Concise review on seaweed photosynthesis: From physiological bases to biotechnological applications

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ABSTRACT

Seaweeds play an important role for the environment, since they are photosynthetic organisms, contributing to the cycling of nutrients and to the protection and feeding of several animals. The potential for biotechnological applications of marine macroalgae biomass is enormous, and to attend the demand of the current market, the knowledge of the physiological characteristics of these organisms is essential to ensure a high productivity in cultivation systems. In this review, we contribute to the knowledge about the photosynthetic characteristics of seaweeds, describing relevant aspects of marine macroalgae and photosynthesis, and the biotechnological use of these organisms.

Introduction

The seaweeds are pluricellular photosynthetic organisms, comprising Rhodophyta (red algae), Chlorophyta (green algae) and Phaeophyceae (brown algae) (Fig. 1), and constitute a diversified group with high morphological and biochemical variations [1]. They are primary producers and through photosynthesis assimilate CO_2 and release O_2, participating in the transformation of light energy into chemical energy and ecological recycling [2]. Since they can uptake different compounds dissolved in seawater, such as CO_2, nitrate, nitrite, ammonium, phosphate, and organic pollutants, these organisms can be used as biofilters to bioremediate the contaminated and/or eutrophicated seawater [3–5].

Different species of seaweed have been used by humans for centuries, for the most diverse purposes, as feeding, natural medicines (such as vermifuges), and for food, pharmacological, cosmetic, bioenergy, agricultural and biotechnological industries [6,7]. Their worldwide application in industry yields billions of dollars, due mainly to: i. human food, such as Kelp (*Laminaria/Saccharina*), Nori (*Porphyra/Pyropia*), Wakame (*Undaria*) and Seagrape aka green caviar (*Caulerpa*); ii. carotenoids compounds such as astaxanthin and ß-carotene; iii. hydrocolloids production, as carrageenan and agar from red seaweeds and alginate from brown seaweeds [8]. In addition, due to the enormous biochemical diversity of these organisms, the fields of application are increasing, ranging from biofuel to cosmetics, food supplements and nutraceuticals [8].

Seaweeds are very important to their environment as primary producers and very interesting to the industry, playing a key role in the circular economy. During photosynthesis they remove the CO_2 and produce the carbon skeletons necessary to synthesize an assortment of molecules with different applications [9,10]. However, to use these organisms for different applications and sustainable cultivation, it is important to know their biochemistry and physiology, including photosynthesis.

Photosynthetic apparatus of seaweeds

The photosynthetic process takes place in chloroplasts, a semi-autonomous organelle responsible not only by autotrophic processes, but also with a role in other metabolism pathways, as lipids, fatty acids, and terpenoids (mevalonate pathway) synthesis [11,12].

There is a great variation in the morphology and structure of chloroplasts between the different groups of macroalgae, which is related to the evolutionary history of these organisms and, in some cases, can be used as a taxonomic character [1] (Fig. 2). In general, it can be observed differences in:

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i Morphology: there is a great variety in the chloroplast morphology between the different groups of seaweeds, that can be discoid, stellate, reticulated, cup-shaped, among others [1,13].

ii Number of membranes: red and green algae chloroplast envelope is formed by two membranes. In the brown seaweeds, the chloroplast envelope, with two membranes, is evolved by more two membranes of chloroplast endoplasmic reticulum. The external membrane is generally continuous to the nuclear membrane, and contain many ribosomes on its cytoplasmatic face [1].

iii Thylakoids: the seaweed's thylakoids don't form grana. Basically, these structures are formed by a set of flattened vesicles embedded in a matrix, the stroma. In the Chlorophyta, they usually occur in groups, with each one containing from three to five thylakoids. In the Phaeophyceae, these groups are normally formed by three thylakoids, while in the Rhodophyta they are not grouped [1,14].

iv Pyrenoid: it is an electron-dense structure that can be present in the stroma of some seaweeds, involved in the CO_2-concentratin mechanism (CCM), due to Rubisco presence and activity [1,15]. In addition, some storage products derived from photosynthesis can be found in it, as starch in the Chlorophyta, or surround it, but in the external side of chloroplast, as laminarin and mannitol in the brown macroalgae [1].

The light-dependent reactions of photosynthesis are the stage in which the formation of high-energy compounds, such as ATP and NADPH, occurs from the capture of light energy. This process ensues through functional units located in the thylakoid membrane called photosystems, which are constituted by protein-associated pigment molecules and have two closely linked components: a reaction center complex and a light harvesting complex (or antenna complex) [16].

Accessory pigments, which varies in the different vegetal groups, are part of the light harvesting complex (LHC) and their main function is to absorb photons and transfer energy to the reaction center complex, where chlorophyll *a* molecules are excited and its electrons are transferred to an electron-accepting molecule, starting the light-dependent reactions [16,17]. There are two types of photosystems, which work simultaneously and continuously: photosystem I (PSI), in which the chlorophyll *a* molecules from the reaction center (P700) have an optimal absorption peak at 700 nm, and photosystem II (PSII), in which the chlorophyll *a* molecules of the reaction center (P680) have the maximum absorption peak at 680 nm [16,17].

Chlorophyll *a* is found in all algae groups. However, these organisms have different accessory photosynthetic pigments in their LHC, which implies in different light absorption characteristics [18], as follows: i. Chlorophyta - Chlorophyll *b* with absorption peaks in 645 nm and 435 nm; ii. Phaeophyceae - Chlorophyll c_1 and c_2 with absorption peaks in 634, 583, and 440 nm and 635, 586, and 452 nm, respectively; iii. Rhodophyta – phycobiliproteins – phycocyanin (PC), phycoerythrin (PE) and allophycocyanin (APC) with absorption peaks in 610 to 620 nm, 540 to 570 nm and in 652 nm, respectively [1]. Carotenoids are also found in seaweeds, with the β-carotene being the most abundant carotene, and fucoxanthin the main xanthophyll found in Phaeophyceae [1].

The LHC varies between the different groups of macroalgae, not only regarding the pigment composition, but also according to its supramolecular arrange [19–22] (Fig. 2). The green seaweeds present the structure more similar with the plants, where the PSII presents, associated with the core complex, the trimeric LHCII and the monomers CP24, CP26 and CP29. There are three different trimeric LHCII, classified according to their location and interaction with the core, as L (loose), M (moderate) and S (strong). For the LHCI, Suga et al. [23] described for a green algae eight Lhca proteins distributed as two tetrameric belts, and more two Lhca proteins that form the Lhca2/Lhca9 heterodimer. The tetrameric belts and heterodimers are on opposite side of the core of PSI.

Rhodophyta presents two kinds of antenna complex, one composed of chlorophyll *a* and linked to the to the reaction centers of the PSI, the LHCI complex, and other bonded to the reaction centers of PSII, the phycobilisome (PBS) (Fig. 2). This last structure, one of the larger protein complexes found in the organisms, is formed by the phycobiliproteins mentioned above, that are chromoproteins formed by a chromophore, a tetrapyrroles known as phycobilin, linked to a protein [24,25].

Fig. 1. General view of specimens of seaweed in their natural environment (picture source: Aline P. Martins).

The phycobiliprotein is a complex and very organized structure, formed by a fundamental component, the trimer $(\alpha\beta)_3$, associated by linkage proteins, which, in turn, forms the hexamers. The trimer is composed by the heterodimer $\alpha\beta$ and according to its organization, it can form different 3D structures, which may have differences in the energy transfer pathway [1,25]. In the core of the phycobilisome, close to the reaction center, the allophycocyanin is located. From the APC to the surface, the PC and PE are distributed [1].

As the other accessory pigments, the phycobiliproteins enhance the zone of light absorbed that can be used in photosynthetic process, and as they absorb the light in the region of green and blue-green light, these pigments allow red algae to photosynthesize and habitat in deep waters [16]. In addition, these complexes function as a cellular nitrogen reserve, being rapidly mobilized in conditions of depletion of this nutrient [26].

Carbon uptake and biomolecules synthesis

Photosynthesis allows the conversion of light to chemical energy. NADPH and ATP, originated from light-dependent reactions of photosynthesis, are utilized in the Calvin cycle and other anabolic pathways to generate the precursor of different compounds [9]. The Calvin cycle represents the chemical phase of photosynthesis in which the Ci will be assimilated, and the pathway begins with the reaction catalyzed by Ribulose-1,5-bisphosphate carboxylase oxygenase (Rubisco), the key enzyme responsible for converting inorganic to organic carbon [17].

As CO_2 is the only substrate of Rubisco in the photosynthesis process, macroalgae need inorganic carbon (Ci) for its physiological requirements and growth. In seawater, the Ci is found as dissolved CO_2, bicarbonate, and carbonate ions, which form the carbonate system. Once dissolved, the CO_2 reacts with water and carbonic acid is formed and promptly dissociates to bicarbonate and hydrogen ions. Then, the bicarbonate ion dissociates to carbonate and hydrogen ions [27–29]. The availability of the Ci species varies mainly according to the alkalinity and pH of the seawater. Due to its high alkalinity, the dominant form of Ci is bicarbonate, which concentration is around 2 mM. The dissolved CO_2 concentration in seawater is around 12 μM [27–29].

Since bicarbonate is the predominant Ci form in seawater, seaweed must have mechanisms to be able to use it. Thus, they can actively uptake the bicarbonate into the cell by a specific transporter, followed by its conversion to CO_2 in a reaction catalyzed by the carbonic anhydrase enzyme. Furthermore, some seaweeds species can convert bicarbonate to CO_2 on the surface of the thallus by the action of extracellular carbonic anhydrase [30]. However, some seaweeds species, around 35%, don't have the carbon dioxide concentrating mechanism (CCM) showed above, and so, they are able to uptake just CO_2, which happens by passive diffusion [31]. The fixed carbon will provide the carbon skeletons needed for the synthesis of proteins, lipids, and carbohydrates (Fig. 3).

Through photosynthetic activity, macroalgae play a very important role in the recycling of nutrients, and effectively contribute to the CO_2 capture and to the climate change mitigation, with a global capture capacity of 173 TgC year^{-1} [32,33]. Kelp species, as *Macrocystis* and *Laminaria*, show a high rate of productivity, reaching values greater than 3000 g C m^{-2} year^{-1} [34]. In brown seaweeds, the fixed carbon can be stored as mannitol and laminarin [1], which can be used for different applications, as bioethanol and hydrogen production [35]. High CO_2 conditions can increase the content of mannitol in *Fucus vesiculosus* [36] and of some phenolic compounds, as phlorotannin, in *Saccharina latissima* and *Nereocystis luetkeana* Kelps [37].

Not only Kelps have high productivity and consequent potential for carbon capture, but also other macroalgae as *Ascophyllum, Fucus, Sargassum, Palmaria, Porphyra,* and *Ulva* [34]. Chemodavov et al. [38] showed that *Ulva* sp. grown offshore in the Mediterranean Sea had a net primary productivity of 838 ± 201 g C m^{-2} year^{-1}, highlighting its contribution for carbon uptake and for producing biomass for bioethanol.

Photosynthetic characteristics of seaweeds

The photosynthetic rate of macroalgae can be analyzed by the oxygen evolution technique, using chambers that allow the control of abiotic factors and electrodes capable of measuring O_2, and by the fluorescence of chlorophyll *a* from photosystem II, using pulse amplitude modulated (PAM) fluorometers [39,40]. Although oxygen evolution and fluorescence of chlorophyll *a* are techniques with different
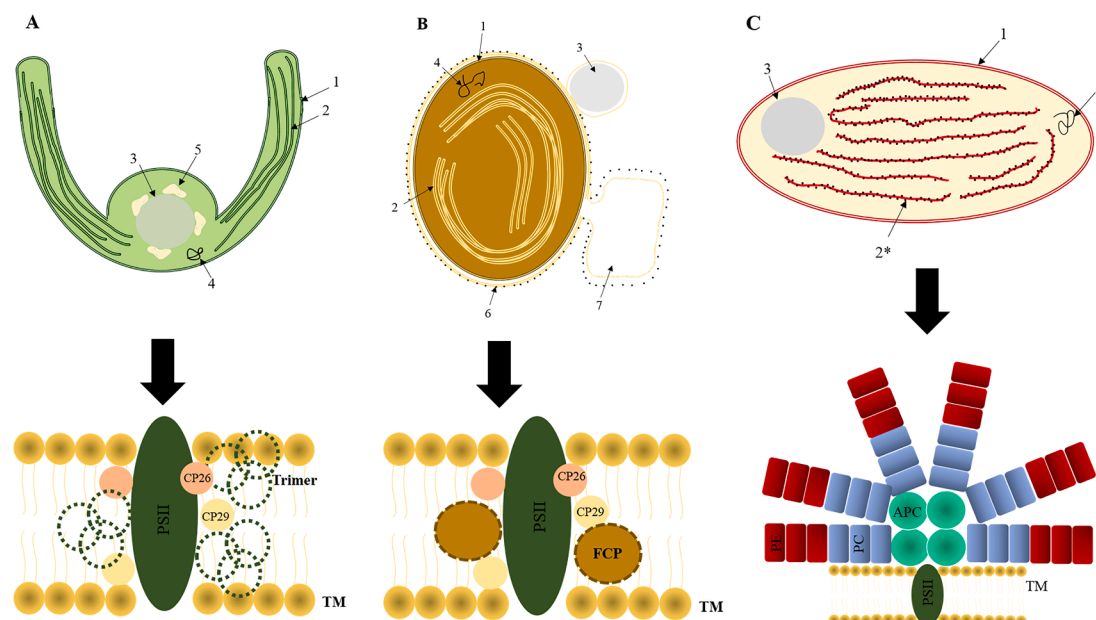

Fig. 2. General scheme of the chloroplast and photosystem II of macroalgae. A. Cup-shaped chloroplast of Chlorophyta. B. Chloroplast of Phaeophyceae. C. Discoid chloroplast of Rhodophyta. 1. Chloroplast envelope; 2. Thilakoids; 2* Thilakoids with phycobilissome; 3. Pyrenoids; 4. DNA; 5. Starch; 6. Two membranes of chloroplast endoplasmic reticulum with ribosomes; 7. External membrane continuous to the nuclear membrane, TM – Tilakoid membrane. FCP - fucoxanthin chlorophyll a/c proteins. Modified from Lee [1] and Patty et al. [2].
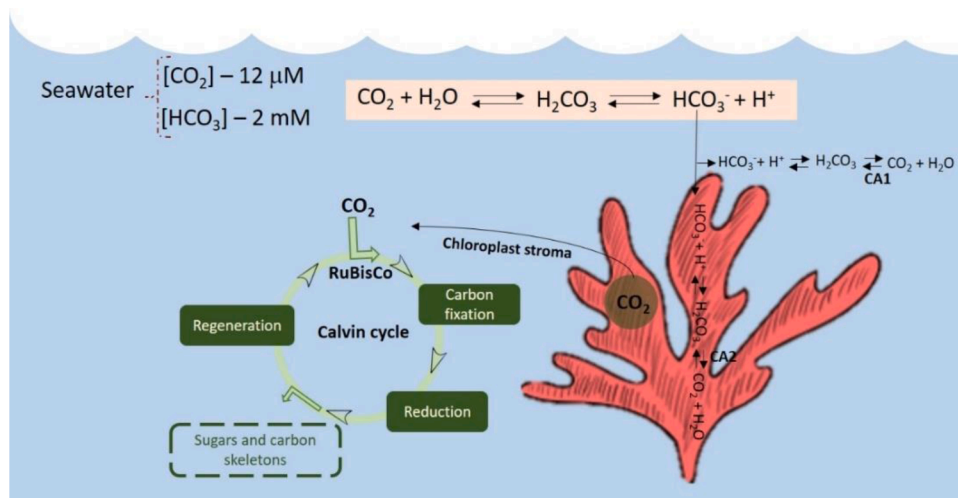
Fig. 3. Summary of the bicarbonate system and carbon fixation by marine macroalgae. CA1. Extracellular carbonic anhydrase; CA2. Intracellular carbonic anhydrase.

advantages and features, both technologies allow to access the electron transport rate (ETR) between photosystem II and photosystem I in response to increasing irradiances and obtain the light curves (photosynthesis x irradiance curves or PI curves) [41].

The light curve analysis provides important information about the photosynthetic process, through the determination of following parameters: photosynthetic efficiency (αETR), saturation irradiance (I_k), maximum photosynthesis (ETRmax) and photoinhibition [41,42]. Other parameters are obtained with chlorophyll *a* fluorescence, as the quantum yield of PSII (effective quantum yield - EQY), which provide information about photosynthetic performance that the plant presents at the time of measurement [43]. By accessing these photosynthetic parameters under different conditions, it is possible to improve de knowledge about the physiological characteristics of seaweeds and its relationship with

Table 1
Variation in the photosynthesis and biochemical composition in different species of seaweeds as a response to CO_2 elevation.

Species	Treatment	Photosynthesis response	Biochemical variation	Reference
Chlorophyta				
Ulva lactuca	High CO_2 25 °C	No alteration	No alteration	[57]
Ulva linza	High CO_2 Different cultivation system	Increase	Not measured	[58]
Ulva prolifera	High CO_2 Monoculture	Increase	Decrease carotenoids and soluble carbohydrates	[51]
Ulva prolifera	High CO_2 Different cultivation system	Increase	Not measured	[58]
Phaeophyceae				
Desmarestia anceps	High CO_2 Different temperature and irradiance	Increase	No alteration	[59]
Dictyota menstrualis	High CO_2 High N	Increase	Increase soluble carbohydrates and lipids	[53]
Ericaria selaginoides (cited as *Cystoseira tamariscifolia*)	High CO_2	Decrease	No alteration	[60]
Padina pavonica	High CO_2	Increase	Decrease phenolic compounds	[60]
Sargassum fusiforme	High CO_2 High irradiance	Decrease	Increase sobuble carbohydrates	[50]
Rhodophyta				
Bostrychia montagnei	High CO_2 Province WTSA	Increase	No variation	[52]
Ellisolandia elongata	High CO_2	No alteration	Increase zeaxanthin and palythine	[60]
Gracilaria parvispora (cited as *G. chouae*)	High CO_2	Increase	Not measured	[61]
Gracilariopsis lemaneiformis	High CO_2	Increase	Not measured	[61]
Gracilariopsis lemaneiformis	High CO_2 25 °C	Increase	Increase phycobiliprotein	[57]
Neopyropia yezoensis	High CO_2 Monoculture	Decrease	Decrease carotenoids and soluble carbohydrates	[51]
Pyropia leucosticta (cited as *Porphyra leucosticta*)	High Ci	Increase	Increase chlorophyll a and insoluble carbohydrates	[49]
Pyropia haitanensis	High CO_2 Different densities	Decrease	Not measured	[62]
Pyropia yezoensis	High CO_2 Low ligh	Increase	Increase phycocyanin and phycoerythrin	[63]

Table 2

Some compounds obtained from seaweed biomass and their respective applications.

Compounds		Applications	Reference
Polysaccharides	Agar	Gelling agent in foods; substrate for culture media; gel for electrophoresis; fermentation process – bioethanol, PHAs, prebiotics; films for food packing.	[6,74–76]
	Alginate	Gelling agent; textile industry; bioethanol; films for food packing.	[6,77,78]
	Carrageenan	Emulsifier; pharmacological activities; bioethanol; films for food packing.	[6,75,76]
	Cellulose	Bioethanol; bioplastic; films for food packing.	[76,79]
	Floridean starch	Immunomodulatory agent; bioethanol.	[78,80]
	Fucoidan	Tissue engineering; drug delivery.	[81]
	Laminarin	Pharmacological, antioxidant and prebiotic activities; cosmetic; bioethanol.	[78,82]
	Starch	Films for food packing; bioethanol.	[76,78, 82]
	Ulvan	Tissue engineering; drug delivery.	[81]
Proteins		Human and animal feed, vegetarian source of protein.	[83,84]
	Lectins	Immune system and histological marker; drug delivery.	[6]
Lipids			
	MUFAs	Biodiesel	[64]
	PUFAs	Nutraceuticals; prevention cardiovascular diseases; antioxidant and antitumor activities.	[6,53]
Pigments	Chlorophyll	Antioxidant properties; food quality indicator (in films).	[76]
	Phycoliliproteins	Antioxidant properties; fluorescent markers.	[85]
	Carotenoids	Antioxidant properties; food quality indicator (in films).	[6,76]
Mycosporine-like amino acids (MAAs)		Photoprotector	[6]
Halogenated compounds		Pharmacological activities; antiparasitic activity.	[6,86]

different abiotic factors, providing information that can contribute to their productivity, and biotechnological application [44–47].

The availability of CO_2 and nutrients in the seawater as well as the salinity, light, and temperature have influence on photosynthesis and cellular metabolism, directly influencing the biosynthesis of algal metabolites [48]. Inorganic carbon, as discussed above, is fixed during the Calvin Cycle, and will be used for the formation of carbon skeletons and biosynthesis of the most different biomolecules [17]. Anthropogenic activities have led to an increase in the concentration of CO_2 in the atmosphere, which may have a distinct effect on photosynthesis and biochemical composition of the different species of macroalgae.

Mercado et al. [49] observed a highest Pmax when *Pyropia leucosticta* (cited as *Porphyra leucosticta*) was growth in current and high Ci availability and highest content of insoluble carbohydrate in high Ci treatment (Table 1). However, the same was not observed for *Sargassum fusiforme* [50] and for *Neopyropia yezoensis* [51], since there was a decrease in Pmax and alpha values with increasing CO_2 availability, which could be a result of pH decrease in seawater. Borburema et al. [52] found similar results for *Bostrychia calliptera* from Tropical Southwestern Atlantic (TSA), which showed a decrease in effective quantum yield and rETR when grown under higher CO_2 availability and low pH. For *B. calliptera* from Warm Temperate Southwestern Atlantic and *B. montagnei* from both regions there was no significant difference in the photosynthetic parameters between the highest and current CO_2 availability and lower and highest pH. However, these specimens showed higher growth and production of certain compounds such as allophycocyanin, polysaccharides and low molecular weight carbohydrates when grown at high pCO_2. According to Borborema et al. [52], the result showed by *B. calliptera* from TSA can indicate a decoupling among photosynthesis and growth. In addition, these seaweeds can contribute to the CO_2 capture from the environment.

The way in which macroalgae respond to the increase in CO_2 may be related to other abiotic factors, such as the availability of nitrogen in seawater. For example, Martins et al. [53] observed higher values of Pmax and saturation of photosynthesis in the brown algae *Dictyota menstrualis* cultivated in higher CO_2 and nitrogen availability. They also verified higher values in the Nitrate Reductase (NR) and Rubisco activities. In this case, there was influence not only of Ci, but also of inorganic nitrogen on photosynthesis. In fact, the metabolic pathways of photosynthesis and nitrogen are connected. Treatments that inhibit photosynthetic carbon fixation, such as CO_2 reduction and photosynthesis inhibitors, deplete the amount of carbon skeletons, which will

lead to a decrease in the assimilation of nitrogen into amino acids [54].

Photosynthesis directly influences the nitrogen metabolism, which can be shown by changes in the activities of NR (the main nitrate assimilation enzyme) and phosphoenolpyruvate carboxylase (PEPC, enzyme related to the formation of organic acids, which will incorporate nitrogen to amino acids) in response to alteration in photosynthetic rate. During photosynthesis, these enzymes are quickly activated due to signals sent from the chloroplast to the cytosol [55]. In addition, the nitrogen source can influence the photosystem's antenna size, as observed by *Ulva lactuca*, which showed a decrease in antenna size when cultivated with urea [56].

Photosynthetic processes also vary as function of light and temperature. Light, in addition to activating photosynthesis and distinct metabolic pathways, plays a fundamental role in the vertical zonation of species, which results from variations in the photosynthetic apparatus of the different groups of macroalgae [40]. Martins et al. [64] studied the photosynthesis of different species of the Brazilian coast and verified that the red seaweeds present the lowest values of EQY, Pmax, alpha and Ik. This result may be related to the vertical distribution of these organisms, in which red macroalgae can be found at greater depths and have a pigmentary apparatus that allows them to photosynthesize at low irradiance, presenting shade-plants patterns [40]. On the other hand, the green seaweed *Ulva lactuca*, a supralittoral species, displayed a high value for all photosynthetic parameters, including saturation irradiance, showing a photosynthetic apparatus capable of resisting to high irradiance [64].

Seaweed species from Antarctica are submitted to intense light variations and usual low temperatures, being subject to a long period of low light during the winter and a shorter period of high light during the summer. The high photosynthetic efficiency (alpha) and the saturation of photosynthesis at low irradiances show the capacity of these organisms to photosynthesize at low irradiance and their low requirement for light, an important characteristic to survive in this environment characterized by long periods of dim light [65].

Gomez et al. [66] studied the physiological characteristics of brown Antarctic seaweeds *Ascoseira mirabilis, Desmarestia menziesii, D. anceps* and *Himantothallus grandifolius* that have a wide range of vertical distribution. They found a difference in photosynthetic efficiency and photosynthesis saturation point values as a function of depth, but they did not observe a zonation pattern, which may be related to the ability of macroalgae to acclimate to different light conditions. Weykam et al. [65] studied the photosynthetic characteristics of 36 seaweeds species

and had similar results that showed by Martins et al. [64], with lower values of Pmax and Ik in Rhodophyta. However, they observed high photosynthetic efficiency, which confirms the best pigment adaptation present in this group to photosynthesize in low light conditions [67]. Furthermore, red seaweeds that present R-phycoerythrin IV, such as *Phyllophora antarctica* and *Iridaea cordata*, present better absorption of blue light, being able to inhabit greater depths than species that have typical R-phycoerythrin [68].

During the summer and intense light conditions, Antarctic macroalgae can downregulation the photosynthesis, through alterations in photosystem II caused by protein D1 degradation, avoiding the damage caused by high irradiance [69]. In addition, they are exposed to UV radiation, without decreasing photosynthesis, which could happen due to the production and high amount of Mycosporine-Like Amino Acids (MAAs) [70,71,72], phlorotannin and high antioxidant activity [66].

Biotechnological application of seaweeds

Several research show the relationship between photosynthesis and the synthesis of different metabolites and biomass production. For example, Nakamura-Gouvea et al. [73] studied the genome of *Gracilaria domingensis*, displaying the pathways of agar and secondary metabolites and the importance of photosynthesis for these processes. The triose phosphate, a Calvin Cycle intermediate, is used in the pathways for the synthesis of carotenoids, floridoside, starch and agar. In addition, the synthesis of some amino acids takes place in chloroplast, contributing to the MAAs (by the shikimate pathway), flavonoids and alkaloids production.

Martins et al. [53] showed that when *Dictyota menstrualis* were cultivated in high N and CO_2 content, there was an increment not only in its photosynthesis, but also in lipids and soluble carbohydrates contents. In turn, when *Sargassum fusiforme* was grown under high CO_2 and low light, there was a decline in both photosynthesis and carbohydrate content and biomass. Indeed, photosynthesis is the key step for the biosynthesis of diverse compounds necessary for cell maintenance and that, consequently, results in a wide range of materials that can be used for industry applications. From the autotrophic process occurs the production of protons and electrons, sugars, oils and biomass, which can be used for different purposes, as biohydrogen, bioethanol, bioplastics, hydrocolloids, biodiesel, nutraceuticals, biomethane, feed, among others [9] (Table 2). Thus, the knowledge of its metabolic basis and how it varies according to biotic and abiotic factors can help in the development of strategies for the improvement of seaweeds cultivation activities and to produce the different compounds of interest.

Final remarks and perspectives

Marine macroalgae are very important organisms for the environment and for humans, being used for centuries for the most different purposes. Knowing its physiological and photosynthetic characteristics is fundamental to understanding its relationship with the environment and to allow their application as well as maximization of the products of interest through biochemical modulation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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