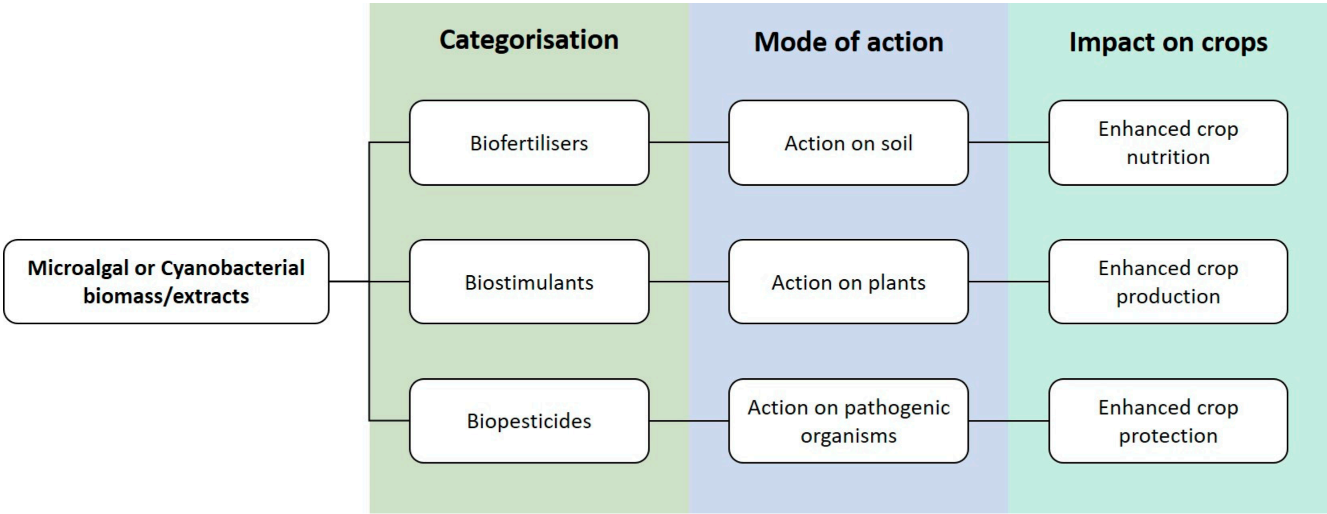

Figure 1. Categorisation of the main activities attributed to algal/cyanobacterial biomass and extracts in crops' production.

Biofertilisers are biologically-based compounds that promote an improvement in crops' productivities through their activity at the soil level. Typically, these compounds and/or microorganisms are responsible for the improvement of soil properties and soils' fertility, providing the essential nutrients (e.g., nitrogen, phosphorus and potassium) for plants' growth [4,8,12,13]. Depending on their beneficial effects and on the microorganisms integrating these formulations, biofertilisers can be classified as [8,14]: (i) plant-growth-promoting bacteria; (ii) compost; (iii) nitrogen-fixators; (iv) phosphate- and potassium-solubilising biofertilisers; and (v) phosphorus-mobilising biofertilisers. The use of biofertilisers in agriculture presents several advantages, such as [14,15]: (i) increased crop productivities per unit of area and time; (ii) reduced energetic requirements; (iii) control and maintenance of adequate soil properties and fertility; (iv) lower risks of soil and water contamination; and (v) crops' protection against pathogenic organisms.

Biostimulants promote crops' productivity by acting directly on the plant. These compounds are responsible for improving respiration, photosynthetic activity, nucleic acid synthesis and ion uptake, enhancing plants' metabolism and, hence, plants' growth [9]. The stimulatory activity of biostimulants can be observed under both optimal and adverse conditions, meaning that these compounds can play an important role in the improvement of plants' resistance and tolerance against stress conditions [3,4]. The application of biostimulants in agriculture has, therefore, the following advantages [3,4]: (i) increased crop productivities; (ii) increased nutrients' utilisation efficiencies; and (iii) enhanced crops' quality. Characterisation and categorisation of biostimulants can be quite complex, as a wide variety of compounds (e.g., polysaccharides, phenolic compounds, hormone-like compounds, vitamins, etc.) have been identified for their biostimulating activity in crops.

Biopesticides are known for their activity against plant pathogens. These compounds, typically presenting antimicrobial, antioxidant, antiviral or antifungal properties, promote crops' development by protecting plants from pathogenic organisms.

3. Microalgal/Cyanobacterial Metabolites and Phytohormones with Potential Interest for Agriculture

Microalgae and cyanobacteria produce a wide variety of metabolites that, due to their biological activity, can be used in agriculture as biofertilisers, biostimulants or biopesticides. Among these metabolites, phenolic compounds, terpenoids, FFAs, polysaccharides, carotenoids and phytohormones are of particular interest, as they have already been identified as plant-growth promotors [2,7,12]. Table 1 presents the main biologically-active compounds that can be extracted from microalgae and cyanobacteria for their benefits in agricultural practices.

Table 1. Microalgal and cyanobacterial metabolites with potential interest for agriculture.

Metabolites	Examples	Microalgal/Cyanobacterial Sources	Biological Activity	Role in Agriculture	Refs.
Phenolic compounds	Polyphenols; phenolic acids; flavonoids; phenylpropanoids	*Botryococcus braunii*; *Chaetoceros calcitrans*; *Chlorella vulgaris*; *Isochrysis galbana*; *Isochrysis* sp.; *Neochloris oleoabundans*; *Odontella sinensis*; *Phaeodactylum tricornutum*; *Saccharina japonica*; *Skeletonema costatum*; *Tetraselmis suecica*	Antibacterial; antioxidant; antifungal	Crops' protection against pathogens or other biotic and abiotic stress conditions	[2,7,16–21]
Terpenoids	Hemiterpenes; monoterpenes; sesquiterpenes; diterpenes; triterpenes; polyterpenes	*Chondrococcus hornemanni*; *Hypnea pannosa*; *Oscillatoria perornata*; *Planktothricoids raciborskii*; *Plocamium cornutum*; *Plocamium leptophyllum*; *Portieria hornemann*; *Pseudanabaena articulate*; *Pseudanabaena* sp.; *Sphaerococcus coronopifolius*; *Synechocystis* sp.; *Thermosynechococcus elongatus*	Antibacterial; anticarcinogenic; antioxidant	Crops' protection against bacteria, insects and other organisms Stimulation of preliminary growth and development of plants Attraction of pollinators	[2,7,22–28]
Free fatty acids	Saturated and unsaturated fatty acids	*Anabaena*; *Chlorella*; *Dunaliella*; *Nannochloropsis*; *Porphyridium*; *Scenedesmus*; *Spirulina*	Antibiotic; anticarcinogenic; antifungal; antioxidant; antiviral	Crops' protection against pathogens or other biotic and abiotic stress conditions	[2,7,29–33]
Polysaccharides	Extracellular polysaccharides; structural polysaccharides; energy-storage polysaccharides	*Aphanothece*; *Arthrospira*; *Chlamydomonas*; *Chlorella*; *Cylindrotheca*; *Dunaliella*; *Navicula*; *Nostoc*; *Phaeodactylum*; *Porphyridium*; *Rhodella*; *Scytonema*	Antibacterial; anticancer; anticoagulant; anti-inflammatory; antioxidant	Improvement of soil quality Plant growth stimulation Crops' protection against biotic and abiotic stress conditions	[2,7,34–46]
Carotenoids	Alpha-carotene; beta-carotene; lutein; lycopene; astaxanthin; zeaxanthin	*Chlorella protothecoides*; *Chlorella pyrenoidosa*; *Chlorella zofingiensis*; *Dunaliella salina*; *Haematococcus pluvialis*; *Muriellopsis* sp.; *Phaeodactylum tricornutum*; *Spirulina* sp.	Anticancer; anti-inflammatory; antioxidant	Soil bioremediation and fertilisation Crops' protection against bacteria, insects and other biotic and abiotic stress conditions Crops' fortification	[7,47–53]
Phytohormones	Auxins; abscisic acid; cytokinins; ethylene; gibberellins	*Arthrospira*; *Chlamydomonas*; *Chlorella*; *Phormidium*; *Protococcus*; *Scenedesmus*	Chemical messengers	Plant growth stimulation Regulation of cellular activities in crops Crops' response to stress conditions	[2,4,7,10,11,54]

3.1. Phenolic Compounds

Phenolic compounds correspond to aromatic hydrocarbons bonded to a hydroxyl group. These compounds can be broadly categorised into phenols and polyphenols, with phenols being sub-divided into phenolic acids, flavonoids and phenylpropanoids [2,7,19,21]. In microalgae, phenols are considered secondary metabolites and their production and release is determined by several physical, chemical and environmental conditions. Phenolic compounds present in microalgae and cynobacteria are associated with their antioxidant properties [18,55], playing an important role in the growth, reproduction and protection against several stress conditions [55]. Goiris, et al. [18] assessed the antioxidant activity of 32 microalgal strains and compared the obtained results with total phenolics and carotenoids contents, concluding that, after carotenoids, phenolic compounds had a significant contribute to the antioxidant capacity of the studied microalgae. Among the studied microalgal species, *Tetraselmis suecica*, *Botryococcus braunii*, *Neochloris oleoabundans*, *Isochrysis* sp., *Chlorella vulgaris* and *Phaeodactylum tricornutum* presented the highest antioxidant capacities, and the highest phenolic contents (between 1.70 and 4.57 mg g^{-1} DW, dry weight basis). More recently, Foo, et al. [17] evaluated the relationship between the antioxidant activity of six algal species (five microalgae and one macroalga) and the presence of bioactive compounds (e.g., carotenoids, phenolic acids, fucoxanthin and fatty acids profile). In this study, the authors concluded that *Chaetoceros calcitrans* and *Isochrysis galbana* presented the highest antioxidant activity, followed by *Odontella sinensis* and *Skeletonema costatum*, with moderate antioxidant activity, and *P. tricornutum* and *Saccharina japonica* with the lowest antioxidant properties. Regarding the influence of bioactive compounds in the antioxidant activity of these algal species, through Pearson correlation and multiple linear regression analyses, the authors concluded that the main contributors to the antioxidant capacity of the studied algae were carotenoids (representing 0.05–6.13 mg g^{-1} DW) and phenolic acids (representing 0.02–12.24 mg g^{-1} DW). For agricultural purposes, phenolic compounds act mainly on crop protection against pathogens or other biotic and abiotic stress conditions, due to their antimicrobial, fungicide and antioxidant properties [7,16,20].

3.2. Terpenoids

Terpenoids are organic compounds that derive from the inclusion of methyl- or oxygen-based functional groups to terpenes. Based on the number of five-carbon isoprene units that constitute them, terpenoids can be classified into: hemiterpenoids (one isoprene unit, C5), monoterpenoids (two isoprene units, C10), sesquiterpenoids (three isoprene units, C15), diterpenoids (four isoprene units, C20), triterpenoids (six isoprene units, C30), tetraterpenoids (eight isoprene units, C40) and polyterpenoids (more than eight isoprene units, >C40) [2,7]. Moreover, terpenoids can be classified according to the number of cyclic structures that constitute them, being the main categories monocyclic, bicyclic, rearranged and linear [7]. These compounds are secondary metabolites of several algal and cyanobacterial species. Among algae, red algae (Rhodophyta) are the richest source of secondary metabolites, with many genera known for their ability to produce terpenoids [28]. For example, 512 sesquiterpenes and 133 diterpenes with different structures have been extracted from the genus *Laurentia* [56]. Other red algae species that produce terpenoids include *Chondrococcus hornemanni*, *Hypnea pannosa*, *Sphaerococcus coronopifolius*, *Plocamium cornutum*, *Plocamium leptophyllum* and *Portieria hornemannii* [28]. In the case of cyanobacte ria, genes encoding the enzymes involved in the terpenoid biosynthetic pathway were identified in *Synechocystis* sp. PCC 6714 and *Thermosynechococcus elongatus*. Similarly, ma- rine cyanobacteria, such as those from the genera *Prochlorococcus*, *Synechococcus* and *Trich-odesmium* are known for their ability to produce isoprene. Finally, some filamentous cyanobacteria (e.g., *Pseudanabaena* sp., *Pseudanabaena articulate*, *Planktothricoids raciborskii* and *Oscillatoria perornata*) were also reported as a source for terpenoids [25]. Due to their bioactivity, especially in terms of antibacterial, antioxidant and anticancer properties, terpenoids are widely used in pharmaceutical and cosmetic formulations [22,23,27]. As precursors of linear terpenes, terpenoids are also being explored as potential candidates to replace fossil fuels [25,57]. In agriculture, the antimicrobial, allelochemical and antioxidant properties of terpenoids make them valuable resources for use as biopesticides, with major impact on crops' protection against bacteria, insects and other organisms [26]. In addition, it has been reported that terpenoids can play an important role during the preliminary growth and development of plants, as well as on the attraction of pollinators [24].

3.3. Free Fatty Acids

FFAs are non-esterified fatty acids typically found in microalgal and cyanobacterial crude extracts. According to the length of the hydrocarbon chain, FFAs can be classified as short, medium, long and very long chain fatty acids. Moreover, they can be divided into unsaturated (e.g., lignoceric, palmitic, capric, behenic, cerotic, caprylic, lauric, stearic, myristic and arachidic acids) and saturated (e.g., cis- and trans-fatty acids) fatty acids [7]. FFAs were identified in microalgal biomass from different genera (e.g., *Anabaena*, *Chlorella*, *Dunaliella*, *Porphyridium*, *Scenedesmus* and *Spirulina*), which include green, red and blue-green algae [29,33]. In addition, several studies have reported that microalgae and cyanobacteria can accumulate up to 70% of fatty acids per dry weight [2]. For example, in the study performed by Feller, et al. [32], extracts from the marine microalgae *P. tricornutum*, *Nannochloropsis oculata* and *Porphyridium cruentum* presented 37.3–82.4% of saturated fatty acids and 27.5–38.5% of polyunsaturated fatty acids. Due to current demands for renewable energy resources, FFAs from microalgae and cyanobacteria have been extensively explored as a resource for biodiesel production, as it can be obtained from the transesterification of fatty acids [58]. In addition to their potential use as a renewable energy resource, FFAs are also recognised for their anticarcinogenic, antibiotic, antifungal, antioxidant and antiviral activities, which make them promising candidates for the development of pharmaceutical, nutraceutical and cosmetic products [2,7,30,31]. Biological activity, namely antimicrobial, antifungal and antioxidant properties, is also an important advantage for agriculture, as application of FFAs extracts can act on crops' protection.

3.4. Polysaccharides

Polysaccharides are polymers of carbohydrate molecules, which correspond to monosaccharide chains bonded by glycosidic interactions. A great diversity of polysaccharides can be obtained, being their characteristics determined by the building blocks, that is, the monosaccharides (e.g., hexose, pentose, uronic acid and methyl pentose) [2,7]. These polysaccharides are used by other organisms as carbon and energy sources, being excreted by algae under both normal and stress conditions. Production of a great diversity of extracellular polysaccharides has been reported for microalgae of different genera, such as *Cylindrotheca*, *Navicula*, *Phaeodactylum*, *Chlamydomonas*, *Chlorella*, *Dunaliella*, *Aphanothece*, *Arthrospira*, *Nostoc*, *Scytonema*, *Porphyridium* and *Rhodella*, being the production yields comprised between 0.01 and 2.9 g L^{-1} [37]. Other polysaccharides have structural functions in the cell walls of different organisms. These include arabinoxylans, cellulose, chitin and pectins, and their production has been associated with marine and freshwater algae, including brown, red, green and blue-green algae [7]. In addition, some polysaccharides (e.g., starch and glycogen) act as energy storage molecules. Starch is typically produced by red and green algae, whereas glycogen is mainly accumulated by species of *Porphyridium* and blue-green algae [7]. Polysaccharides' synthesis by microalgae and cyanobacteria accounts for 0.5–20 g L^{-1} [37]. These polymers have been widely applied as thickening, gelling, stabiliser and emulsifier agents [45]. Moreover, antibacterial, anticoagulant, antioxidant, anticancer and anti-inflammatory properties have been described for these compounds [38,43,44]. In agriculture, polysaccharides have a preponderant role in the improvement of soil quality, with major activities as soil conditioners, nutrient carriers and as safe release systems for agrochemicals [35,36,41,42]. Despite their impact on soils, some studies have also demonstrated that polysaccharides can act on plant growth stimulation and on plant defence against biotic and abiotic factors [34,36,39,40,46].

3.5. Carotenoids

Carotenoids are accessory pigments used by algae during photoautotrophic growth. These compounds are obtained through polymerisation of five-carbon isoprene units [51,59]. Although they are essential for photosynthetic organisms, production of these compounds has also been described for bacteria and fungi [48,60]. Their role in algae is associated with light harvesting, protein assembly in photosystems and protection against photo-induced free radicals exposure [49]. The main carotenoids obtained from microalgae include alpha- and beta-carotene, lutein, lycopene, astaxanthin and zeaxanthin. *Spirulina* and *Dunaliella* species are the major sources of alpha- and beta-carotene (up to 10% DW), respectively. Lutein is typically obtained from *Chlorella protothecoides*, *Scenedesmus almeriensis* and *Muriellopsis* species, which can accumulate between 4.3 and 5.4 mg g^{-1} DW. Lycopene, in turn, can be found in several green algae, such as *Chlorella marina*, *Chlorella regularis* and *Dunaliella salina*. Similarly, astaxanthin is mainly produced by green algae, such as *Haematococcus pluvialis* and *Chlorella zofingiensis*, being *H. pluvialis* the major source of this compound, accumulating up to 3% DW. Finally, zeaxanthin is obtained from red and green microalgae, such as *P. cruentum* and *Chlorella ellipsoidea*. According to several studies, zeaxanthin in *P. cruentum* accounts for 97.4% of the total carotenoids content of this microalga. On the other hand, *C. ellipsoidea* can accumulate up to 4.26 mg g^{-1} DW of zeaxanthin [47,49,51,52]. Carotenoids from microalgae have been extensively used in food, feed, cosmetics, nutraceutical and pharmaceutical applications, due to the antioxidant, anti-inflammatory and anticancer properties exhibited by these compounds [47–49,52]. Regarding agricultural practices, carotenoids have been applied in soils' bioremediation and also as antioxidants, fertilisers and biopesticides, with major impacts on soil improvement and crops' protection.

They are also applied to increase the availability of provitamin A, contributing to the development of biofortified crops [50,53].

3.6. Phytohormones

Phytohormones are considered signal molecules that are responsible for the regulation of several cellular processes in plants. Typically, these molecules are produced in small amounts and their presence has been firstly identified in higher plants [11]. However, the booming in algal research in the last decades, especially microalgal genomic studies, has demonstrated that these signalling molecules are also produced by a wide diversity of microalgae and cyanobacteria. In fact, the most popular phytohormones (i.e., auxins, abscisic acid, cytokinins, ethylene and gibberellins) have already been identified in multiple algal lineages, such as brown, red and green algae, cyanobacteria and diatoms [10,11]. Although research studies on the physiological responses promoted by microalgal phytohormones are still very scarce, the similarities found between phytohormones profiles in higher plants and algae suggest that their roles may be very similar. In higher plants, auxins, especially indole-3-acetic acid, are responsible for the regulation of growth and development [11]. In microalgae, these molecules also act as growth regulators, as auxins from *C. vulgaris*, *D. salina*, *Nannochloropsis oceanica*, *Scenedesmus obliquus* and *Scenedesmus quadricauda* have promoted an increase in cell size and chlorophyll and protein contents, as well as cell division, which resulted in higher biomass productivities [61–65]. Abscisic acid is commonly associated with the cellular response to environmental stress factors, such as high salinity levels, drought and nutrients scarcity [10,11]. Typically, this molecule induces cellular mechanisms to increase the plants' tolerance to these stress conditions and avoid their harmful effects. In higher plants, it has been demonstrated that abscisic acid can improve the tolerance to temperature and salt stresses through the control of water and ions uptake [66]. In microalgae and cyanobacteria, this molecule is quite effective in the control of cells' response to salt, osmotic, oxidative, drought and nutrients' stresses [67,68]. Common responses induced by the activation of the abscisic acid pathway include the production of carotenoids, which typically act as protecting agents against oxidative stress [62]. Regarding cytokinins, these molecules mediate several processes in higher plants, namely cell division, growth, biogenesis, chloroplasts differentiation, regulation of seed dormancy, among others [10]. Therefore, the role of these hormones in plants' growth and development is crucial. Besides these activities, cytokinins also improve the plants' tolerance to adverse environmental conditions [10,11]. In microalgae and cyanobacteria, the role of these hormones is very similar, as they also stimulate cell division and photosynthetic activity and protect cells from environmental stress conditions [69]. For example, cytokinins from *Acutodesmus obliquus*, *C. vulgaris* and *Gracilaria caudata* have been associated with increased pigments' contents in these organisms, which resulted in higher photosynthetic rates and, hence, higher biomass productivities [70–72]. Additionally, a cytokinin produced by *D. salina*, kinetin, induced the accumulation of the photo-protective pigment beta-carotene in this microalga [62]. Ethylene is known for its multiple responses in plants, which range from the regulation of plants' growth and ageing, to the improvement of plants' tolerance to both biotic and abiotic stress factors [10]. In microalgae and cyanobacteria, the role of ethylene is not well documented. However, some studies have evidenced that this molecule may act as a growth stimulation agent in *Chlamydomonas reinhardtii*, *Chlorella* sp. and *Spirogyra platensis* [73–75]. Gibberellins from plants and microalgae/cyanobacteria have similar functions, which are mainly related with growth stimulation and induction of pigments and proteins accumulation [10,11]. In the case of microalgae and cyanobacteria, gibberellins from *C. ellipsoidea*, *Chlorella pyrenoidosa*, *C. vulgaris* and *Microcystis aeruginosa* have been associated with increased cell number and size and higher growth rates [76–79]. The regulation activities promoted by phytohormones extracted from microalgae and cyanobacteria highlight additional benefits of using these organisms (or their extracts) in agricultural fields, especially in what concerns growth stimulation and plants' protection against biotic and abiotic factors.

4. The Impacts of Microalgae/Cyanobacteria and Their Extracts on Crops' Production

As reported in Section 3, microalgae and cyanobacteria are an important source of biologically-active compounds that can significantly improve agricultural productivities. The wide diversity of compounds found in microalgae/cyanobacteria, together with their multiple functions in crops' production, allow their use as pure extracts or as a crude algal compost. Moreover, this diversity of metabolites impacts crops' production at different levels: (i) some extracts and microorganisms induce higher crops' productivities through an improvement in the soil quality; (ii) others enhance crops' development through the protection against biotic and abiotic stress conditions; and (iii) some metabolites act directly on plant growth stimulation. The next sections present how different metabolites can improve crops' production at these three levels, focusing on specific application examples.

4.1. Soil Improvement

Some algal and cyanobacterial species and their extracts are known for their positive effect at the soil level. Well-known activities include their ability to (i) fix atmospheric nitrogen into nitrogen species that can be easily assimilated by plants; (ii) provide essential nutrients for plants; and (iii) improve soil physical and chemical properties. Table 2 presents some application examples where microalgae and cyanobacteria (and their extracts) have contributed to an improvement in crops' productivities by action at the soil level.

Table 2. Impacts of microalgae and cyanobacteria (and their metabolites) on soils' improvement.

Mode of Action	Algae/Algal Extracts	Target Crop/Soil	Observed Improvements	Ref.
Nitrogen fixation	Cyanobacterial inoculum composed by *Aulosira fertilissima*, *Anabaena sphaerica*, *Nostoc hatei*, *Cylindrospermum majus* and *Westiellopsis prolifica*	Rice	Increase in nitrogen availability in the soil Increase in grain and straw yields	[80]
	Wild type and herbicide-resistant strains of *Anabaena variabilis*	Rice	Increase in grain, straw and seeds yields Increase in plant height and leaf length	[81]
	Nostoc sp. vegetative cells	Rice	Increase in grain yields comparable to those obtained with a chemical fertiliser	[82]
	Nostoc entophytum and *Oscillatoria angustissima*	Pea	Increase in nitrogen fixation Increase in growth parameters, germination percentage and photosynthetic pigments Increase in nutritional value of pea seeds	[83]
	Anabaena torulosa biofilm	Wheat	Increase in nitrogen availability in the soil	[84]
	Cyanobacterial-bacterial biofilms including the species: *Calothrix* sp., *Anabaena laxa*, *Anabaena torulosa*, *Anabaena doliolum*, *Nostoc carneum*, *Nostoc piscinale*, *Trichoderma viride*, *Pseudomonas fluorescens* and *Azotobacter chroococcum*	Soybean and mungbean	Increase in nitrogen availability in the soil Increase in plant fresh weight	[85]
Nutrients' availability in soils	*Calothrix ghosei*, *Hapalosiphon intricatus* and *Nostoc* sp.	Wheat	Increase in organic carbon content in the soil Increase in grain yield	[86]
	Cyanobacterial consortia including the species: *Anabaena doliolum*, *Cylindrospermum sphaerica* and *Nostoc calcicola*	Wheat and millet	Increase in nitrogen and phosphorus availability in the soil Decrease in soil density Improvement of water retention capacity Increase in grain yields Improvement of nutritional properties (increase in protein content of grain and leaves)	[87]
	Microalgal-bacterial flocs and *Nannochloropsis oculata*	Tomato	Increase in ammonium, phosphorus and potassium availability in the soil Improvement of fruit quality (increase in sugar and carotenoids contents)	[88]
	Consortia and biofilms including the species: *Azotobacter* sp., *Anabaena* sp., *Providencia* sp. and *Calothrix* sp.	Okra	Increase in zinc and iron availability in the soil Beneficial changes in the microbiome Increase in root yield and weight	[89]
	Microalgal-cyanobacterial unicellular and filamentous consortia including species of: *Chlorella*, *Scenedesmus*, *Chlorococcum*, *Chroococcus*, *Phormidium*, *Anabaena*, *Fischerella* and *Spirogyra*	Wheat	Increase in nitrogen, phosphorus and potassium availability in the soil Increase in organic carbon content in the soil Improvement of product quality (increase in nitrogen, phosphorus and potassium contents in roots, shoots and grains)	[90]

Table 2. *Cont.*

Mode of Action	Algae/Algal Extracts	Target Crop/Soil	Observed Improvements	Ref.
	Microalgal-cyanobacterial unicellular and filamentous consortia including species of: *Chlorella*, *Scenedesmus*, *Chlorococcum*, *Chroococcus*, *Phormidium*, *Anabaena*, *Fischerella* and *Spirogyra*	Wheat	Increase in zinc, iron, copper and manganese availability in the soil Increase in organic carbon content in the soil Increase in grain yield Improvement of plant nutritional value (increase in grain micronutrient contents)	[91]
	Chlorella sorokiniana	Soil from a vineyard	Increase in nitrogen availability in the soil	[92]
Soil physical and chemical amendments	*Microcoleus vaginatus*, *Phormidium tenue*, *Scytonema javanicum*, *Nostoc* sp. and *Desmococcus olivaceus*	Unconsolidated sand	Increase in crust cohesion Increase in the resistance to wind erosion	[93]
	Nostoc strains	Poorly aggregated tropical soils	Increase in aggregates' stability	[94]
	Phycocyanin extract from *Spirulina platensis* and inactive biomass of *Spirulina platensis*	Soil contaminated with diesel and biodiesel	Reduction in diesel and biodiesel concentration using *S. platensis* and phycocyanin, respectively	[95]

4.1.1. Nitrogen Fixation

Blue-green algae (or cyanobacteria) are able to fix atmospheric nitrogen (N_2), converting it into organic nitrogen forms, which are more easily assimilated by higher plants. Therefore, the use of cyanobacteria in soils increase the availability of nitrogen, which is one of the essential nutrients for plants' growth [6,8,96,97]. The beneficial effects of cyano-bacteria in agricultural soils (for the production of different crops) has already been demonstrated [90]. For example, using a cyanobacterial inoculum in a rice paddle, Jha and Prasad [80] concluded that this inoculum improved the grain and straw yields and increased the availability of nitrogen in the soil. Similarly, using *Anabaena variabilis* strains in a rice field, Singh and Datta [81] demonstrated that the used strains promoted an overall improvement in the rice crops (e.g., increase in plant height and leaf length, and improvement of seeds, grain and straw productivities). When applying *Nostoc* sp. vegetative cells to a rice field, Innok, et al. [82] obtained an increase in grain yields comparable to the one obtained with a chemically-based nitrogen fertiliser. Although the majority of the studies refer to the use of cyanobacteria in rice fields, recent studies have also referred the positive effect of cyanobacteria in other cultures. Osman, et al. [83] inoculated the soil intended for pea plant production with the cyanobacterial species *Nostoc entophytum* and *Oscillatoria angustissima,* observing a significant increase in the germination percentage, photosynthetic pigments and growth parameters of this plant. In addition, the authors observed that this increase was associated with a higher N_2 fixation activity by both cyanobacteria. In the study performed by Swarnalakshmi, et al. [84], the use of a biofilm composed by the cyanobacterium *Anabaena torulosa* in a wheat crop significantly increased the availability of nitrogen in the soil. Prasanna, et al. [85] evaluated the potential of several cyanobacterial-bacterial consortia as fertilisers for soybean and mungbean production, presenting positive results in terms of nitrogen availability in the soil and plant fresh weight. Considering the improvements observed in terms of nitrogen availability, it is possible to conclude that cyanobacteria could be used in replacement of chemical nitrogen fertilisers, which can reduce crops' production costs by 25–40%. The use of these microorganisms also promotes nitrogen recycling, avoiding the continuous production of chemically-based nitrogen fertilisers. Finally, cyanobacteria are known for their ability to form soil crusts that avoid nitrogen leaching/runoff and, therefore, the risks of water contamination with nitrogen [96].

4.1.2. Nutrients' Availability in Soils

The use of microalgae and cyanobacteria in soils can also increase the availability of other essential nutrients for plants. As photosynthetic microorganisms, microalgae and cyanobacteria uptake nitrogen and phosphorus from different environments (even from sites where these nutrients are limiting) and store them in their biomass. As these nutrients are essential for the development of higher plants, microalgal/cyanobacterial biomass can be considered as an important source of these nutrients, avoiding the use of the traditional chemical fertilisers [4,8,97]. Other essential microelements for plants' growth and development (e.g., potassium, magnesium, sulphur and iron) can also be found in microalgal/cyanobacterial biomass. These elements are typically involved in redox reactions, playing an important role in plants' metabolism. Therefore, the use of microalgae and cyanobacteria in soils can improve the availability of both macro- and micronutrients for plants' growth. This improvement in nutrients' availability has already been reported in the literature [88,89,91,92]. Coppens, et al. [88] applied microalgal-bacterial flocs and *N. oculata* biomass to a tomato culture and evaluated their impact on soil composition and fruit development. The authors concluded that the presence of the photosynthetic organisms increased the availability of nitrogen, phosphorus and potassium in the soil and improved the fruit quality, by an increase in the sugar and carotenoids contents. However, a lower tomato yield was obtained when compared to the one achieved using an inorganic fertiliser. In the study performed by Manjunath, et al. [89], the use of cyanobacterial-bacterial biofilms and consortia to okra crops resulted in an increase in zinc and iron contents in the soil and contributed to an increased root yield and weight. More recently, Marks, et al. [92] evaluated the influence of applying a *Chlorella sorokiniana* culture in a vineyard soil on its composition, concluding that the presence of this microalga increased the concentration of nitrogen in the referred soil.

Microalgae and cyanobacteria can also act as a source of organic matter to higher plants, which should be supplied in adequate concentrations for a proper plants' growth [96,97]. Firstly, these photosynthetic microorganisms fix atmospheric CO_2, converting it into organic biomass. Moreover, these organisms tend to excrete extracellular polymeric substances, increasing the organic carbon levels in soils and promoting the growth of other microorganisms. Finally, microalgal and cyanobacterial biomass present in agricultural fields may be degraded by other organisms and grazers, which also increases the organic carbon content in the soils. The increase of organic carbon contents in soils using microalgae and/or cyanobacteria has already been described in the literature [86,87,91]. For example, Karthikeyan, et al. [86] demonstrated that the use of cyanobacterial suspensions (*Calothrix ghosei*, *Hapalosiphon intricatus* and *Nostoc* sp.) in wheat production increased organic carbon concentration in the soil, while promoting higher grain yields. More recently, Renuka, et al. [91] evaluated the effect of unicellular and filamentous microalgal-cyanobacterial consortia on soil composition and grain quality of a wheat crop. Besides an increase in micronutrient availability in the soil (mainly zinc, iron, copper and manganese), the studied consortia also enhanced its organic carbon content. This improvement in soil quality resulted in an increased grain yield and in a higher quality product, as the obtained grains presented an improved nutritional composition.

4.1.3. Soil Physical and Chemical Amendments

Microalgae and cyanobacteria also play an important role in the recovery of damaged soils, as they are able to: (i) modulate soils' pH; (ii) control soils' salinity or protect plants from high salinity levels; and (iii) remove heavy metals and other contaminants from soils [7,85,97,98]. Regarding the pH control, several studies have reported either an increase or decrease in soils' pH when using microalgal/cyanobacterial biomass. However, it is important to highlight the beneficial effect of this biomass in controlling the acidic/basic nature of different soils [7,99]. In terms of soils' salinity, several studies have reported an improvement in plants' growth in soils presenting high salinities [97]. This improvement may be a result of (i) a reduction in the soils' salinity (by increasing the water retention capacity of soils); or (ii) an increase in plants' tolerance to high salinity levels (which may be achieved by gibberellic acid, a phytohormone commonly found in microalgae and cyanobacteria). Finally, microalgae and cyanobacteria are able to sequester trace elements (e.g., iron, zinc, copper and manganese), heavy metals (e.g., cadmium, lead and chromium), hydrocarbons and other compounds from the surrounding environment. Therefore, when applied to soils, microalgae and cyanobacteria may contribute to its remediation and to an increase in soils' quality and fertility [7,8,98,100]. Decesaro, et al. [95] evaluated the potential of inactive *Spirulina platensis* cells and phycocyanin extracts from the same species on hydrocarbons removal from a soil contaminated with diesel and biodiesel. Compared to the control, phycocyanin extracts and inactive cells have effectively removed hydrocarbons from the contaminated soils, with the extracts being more effective in biodiesel removal (88.8%) and *S. platensis* inactive cells in diesel removal (63.9%).

Besides their importance in the enrichment of soils with essential nutrients and in the reclamation of soil properties, microalgae and cyanobacteria can also improve some soil characteristics, such as aggregation, porosity, permeability, ventilation and humidity level [6,7,97,101]. Typically, the improvement of these characteristics is associated with the polysaccharides excreted by several microalgal/cyanobacterial species [6,97]. When excreted to the soils, these polysaccharides tend to form an adhesive and gelatinous sheath that contributes to soils' aggregation and prevents them from erosion [6]. These polysaccharides also play an important role in soils' aeration and in their ability for water retention, which is crucial to maintain soils' temperature, pH and salinity [6,7,97,101]. The improvement of these soil properties significantly enhances crops' productivities, as they stimulate root growth and boost the soil microbial activity. Therefore, microalgae and cyanobacteria have been widely used in the restoration of soils' properties and in the improvement of soils' fertility. Hu, et al. [93] demonstrated that the resistance to wind erosion of unconsolidated sand was increased in the presence of desert soil algae, such as *Microcoleus vaginatus*, *Phormidium tenue*, *Scytonema javanicum*, *Nostoc* sp. and *Desmococcus olivaceus*, concluding that this increase was associated with higher crusts' cohesion in the samples treated with the referred algae. Similarly, Issa, et al. [94] inoculated a poorly aggregated soil with *Nostoc* strains, achieving a higher degree of aggregation in the inoculated soil when compared to the non-inoculated one.

4.2. Crops' Protection

Crops protection against biotic and abiotic factors is crucial for the improvement of agricultural productivities. Some plants have their defence and resistance mechanisms, but to achieve the ambitious target productivities, external protection agents should be employed on food crops. Considering the wide variety of bioactive compounds that can be found in microalgae and cyanobacteria, the use of these microorganisms (or their extracts) can promote an adequate crops' protection against both biotic and abiotic factors. Table 3 presents some examples of the application of microalgae and cyanobacteria (biomass and/or extracts) on crops' protection and productivity.

Table 3. Impacts of microalgae and cyanobacteria (and their metabolites) on crops' protection.

Mode of Action	Algae/Algal Extracts	Target Crop	Observed Improvements	Ref.
Protection against biotic factors	*Laminaria digitata*	Grapevine	Fungicidal activity against *Botrytis cinerea* and *Plasmopara viticola*	[102]
	Methanolic extract from *Sargassum wightii*	Rice	Antibacterial activity against *Xanthomonas oryzae*	[103]
	Oscillatoria, *Anabaena*, *Nostoc*, *Nodularia* and *Calothrix* species	Pepper	Fungicidal activity against *Alternaria alternate* and *Botrytis cinerea*	[104]
	Oscillatoria chlorina	Tomato	Fungicidal activity against *Meloidogyne arenaria* Improved plant growth	[105]
	Extracts from *Ulva armoricana*	Bean, grapevine and cucumber	Fungicidal activity against *Erysiphe polygoni*, *Erysiphe necator* and *Sphareotheca fuliginea* Reduced foliar disease	[106]
	Anabaena variabilis and *Anabaena oscillarioides*	Tomato	Reduction in fungal disease severity Improved plant growth (increased height and fresh weight of plants)	[107]
	Spatoglossum variabile, *Stokeyia indica* and *Melanothamnus afaqhusainii*	Watermelon and eggplant	Fungicidal activity against the root rotting fungi, *Fusarium solani*, *Fusarium oxysporum* and *Macrophomina phaseolina* Antinematodal activity against *Meloidogyne* spp. Improved plant growth (increased fresh weight of shoots, increased length of vines in watermelon and increased shoot length in eggplant)	[108]

Table 3. *Cont.*

Mode of Action	Algae/Algal Extracts	Target Crop	Observed Improvements	Ref.
	Anabaena laxa and *Calothrix elenkinii*	Coriander, cumin and fennel	Increase in the activity of β-1,3 endoglucanase in shoots and roots Increase in fungicidal activity Increase in germination rates Increase in shoot and root length Increase in plant dry weight	[109]
	Anabaena torulosa, *Anabaena laxa*, *Anabaena azollae*, *Anabaena oscillarioides* and *Calothrix* sp.	Wheat	Increase in nitrogen fixation Increase in the activity of hydrolytic and defence enzymes (endoglucanase, peroxidase, polyphenol oxidase and phenylalanine ammonia lyase) Increase in fresh and dry weight of plant	[110]
	Calothrix elenkinii	Rice	Increase in the activity of hydrolytic and defence enzymes (peroxidase, polyphenol oxidase and phenylalanine ammonia lyase) Increase in nitrogenase activity and indole acetic acid production Increase in plant growth	[111]
	Aqueous extract from *Cystoseira myriophylloides* and *Fucus spiralis*	Tomato	Antibacterial activity against *Agrobacterium tumefaciens*	[112]
	Polysaccharides' extract from *Chlorella vulgaris*, *Chlorella sorokiniana* and *Chlamydomonas reinhardtii*	Tomato	Increase in the activity of hydrolytic and defence enzymes (β-1,3 endoglucanase, peroxidase, ascorbate peroxidase and phenylalanine ammonia lyase) Improvement of plant nutritional value (increase in polyunsaturated fatty acids contents)	[40]
Protection against abiotic factors	*Scytonema hofmanni*	Rice	Alleviation of salt stress comparable to the one obtained with gibberellic acid	[113]
	Seaweed extracts	Cucumber	Low temperature stress was not observed in treated plants Improvement of plant productivity (increase in the number of fruit per plant, fruit weight and total yield)	[114]
	Extracts from *Ascophyllum nodosum*	Wheat	Alleviation of drought stress Increase in growth, yield and nutrients uptake	[115]
	Extracts from *Ulva rigida* and *Fucus spiralis*	Beans	Alleviation of drought stress Increase in the activity of antioxidant enzymes and in the polyphenol content (mediators of plants' protection mechanisms) Improvement of plant growth	[116]
	Sargassum muticum and *Jania rubens*	Chickpea	Alleviation of salt stress Increase in the activity of enzymes (superoxide dismutase and peroxidase) and amino acids (serine, threonine, proline and aspartic acid) associated with plants' stress responses Improvement of plant growth	[117]
	Polysaccharides extracted from *Dunaliella salina*	Tomato	Alleviation of salt stress Activation of metabolic pathways involved in plants' tolerance to stress Mitigation of the decrease in length and dry weight of shoots and roots	[34]
	Oscillatoria agardhii	Wheat	Alleviation of drought stress Increase in the activity of hydrolytic and defence enzymes (catalase, superoxide dismutase and peroxidase) Increase in grain yield Improvement of plant quality parameters	[118]

4.2.1. Protection against Biotic Factors

Biotic factors that can negatively impact crops' productivities include the presence of organisms, such as insects, nematodes, bacteria and fungi [7,36,119]. Protection against these pathogenic organisms is commonly addressed by polysaccharides, which recognise the signalling molecules present in the pathogenic organism cell wall, and induce several defence responses [36]. Common defence responses include the regulation of signalling pathways, gene expression and induction of specific biosynthetic pathways, which typically result in the production secondary metabolites with antioxidant, antimicrobial and fungicidal properties (e.g., phenolic compounds, terpenoids and other compounds) [7,36,40,96,120]. When applied in agricultural crops, microalgae and cyanobacteria may promote these defence mechanisms, as these microorganisms are a great source of polysaccharides [36,121]. In fact, induction of plant defence mechanisms in the presence of microalgae and cyanobacteria has already been described in the literature. For example, in the study performed by Kumar, et al. [109], inoculation of spice crops' seeds with the cyanobacteria *Anabaena laxa* and *Calothrix elenkinii* significantly improved the activity of the enzyme β-1,3-endoglucanase in shoots and roots, which is responsible for the breakdown of the cell wall components of pathogens. Moreover, the authors reported an increase in the fungicidal activity, plant dry weight and shoot and root length. Similarly, Priya, et al. [111] demonstrated an increase in the activity of plant defence enzymes, namely peroxidase, polyphenol oxidase and phenylalanine ammonia lyase, in shoots and roots of rice plants treated with *C. elenkinii*. Increased activity of these enzymes is associated with the up-regulation of metabolic pathways that induce the production of thousands of metabolites, such as phenolic compounds, that have a toxic effect against pathogenic organisms. For example, phenylalanine ammonia lyase results in the up-regulation of the phenylpropanoid pathway, which is responsible for the production of phytoalexins, phenolic substances known for their antimicrobial and antioxidant properties [36]. More recently, Farid, et al. [40] demonstrated that elicitation of plant defence mechanisms may be a result of algal polysaccharides' activity. In this study, the authors concluded that: (i) polysaccharides extracted from *C. vulgaris* and *C. sorokiniana* promoted an increase in β-1,3-endoglucanase activity of tomato plants; (ii) polysaccharides extracted from *C. sorokiniana* induced an increased activity of phenylalanine ammonia lyase; and (iii) polysaccharides extracted from *C. vulgaris* and *C. reinhardtii* induced an increased activity of peroxidase and ascorbate peroxidase.

Although the majority of plant defence mechanisms may be promoted by microalgal/cyanobacterial polysaccharides, several metabolites presenting antioxidant, antimicrobial and cytotoxic properties are commonly found in microalgal/cyanobacterial biomass [119]. For example, the fatty acids' contents, especially the type and amount of myristic, palmitic, oleic and eicosapentaenoic acids, are the major contributors to the antimicrobial properties commonly associated to microalgae and cyanobacteria [122,123]. Due to their antioxidant nature, carotenoids may also have antibacterial activity [112]. Phenolic compounds, in turn, are responsible for the degradation of pathogenic organisms' cell walls [119]. Therefore, the use of microalgae and/or cyanobacteria in food crops can induce plants' defence mechanisms not only through the activity of their polysaccharides, but also through the activity of these biologically-active compounds, as it has already been documented in the literature. Arunkumar, et al. [103] demonstrated that a methanolic extract from the brown seaweed *Sargassum wightii* exhibited activity against *Xanthomonas oryzae*, which is a common bacterial blight of rice. More recently, Baloch, et al. [108] reported a significant suppressive effect of the seaweeds *Spatoglossum variabile*, *Stokeyia indica* and *Melanothamnus afaqhusainii* against eggplant and watermelon pathogens (e.g., the root rotting fungi, *Fusarium solani*, *Fusarium oxysporum* and *Macrophomina phaseolina*, and the root knot nematode, *Meloidogyne* spp.). Besides the inhibitory effect against these organisms, the authors reported an improved plant growth (increased fresh weight of shoots, increased length of vines in watermelon and increased shoot lengths in eggplant).

4.2.2. Protection against Abiotic Factors

Besides biotic factors, plants' exposure to extreme environmental conditions (e.g., very cold and hot temperatures, high salinity conditions and drought) can negatively impact crops' production and development [9,124]. In the case of extreme temperatures, low temperatures may reduce the metabolic activity of higher plants and damage the cell membranes, as the phospholipidic layer that constitutes these membranes become unstable. Exposure to high temperatures may also be harmful for cell membranes and influence the synthesis and activity of plants' proteins and enzymes [124]. High salinity levels are commonly associated with the osmotic stress in plants, which affects the nutritional composition of plants (typically, salt-stressed plants exhibit lower chlorophyll contents than the non-stressed ones) and, hence, plants' metabolism and growth [9,124,125]. Drought is also responsible for the osmotic stress in plants. However, it also affects plants' ability for gas exchange, significantly influencing the photosynthetic and transpiration rates and, therefore, the plants' yield [9,124]. Considering the negative impacts of extreme environmental conditions on plants' growth and development, increasing the tolerance of higher plants to these harsh conditions is crucial for the improvement of agricultural productivities. For this purpose, the use of biostimulants can be a very promising option, as these compounds are able to [124,126]: (i) promote the accumulation of antioxidant compounds, thus increasing the plants' tolerance to stress conditions; and (ii) improve the overall performance of higher plants, thus stimulating their growth. Although several biological compounds are known for their stimulatory activity, the use of secondary metabolites produced by microalgae and cyanobacteria has attracted researchers worldwide, due to their wide variety and to their ability to induce several plant response mechanisms and metabolic pathways. In fact, the use of algal-based products as biostimulants has been successfully applied in food crops under temperature, salt and drought stress conditions [34,113–118]. In the study performed by Arroussi, et al. [34], the polysaccharides excreted by *D. salina* induced the jasmonic acid pathway, a metabolic pathway involved in plants' response to stress, reducing the salt stress damages in tomato cultures. Moreover, this algal-based treatment promoted an improvement in roots and shoots' length. Similarly, the use of seaweed extracts from *Ulva rigida* and *Fucus spiralis* in bean plants under drought stress increased the tolerance of this plant to drought and improved its growth [116].

4.3. Direct Growth Stimulation

Apart from their beneficial effects at the soil level and on plants' protection, the use of microalgae and cyanobacteria (and/or their extracts) can directly stimulate plants' growth and development, through an improvement in germination rates and plant characteristics (e.g., increased shoot and root length, increased leaf area and higher nutritional contents). These improvements are achieved as a result of the activity of microalgal/cyanobacterial metabolites, which are able to trigger several metabolic responses, such as respiration, photosynthesis, nucleic acid synthesis, chlorophyll production and ions uptake [9]. Table 4 presents some examples where microalgae and cyanobacteria (biomass and/or extracts) have been successfully applied in direct growth stimulation of higher plants.

Table 4. Impacts of microalgae and cyanobacteria (and their metabolites) on direct growth stimulation of plants.

Algae/Algal Extracts	Target Crop	Observed Improvements	Ref.
Anabaena strains (*Anabaena spiroides*, *Anabaena osillarioides*, *Anabaena torulosa* and *Anabaena variabilis*)	Rice	Increase in germination rate Increase in plant height and shoots length Increase in fresh and dry weights of leaf, stem and root Improvement of soil properties (increase in soil moisture and porosity)	[127]
Laurencia obtusa, *Corallina elongata* and *Jania rubens*	Maize	Increase in plant length and fresh and dry weight Increase in the number of leaves Improvement of plant nutritional value (increase in potassium, phosphorus and nitrogen contents)	[128]
Exopolysaccharides extracts from *Dunaliella salina*	Wheat	Increase in germination rate and seedling growth Increase in root and coleoptiles height Increase in tolerance to salt stress	[129]
Aqueous extracts from *Gracilaria corticata* and *Enteromorpha flexuosa*	Maize and sunflower	Increase in shoot and root length and dry weight Improvement of plant nutritional value (increase in photosynthetic pigments, carbohydrate, proteins and nutrients contents)	[130]
Liquid extracts from *Stoechospermum marginatum*	Brinjal	Increase in shoot and root length Increase in fresh and dry weight of leaves Increase in leaf area Improvement of leaves nutritional value (increase in moisture, photosynthetic pigments, protein, amino acids, reducing sugars and ascorbic acid contents)	[131]
Total polysaccharides extract from *Spirulina platensis*	Tomato and pepper	Increase in plants' size Increase in roots' weight Increase in size and number of nodes	[39]
Ulva lactuca and *Jania rubens*	Spinach	Increase in plant yield and height Improvement of plant nutritional value (increase in chlorophyll and nitrogen contents)	[132]
Arthrospira platensis	Lettuce	Increase in seedling growth Increase in spermine content in leaves	[133]
Chlorella vulgaris and *Spirulina platensis*	Maize	Increase in germination rate and plant yield Increase in fresh and dry weights of shoot, root and whole plant Increase in shoot length and in the number of leaves	[134]

Commonly involved metabolites include plant growth promoting factors, such as phytohormones, but also some amino acids, vitamins (e.g., vitamin B12 and biotin), polysaccharides and polypeptides [97]. Treatment of a paddy field with *Anabaena* isolates resulted in an overall increase in seeds' germination rate and in an improvement of plant properties, such as plant height, root length and fresh and dry weights of leaves, stems and roots [127]. In addition, an improvement of soil properties, namely moisture and porosity, was observed. In the study performed by Omar, et al. [130], aqueous extracts of *Gracilaria corticata* and *Enteromorpha flexuosa* were applied to maize and sunflower seeds. Although extracts from both species resulted in increased root and shoot lengths and dry weights, these effects were more pronounced in plants treated with *E. flexuosa* extracts. After evaluating the composition of both extracts, the authors attributed the most promising effects of *E. flexuosa* extracts to the higher contents of phytohormones (indole-3-acetic acid, gibberellins and cytokinins) determined for this organism. Elarroussia, et al. [39] evaluated the effect of applying a solution of total polysaccharides extracts obtained from *S. platensis* in tomato and pepper cultures. With this study, the authors demonstrated that application of the extracts' solution resulted in an increase in the size of both tomato and pepper plants. In addition, increased root weight, size and number of nodes was registered for the treated plants.

5. Major Limitations to the Use of Microalgae and Cyanobacteria in Agriculture

Although the beneficial effects of microalgae and cyanobacteria (or their extracts) in agricultural practices is undeniable, one of the major limitations to the use of these microorganisms or compounds is the high costs typically associated with microalgal/cyanobacterial biomass production and compounds' extraction. For example, autotrophic growth of microalgae and cyanobacteria can be quite expensive and biomass productivities achieved are not very high. Moreover, biomass recovery after the production process can be costly and energetic-demanding, representing a large fraction of the overall biomass production costs. On the other hand, application of microalgal/cyanobacterial extracts requires the extraction of the interest metabolites, being the most commonly used methods very expensive [7,96]. The high costs associated with microalgal biomass production and processing contribute to an increase in the biofertilisers/biostimulants/biopesticides cost to values that cannot compete with the actual price of chemically-based compounds. For these reasons, applications with higher revenues (e.g., obtention of bioactive compounds for the nutraceutical, pharmaceutical and cosmetics' industries) are typically preferred for microalgal/cyanobacterial biomass.

Another problem arising from the use of microalgal and cyanobacterial extracts is related with the sustainability of the most commonly used extraction procedures. Usually, extraction of the bioactive compounds requires and disposes large amounts of organic solvents.

Finally, the use of microalgal/cyanobacterial products is not broadly applied in agriculture because little is known about the interactions established between microalgae/cyanobacteria (and their extracts), plants and the environment. Although a lot of studies have been carried out in this area, the great diversity of photosynthetic organisms already isolated and identified and the infinite number of metabolites that can be extracted from them difficult a deep understanding of these interactions and, hence, their application in agriculture [7].

6. Conclusions

This manuscript presents a detailed review on the potential benefits of using microalgae and cyanobacteria in the improvement of agricultural productivities in a sustainable and effective way. Microalgae and cyanobacteria are an important source of a wide variety of bioactive compounds that can regulate several plant response mechanisms: (i) the improvement of soil quality and plants' nutrition; (ii) plants' protection against biotic and abiotic factors; and (iii) growth stimulation. Therefore, the use of microalgal/cyanobacterial biomass (or their extracts) can be a sustainable and viable alternative to the chemically-based fertilisers, pesticides and growth stimulants. Additionally, the use of these biologically-based substances/organisms constitutes an important step towards the improvement of agricultural productivities, which is essential to meet the continuously increasing targets for food products determined by the world population increase. Despite all the benefits, the use of these photosynthetic microorganisms in agriculture is still limited because: (i) biomass production and processing costs are still quite expensive; and (ii) the wide diversity of microalgae/cyanobacteria and their products difficult a deep understanding of the interactions between these microorganisms (or their extracts) and higher plants. To use microalgal and cyanobacterial biomass in the agricultural field and avoid the high process costs, one possible way is to promote the biorefinery concept, in which the obtained biomass should be fully exploited, towards the obtention of different products, for different applications, at the same time. Additionally, for a better definition of the most adequate substances for agricultural activities, more research studies focusing on the effect of each metabolite/biomass on crops are required.

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