Trends in
Plant Science

CellPress

Review

Reuniting the Biogeochemistry of Algae for a Low-Carbon Circular Bioeconomy

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Given their advantages of high photosynthetic efficiency and non-competition with land-based crops, algae, that are carbon-hungry and sunlight-driven microbial factories, are a promising solution to resolve energy crisis, food security, and pollution problems. The ability to recycle nutrient and CO_2 fixation from waste sources makes algae a valuable feedstock for biofuels, food and feeds, biochemicals, and biomaterials. Innovative technologies such as the bicarbonate-based integrated carbon capture and algae production system (BICCAPS), integrated algal bioenergy carbon capture and storage (BECCS), as well as ocean macroalgal afforestation (OMA), can be used to realize a low-carbon algal bioeconomy. We review how algae can be applied in the framework of integrated low-carbon circular bioeconomy models, focusing on sustainable biofuels, low-carbon feedstocks, carbon capture, and advances in algal biotechnology.

Highlights

Algae are promising players in the framework of an integrated circular bioeconomy.

Wastewater and flue gas are alternative low-carbon feedstocks for algae cultivation.

Bicarbonate-based integrated carbon capture and algae production system (BICCAPS), integrated algal bioenergy carbon capture and storage (BECCS), and ocean macroalgal afforestation (OMA) are algae-based carbon-capture technologies.

The evolution of the biotechnology industry and government policies are promoting the growth of bioeconomies.

Algal Potential for a Low-Carbon Circular Bioeconomy

Algae hold enormous promise to resolve the energy crisis, food security, and pollution problems. Algae are being applied in the framework of integrated low-carbon circular bioeconomy models, focusing on sustainable biofuels, low-carbon feedstocks, carbon capture, and advances in algal biotechnology. Their ability to recycle nutrient and CO_2 makes algae a valuable feedstock for biofuels, food and feeds, biochemicals, and biomaterials. Innovative technologies, such as BICCAPS, integrated algal **bioenergy carbon capture and storage** (BECCs, see Glossary), as well as OMA, have enormous potential for realizing a low-carbon algal bioeconomy.

Our society is currently based on a 'linear fossil-based economy' that is heavily dependent on non-renewable fossil resources for energy, chemicals, materials, and other industrial products [1]. Statistically, resource use will increase by an average of 0.4% for every 1% rise in **gross domestic product** (GDP). Explosive population growth together with rapid urbanization and industrialization has led to crucial issues such as global food insecurity, energy crisis, climate change and extreme weather, and pollution problems [2]. Following pressure from policymakers and society to mitigate these issues, the modern industrial community is now working towards a resource-conserving and low-carbon circular bioeconomy. In a circular bioeconomy, renewable bio-based resources are used as feedstock for products and services, while material and energy flows are cascaded and recycled in a closed-loop system to achieve sustainable production [3]. This can be further enhanced with the biorefinery concept – the integrated and sequential extraction of every part of the biomass to synthesize bioenergy (biofuels, power, and heat) and high value-added products (chemicals, feed, food) with little to zero waste. The development of high-value coproducts through the integration of unit operations in the biorefinery framework can improve resource recovery, cost-effectiveness, and process efficiency.

Algae are sunlight-driven cell factories that can convert organic or inorganic carbon into valuable products. Owing to their immense potential, algae play an increasingly significant role in the above-mentioned issues. Algae can provide a food source for both humans and livestock, feedstock

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for biofuels, commodity and fine chemicals (cosmetics, nutraceuticals, pharmaceuticals), as well as being agents for pollution treatment, remediation, and detection (sensing) [4]. Given their ability to adapt and grow in harsh environments (e.g., seawater, brackish water, greywater, etc.), algae can recover nutrients and sequester CO_2 from wastewater and industrial exhaust, utilizing them as a low-carbon feedstock, thus minimizing arable land and water use. These factors make algae promising players in the framework of integrated low-carbon circular bioeconomy models (Figure 1, Key Figure). We provide a critical analysis of the role of algae in a low-carbon circular bioeconomy, with a focus on (i) algal biofuels as a promising solution for achieving sustainable energy, (ii) waste streams as a feedstock for a low-carbon circular bioeconomy, (iii) carbon-capture technologies using algae, and (iv) advances and developments in algal biotechnology.

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Algal Biofuels as a Promising Solution to the Demand for Sustainable Energy

Recent findings have revealed that 80% of global energy consumption derives from fossil fuels such as diesel, gasoline, and kerosene that are responsible for the release of 29 gigatons of CO_2 annually [5,6]. The escalating energy demand will reach an estimated 16 700 **million tonnes of oil equivalent** (Mtoe) by the year 2035 [7–9]. Many countries such as Australia, Austria, Brazil, Germany, Italy, South Korea, and the USA have already started to use biofuels including bioethanol and biodiesel in the transportation sector [10]. However, the utilization of food crops such as canola, corn, maize, olive oil, rapeseed, soybean, and sugarcane as feedstocks for biofuel has sparked much debate on food security as well as regarding competitive use of water and arable land, and eventually its sustainability [11].

To address these issues, algae have emerged as a promising solution to a clean energy future that have the potential to produce a variety of biofuels including bioalcohols, biodiesel,

Key Figure

The Concept of an Algae-Based Low-Carbon Circular Bioeconomy

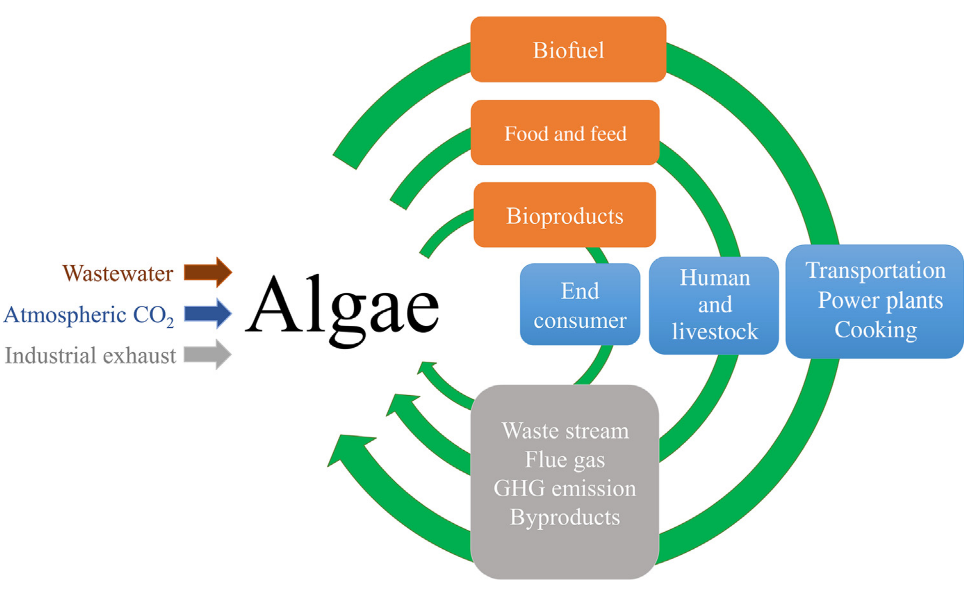

Figure 1. Abbreviation: GHG, greenhouse gas.

biomethane, and biohydrogen. Compared with terrestrial or oleaginous crops, microalgae have a higher photosynthetic efficiency and growth rate, as well as higher biomass and better productivity of lipid (58 700 l/ha compared with 172 and 446 l/ha for corn and soybean, respectively) [12,13]. The absence of lignin in algae is also advantageous for pretreatment and enzymatic hydrolysis in biofuel production relative to terrestrial plants, reducing overall production cost [14]. However, the wide-scale application and commercialization of algal bioenergy faces several bottlenecks, including the high costs of harvesting and dewatering, pretreatment, conversion, operation, and maintenance [8]. Therefore, the interest of utilizing algae as a sustainable and renewable feedstock for biofuel production has stimulated a new focus on the biorefinery perspective, where the multiple and complementary product outputs of an integrated biorefinery can provide a more economical and sustainable approach for biofuel and bioproduct production.

Biodiesel

Microalgae can accumulate substantial amounts of **triacylglycerides** (TAGs) that have a higher fatty acid content and an absence of N, P, and S that might affect the quality of the biodiesel produced by esterification/transesterification [5]. Algal biodiesel produces much less carbon monoxide, sulfur dioxide, and unburned hydrocarbons, releasing 41% less **greenhouse gas** (GHG) emissions compared to conventional gasoline. The microalgal lipid profile has lower levels of saturated fatty acids (such as C16:0 and C18:0) that is advantageous for winter operability, and its high levels of monosaturated fatty acids (such as C18:1) and low levels of polyunsaturated fatty acids (such as C18:3) are preferable for oxidation stability [15].

Microalgae strains such as *Chlorella*, *Crypthecodinium*, *Cylindrotheca*, *Dunaliella*, *Isochrysis*, *Nannochloris*, *Nannochloropsis*, *Neochloris*, *Phaeodactylum*, *Porphyridium*, *Schizochytrium*, and *Tetraselmis* have a high lipid content of up to 20–50% dry weight of algal biomass [10]. Although macroalgae usually have a lower lipid content than microalgae, researchers have also reported biodiesel production from macroalgae such as *Asparagopsis taxiformis*, *Enteromorpha compressa*, *Fucus spiralis*, *Himanthalia elongate*, *Pelvetia canaliculata*, and *Ulva lactuca* [16].

Bioalcohols

Carbohydrates from algae can be converted into bioalcohols such as bioethanol and biobutanol that can be mixed with oil or used directly without any modifications [8]. Several carbohydrate-rich microalgae species such as *Chlorella vulgaris* and *Chlamydomonas reinhardtii* are potential candidates for bioalcohol production [8]. Similarly, the ease of harvesting macroalgae such as *Gracilaria* spp., *Kappaphycus alvarezii*, *Laminaria japonica*, *Sargassum* spp., and *Ulva* spp., combined with their high content of polysaccharides and sugar alcohols (up to 75%) owing to the presence of extracellular carbohydrates, make them promising feedstocks for bioalcohol production [5]. Techniques such as **simultaneous saccharification and fermentation** (SSF) and **separate hydrolysis and fermentation** (SHF) are the conventional methods for bioethanol production from macroalgae [9,16].

Biogas

Both fresh biomass and spent algal biomass can be employed as feedstock for biogas production by microbial consortia via anaerobic digestion [17]. Algae have been used to integrate biogas production and the treatment of wastewater such as municipal or urban wastewater [18,19], piggery wastewater [20,21], and textile wastewater [22]. The wide range of substrates and products of anaerobic digestion allows the process to be placed at different stages of the biorefinery chain [23]. However, anaerobic biodegradation is limited by the complex cell-wall structure of algae, and microalgal strains such as *Dunaliella* spp. (that lacks cell wall), and *Chlamydomonas* spp. (whose cell walls do not contain cellulose) are promising feedstocks for

Glossary

Bioenergy carbon capture and storage (BECCS): the process of extracting bioenergy from biomass and capturing and storing the carbon, thereby removing it from the atmosphere.

Greenhouse gases (GHGs): gases that absorb and emit radiant energy in the thermal infrared range. The primary greenhouse gases in Earth's atmosphere are water vapor (H_2O), carbon dioxide (CO_2), methane (CH_4), nitrous oxide (N_2O), and ozone (O_3).

Gross domestic product (GDP): the total monetary or market value of all the finished goods and services produced within a country's borders in a specific time-period. As a broad measure of overall domestic production, it functions as a comprehensive scorecard of a given country's economic health.

Life-cycle assessment (LCA): a methodology for assessing environmental impacts associated with all the stages of the life cycle of a commercial product, process, or service.

Million tonnes of oil equivalent (Mtoe): the tonne of oil equivalent (toe) is a unit of energy defined as the amount of energy released by burning 1 tonne of crude oil. It is approximately 42 GJ or 11 630 megawatt hours.

Separate hydrolysis and fermentation (SHF): a method by which enzymatic hydrolysis and fermentation are performed sequentially.

Simultaneous saccharification and fermentation (SSF): a process that combines enzymatic hydrolysis with fermentation to obtain value-added products in a single step.

Triacylglycerides (TAGs): esters between glycerol and three fatty acids. Triglycerides are the main constituents of body fat in humans and other vertebrates, as well as of vegetable fat.

Volatile solid (VS): the weight lost following heating a sample to dryness at 550°C (ignition/pyrolysis). Determinations of fixed and volatile solids do not distinguish precisely between inorganic and organic matter because the loss on ignition is not confined to organic matter. It includes losses caused by the decomposition or volatilization of some mineral salts.

biogas production. The yield of biogas methane from these microalgae generally ranges between 0.32 and 0.44 l/g **volatile solid** (VS) [23]. By contrast, macroalgae such as *Ulva* (*Chaetomorpha* and *Cladophora*) and *Macrocystis pyrifera* also give high yields of methane (up to 0.48 and 0.31 l/g VS, respectively) [24].

Biohydrogen

Algae play a dual role in biohydrogen production – as a producer via direct biophotolysis and as the substrate for other hydrogen-producing microorganisms via photo- or dark fermentation. Hydrogen production by microalgae depends on hydrogenase enzyme activity that is highly sensitive to oxygen. A large number of microalgae such as *Anabaena*, *Botryococcus*, *Chlamydomonas*, *Chlorella*, *Chlorococcum*, *Nostoc*, *Scenedesmus*, *Synechocystis*, *Tetraspora*, and others harbor hydrogenase activity and can produce biohydrogen [25]. In addition to biohydrogen, the biorefinery approach can generate other valuable byproducts such as biomethane and fatty acid-rich intermediates (e.g., acetate, butyrate, and propionate) [2].

Waste Streams as Feedstocks for a Low-Carbon Circular Bioeconomy

There is increasing interest in valorization of waste streams by resource recovery and converting unwanted wastes into value-added products including biofuels, biopolymers, and biochemicals. Therefore, phycoremediation utilizing algae has emerged as a promising waste-treatment process owing to their ability to adapt to harsh environments [14]. The spent biomass can be further utilized as a biofertilizer and feedstock for the production of biofuels [26]. Strain screening and selection, as well as genetic engineering, can enhance microalgae performance, and modification of medium composition and optimization of cultivation conditions have been employed to improve waste-stream nutrient utilization by microalgae [5].

Wastewater as a Low-Cost Algae Feedstock

Wastewater contains a high concentration of organic matters, nutrients (ammonia, nitrate, phosphate, and trace minerals), salts, suspended solids, toxic compounds, heavy metals, and pathogenic microorganisms [27]. Nutrient-rich wastewaters such as urban wastewater, agriculture/aquaculture wastewater (dairy, poultry, piggery, and mariculture), food industry wastewater, anaerobically digested sewage sludge, and municipal landfill leachates have been utilized for simultaneous phycoremediation and added-value product synthesis through microalgae cultivation. In addition, Graham and coworkers reviewed the feasibility of using wastewater from the oil and gas industry as a growth medium for microalgae cultivation [28]. Using real pilot-scale data from a 10 ha facility, **life-cycle assessment** (LCA) of biomethane production from microalgae utilizing municipal wastewater demonstrated that the climate and fossil fuel replacement benefits warrant further development and optimization despite technical and environmental obstacles [29]. Table 1 briefly summarizes the performance of algae in wastewater phycoremediation with simultaneous added-value product synthesis.

Flue Gas as a Low-Cost Algal Feedstock

Other than CO_2 as the main component (approximately 10–25% v/v), industrial flue gas generally contains toxic pollutants such as heavy metals, particulate matter, fly ash, soot, NO_x, and SO_x that hinder microalgal growth. Microalgal species that thrive in acidic conditions and thermophilic algae are therefore preferable for flue gas phycoremediation because of their tolerance to the elevated CO_2 concentrations and high temperatures of waste gases from thermal power plants. Algae such as *Galderia* spp. and *Viridella* spp. have great potential for CO_2 fixation from CO_2-rich streams [44]. By contrast, microalgal species such as *Chlorella fusca*, *Desmodesmus* spp., *Nannochloropsis salina*, and *Spirulina* spp. are more specific for the removal of NO_x, SO_x, and

Table 1. Performance of Algae in Wastewater Phycoremediation with Simultaneous Added-Value Product Synthesis[a,b]

Microalgae	Wastewater	Nutrient removal	Added-value product synthesis	Refs
Acutodesmus dimorphus	Dairy industry wastewater	COD and TN removal of 90% and 100%, respectively	Biodiesel and bioethanol of 195 and 78 g/kg biomass, respectively	[30]
Arthrospira platensis	Dairy farm wastewater	COD, TN, and TP removal of 98.4%, 98.8%, and 100%	Biomass and lipid productivity of 0.52 g/l/day and 158 mg/l/day	[31]
A. platensis	Plant-based food industry wastewater	TN and TP removal of 100% and 82%	Phycobiliprotein content of 30.3%	[32]
Chlamydomonas reindhardtii	Piggery wastewater	Almost total removal of TN and TP	Carbohydrate, lipid, and protein content of 50–60%, 35–40%, and 23–25% Biomethane yield of 171 ± 6 ml CH_4 g COD^{-1}	[20]
Chlorella PY-ZU1	Food waste	COD, TN, and TP removal of 68%, 99%, and 99%	Protein and lipid content of 17.2 and 32.2%	[33]
C. vulgaris	Piggery wastewater	Almost total removal of TN and TP	Carbohydrate, lipid and protein content of 50–60%, 35–40%, 23–25% Biomethane yield of 171 ± 6 ml CH_4 g COD^{-1}	[20]
C. vulgaris	Pulp and aquaculture wastewater (ratio 3:2)	COD, TN, TP, and TOC removal of 75.5%, 76.6%, 92.7%, and 70.7%	Carbohydrate, lipid, and protein content of 19.1, 9.1, and 47.5%	[34]
Dunaliella sp.	Synthetic mariculture wastewater	COD, TN, and TP removal of 82%, 97%, and 94%	Lipid productivity of 19.4 mg/l/day	[35]
D. tertiolecta	Coal seam gas industry wastewater	TN, TP, and TOC removal of 2.81, 1.16, and 29 mg/l/day	Biomass productivity and lipid content of 49.7 mg SS/l/day and 22%	[36]
Microalgal consortium of *C. vulgaris* and *Scenedesmus* sp.	Poultry wastewater	COD, TN, and TP removal of 91%, 91%, and 73%	650 mg crude protein/g volatile suspended solid	[37]
Microalgal consortium of *Euglena gracilis* and *Selenastrum*	Aquaculture wastewater	COD, TN, and TP removal of 56–68%, 75–89%, and 84–96%	Lipid and tocopherol yield of 84.9 mg/l and 877.2 μg/l	[38]
Microalgal consortium	Lignocellulosic fermentation effluents	TOC removal of 27%	55, 41, and 26 mg/l/day of carbohydrates, lipids, and proteins 25.8 mg/l of total chlorophyll and 5.9 mg/l of carotenoids	[39]
Nannochloropsis sp.	Synthetic mariculture wastewater	COD, TN, and TP removal of 81%, 94%, and 97%	Lipid productivity of 13.0 mg/l/day	[35]
Nostoc sp.	Plant-based food industry wastewater	TN and TP removal of 94% and 99%	Phycobiliprotein content of 19.9%	[32]
Porphyridium purpureum	Plant-based food industry wastewater	TN and TP removal of 98% and 100%	Phycobiliprotein content of 9.3%	[32]
Scenedesmus sp.[a]	Non-sterile domestic wastewater	TN and TP removal of 96.8% and 97.7%	Biomass and lipid productivity of 0.223 g/l/day and 34.3 mg/l/day	[40]
Scenedesmus sp.	Domestic wastewater	COD, NH_4, NO_3, and PO_4 removal of 69–96%, 94–98%, 57–70%, and 73–82% CO_2 removal rate 368 mg/l/day	Biomass and lipid productivity of 0.196 g/l/day and 65.2 mg/l/day	[41]
Scenedesmus sp.	Piggery wastewater	NH_4, PO_4, and CO_2 removal of 21.2, 3.5, and 219 mg/l/day H_2S completely removed	Biogas upgrading	[21]
Scenedesmus sp. *Novo*			63–94.3 pg lipid/cell, 0.34–1.08 pg carotene/cell	[42]
S. bijuga	Food wastewater	TN and TP removal of 100% and 90.5%	Biomass and lipid productivity of 50.8 and 15.6 mg/l/day	
S. obliquus	Food wastewater	TN and TP removal of 38.9 and 12.1 mg/l	Carbohydrate and lipid productivity of 14.7 and 13.3 mg/l/day	[43]

(continued on next page)

Table 1. (continued)

Microalgae	Wastewater	Nutrient removal	Added-value product synthesis	Refs
S. obliquus	Piggery wastewater	Almost total removal of TN and TP	Carbohydrate, lipid, and protein content of 50–60%, 35–40%, and 23–25% Biomethane yield of 171 ± 6 ml CH_4 g COD^{-1}	[20]
Tetraselmis sp.	Synthetic mariculture wastewater	COD, TN, and TP removal of 91%, 91%, and 73%	Lipid productivity of 29.5 mg/l/day	[35]

[a]Ultrasonic treatment during logarithmic growth phase (days 3 and 4 of cultivation) under operating conditions of 18 Hz and 20 W power for 10 minutes.
[b]Abbreviations: COD, chemical oxygen demand; SS, suspended solids; TOC, total organic carbon; TN, total nitrogen; TP, total phosphorus.

volatile organic compounds (VOCs) [45]. Table 2 presents the performance of algae in utilizing flue gas as a low-cost feedstock.

Carbon-Capture Technologies from Algae

CO_2 constitutes up to 68% of total emissions of anthropogenic greenhouse gases, and is expected to reach 40.3 Gt by 2030 and 50 Gt by 2050 [53,54]. Algae-based biological CO_2 sequestration has attracted much interest owing to its outstanding CO_2-fixation ability compared to terrestrial plants (10–50-fold greater): 1 kg of dry algal biomass utilizes ~1.83 kg of CO_2 [53,55]. Microalgal species such as *Botryococcus braunii*, *Chlorella vulgaris*, *Nannochloropsis oculate*, and

Table 2. Performance of Microalgae in Flue Gas Sequestration with Simultaneous Biofuel Production[a]

Microalga	Flue gas	Carbon fixation	Lipid content and productivity	Fatty acid assay	Refs
Chlorella sp.	Coal-fired flue gas with 13% v/v CO_2		23.5%; 42 mg/l/day	C_{16}–C_{18} content >70% SFA 35.0% MUFA 22.1% PUFA 30%	[46]
C. pyrenoidosa	Diluted simulated flue gas with 15% v/v CO_2, 0.03% v/v NO, 0.03% v/v SO_2	95.9% CO_2 removal efficiency	38%; 39.1 mg/l/day	C_{16}–C_{18} content 99.5% SFA 43.7% MUFA 30.9% PUFA 25.5%	[47]
Heterosigma akashiwo CCMP 2393	Simulated flue gas with 12% v/v CO_2, 150 ppm NO			SFA 41–47% MUFA 15–21% PUFA 32–44%	[48]
Mixed microalgae consortia	1% Coal-fired flue gas with 11.2% v/v CO_2, 388.8 mg/Nm^3 CO, 423.9 mg/Nm^3 NO_x, 781.8 mg/Nm^3 SO_x		16.6–28.0%; 7.86–14.0 mg/l/day	SFA 25.2–26.3% MUFA 26.5–28.1% PUFA 45.7–48.4%	[49]
Scenedesmus sp.	2.5% Coal-fired flue gas with 12% v/v CO_2, 0.55% v/v CO, 61 ppm NO_x, 0.3% v/v SO_x	CO_2 fixation 0.349 g/l/day	35.6%; 66.1 mg/l/day	C_{16}–C_{18} content of 86.8% SFA 48.2% MUFA 25% PUFA 26.8%	[50]
S. obliquus	Coal-fired flue gas with 14.1% v/v CO_2	Inorganic carbon removal of 35.8 mg/l	22.8%; 9.9 mg/l/day	C_{16}–C_{18} content of 82.85% SFA 28.4% MUFA 21.5% PUFA 50.1%	[51]
S. quadricada	Air-mixed coal-fired flue gas with 7% v/v CO_2, 210 ppm NO_x, 120 ppm SO_x	85% Carbon utilization efficiency	24.2%; 57.5 mg/l/day	Biodiesel yield of 0.21 g/l C_{16}–C_{18}	[52]

[a]Abbreviations: MUFA, monounsaturated fatty acid; mg/Nm^3, milligrams per (normal) cubic meter (i.e., at 25°C and 1 atmosphere pressure); PUFA, polyunsaturated fatty acid; SFA, saturated fatty acid.

Scenedesmus obliquus are some of the most promising strains for both carbon sequestration and biofuel production [44].

BICCAPS

BICCAPS is a novel concept that can solve this problem. In BICCAPS, CO_2 is captured as bicarbonate solution and stored as a liquid that can be easily transported and utilized as a feedstock for the cultivation of algae or cyanobacteria [56]. In some cases, amine solutions such as mono-, di-, and triethanolamine have been used because they quickly convert CO_2 to bicarbonate [57–59]. BICCAPS has the dual benefits of solvent recycling and value-added bioproduct accumulation, leading to a reduction in the operating cost of CO_2 mitigation [60]. However, the algae or cyanobacteria strains utilized in this culture system must be able to tolerate high alkalinity and high ion concentrations, and halophilic and alkaliphilic algae species from natural soda lakes may be suitable for this purpose [56]. A mixed algal consortium of *Chlorella* spp. and *Scenedesmus obliquus* was able to fix 2.42 g HCO_3^- per g dry weight of microalgal biomass [61]. Table 3 lists the applications of BICCAPS for carbon fixing using different microalgal strains.

Integrated Algal BECCS

BECCS is another innovative carbon capture and storage technology, and this has been proposed as a promising greenhouse gas capture technology by coupling energy generation from biomass to the capture and storage of CO_2 in geological or other long-term reservoirs. This technology can be applied to ethanol production and biomass gasification, as well as to flue gas streams from pulp industries and waste incineration [74]. Therefore, integrating BECCS with algal production, which does not require fresh water or arable land, can help to achieve net negative emissions of CO_2 without impacting on food security. LCA and technoeconomic analysis of BECCS showed that a 2680 ha eucalyptus forest equates to a 121 ha algal facility in terms of carbon capture and storage [75]. The system generated 61.5 TJ of electricity and yielded as much protein as soybeans cultivated on the same footprint, and sequestered 29 600 tons of CO_2 annually. The potential of BECCS to generate energy and reduce the carbon footprint represents a milestone in achieving environmental sustainability.

Ocean Fertilization and Macroalgal Afforestation

The photosynthetic action of marine algae combined with the ocean solubility pump constitutes at least 50% of Earth's annual carbon fixation [53,74]. Innovative strategies to fertilize the surface water of the ocean with 'limiting nutrient' have been proposed as a means to promote algal growth and enhance the biological CO_2 pump [44]. The 'limiting nutrient' is usually thought to be N, followed by P for the majority of open ocean, whereas Fe is limiting in high-nutrient low-chlorophyll regions (such as Equatorial Pacific, North Pacific, and the Southern Ocean). Because only trace amounts of Fe are necessary to stimulate carbon fixation following the Redfield ratio (C:N:P:Fe = 106:16:1:0.001), most attention has been paid to *in situ* ocean Fe fertilization. OMA is a concept proposed by de Ramon N'Yeurt and coworkers that aims to reduce the concentration of atmospheric CO_2 to under 350 ppm by 2085 through the expansion of natural populations of microalgae [76]. In addition to carbon sequestration and contaminant bioremediation, OMA can also mitigate coastal eutrophication, minimize ocean acidification, and control the spread of harmful algal blooms. Based on the macroalgal forest that covers 9% of the Earth's ocean surface, LCA and economic analysis have demonstrated the potential of OMA for an annual production of 12 billion tons of biomethane, storage of 19 billion tons CO_2, and 34 billion tons of CO_2 captured from the biomethane combustion exhaust. The algal biomass after anaerobic digestion for biomethane production is recycled to expand the algal forest and facilitate sustainable fish production, potentially at a level of 200 kg/person/year for 10 billion people. Similarly to the concept of OMA, the Coastal CO_2 Removal Belt that comprises both natural and man-made *Ecklonia cava*

Table 3. Applications of BICCAPS to Carbon Fixation by Utilizing Microalgae

Microalgae	Solvent type and concentration	Biomass productivity (g/l/day)	Carbon fixing capability	Refs
Ankistrodesmus falcatus	$NaHCO_3$ (10 g/l)	0.00355		[62]
Chlorella sp. L38	NH_4HCO_3 (0.02 M)	0.055	99.4% Carbon utilization efficiency with a fixation capacity of 0.158 g/l/day	[63]
C. pyrenoidosa	$NaHCO_3$ (3.33 g/l)		86.3% CO_2 removal efficiency	[64]
C. sorokiniana PAZ	HCO_3^- (1.127 g/l)	0.0891		[65]
C. vulgaris	$NaHCO_3$ (1 g/l)	0.996	CO_2 fixation of 0.69 g/ml/day	[66]
Dunaliella salina JDS 001	$NaHCO_3$ (5 g/l)	0.186	91.4% Carbon utilization efficiency with a fixation capacity of 0.109 g/l/day	[67]
Euhalothece ZM001	$NaHCO_3$ (84 g/l)	1.21		[68]
Mixed *Chlorella* sp. and *Scenedesmus obliquus*	$NaHCO_3$		HCO_3^- removal efficiency of 63.9% with a fixation capacity of 0.015 g/l/h	[61]
Neochloris oleoabundans	$NaHCO_3$ (25.2 g/l)	0.223		[69]
Scenedesmus sp.	Triethanolamine (1 mM)[a]	0.52	CO_2 fixation of 0.972 g/l/day	[59]
Spirulina sp. DUT001	$NaHCO_3$ (42 g/l)	1.0	CO_2 fixation of 0.81 g/l/day	[70]
Spirulina sp. LEB18	Monoethanolamine (0.41 mM)	0.110	29.8% carbon utilization efficiency with a fixation capacity of 0.197 g/l/day	[58]
	NaOH (0.41 mM)	0.121	31.7% carbon utilization efficiency with a fixation capacity of 0.210 g/l/day	
	Diethanolamine (1.64 mM) plus K_2CO_3 (0.41 mM)	0.174	43.7% carbon utilization efficiency with a fixation capacity of 0.319 g/l/day	[57]
S. platensis	Equimolar mixture of $NaHCO_3$ and $KHCO_3$ (0.1 M)	0.00737	Inorganic carbon conversion of 4.192 mM/day	[71]
	NH_4HCO_3 (0.3 M)	0.0972	40.5% Carbon utilization efficiency with a fixation capacity of 0.179 g/l/day	[72]
Synechococcus PCC 7002	$NaHCO_3$ (22 g/l)	1.12		[73]

[a]Repeated addition of triethanolamine.

kelp forests has been developed in the coastal region of southern Korea with the potential as a carbon sink of ~10 t/ha/year [77]. In context of a low-carbon circular bioeconomy, it is environmentally and economically desirable to combine algal CO_2 fixation and nutrient recovery from waste streams and the atmosphere with concurrent value-added product synthesis. Integration of algae biotechnology into waste-stream management and carbon-capture technologies represents an opportunity for green energy generation, pollutant removal, CO_2 sequestration, and simultaneous biomass accumulation, leading to low-carbon and economically viable production of bioenergy and bioproducts.

Advances and Developments in Algal Biotechnology

The growth of the bioeconomy is closely connected to the evolution of the biotechnology industry. Significant breakthroughs have been made in high-throughput screening and rapid sampling methodologies, novel culture techniques, strain development, bioreactor design, genetic engineering, genome editing, and sequencing technology, metabolic engineering, systems-biology engineering, directed evolution, and *in silico* model prediction that have led to a revolution in the field of algal bioeconomies. Furthermore, systems biology utilizing several genome-wide tools, including omic and computational analyses that cover genomics, metabolomics, proteomics, and transcriptomics, have facilitated the analysis of cellular metabolism and physiological data at the systems level.

Genetic and Metabolic Engineering Strategies

A wide range of bioengineering techniques has been adopted to genetically improve microalgae for higher growth rates and enhanced accumulation of valuable products. These modifications can also provide microalgae with greater tolerance to inhibitors (such as heavy metals). Moreover, novel algal strains can be created through domestication, gene editing, hybridization, and mutation breeding. Several attempts have been made to optimize algal biofuel production, for example by enhancing lipid accumulation through strain optimization, pathway prediction and reconstruction, varying stress conditions, and carbon flux modifications. Furthermore, engineering can be used to modify the degree of saturation and the chain length of the accumulated lipids [14]. Similar strategies have been employed to enhance the photosynthetic efficiency of microalgae and minimize the negative impact of photoinhibition on their growth, with a focus on reducing the size of light-harvesting chlorophyll antenna [78]. These strategies have undoubtedly made algae an even stronger 'powerhouse' for carbon capture, phycoremediation, and value-added product synthesis.

Innovative Technologies

Innovative technologies such as ultrasonic and bioelectromagnetic stimulation can improve algal growth and intracellular compound accumulation. Ultrasonic waves can promote the transport of substrates across the cell membrane and enhance biochemical reactions within the cells [40]. Pulsed electric fields (PEFs) can enhance algal biomass dehydration, the extraction and fractionation of valuable components, and biomass pretreatment (disintegration of cell and cell organelles) for biogas yield improvement [79]. These innovative technologies have demonstrated their potential in the life cycle of an algal bioeconomy, and warrant further research and development.

Challenges and Future Perspectives

The expansion of a low-carbon circular bioeconomy can have a pronounced socioeconomic and environmental impact in which algae-based technology plays a significant role [1]. However, several major barriers to the growth and expansion of the algal bioeconomy need to be overcome. Table 4 presents the major challenges faced by the algal bioeconomy together with potential solutions.

LCA is a useful tool to evaluate the environmental performance of algae to end-product systems. Collota and coworkers commented that many LCAs of microalgae-based biofuel production do not cover the whole 'cradle-to-grave' cycle [80]. Furthermore, these studies focused on a limited number of environmental impact factors, predominantly global warming potential, and neglected water- and land-use parameters that play an important role in an algal production system. In

Table 4. Major Challenges Faced by an Algal Bioeconomy and Suggested Solutions

Challenges	Suggested solutions
Inability of sufficient algal biomass production at a feasible cost with minimum environmental impact	Practice the 'systems approach' in algal biomass production and logistics Utilize byproducts and waste streams for algae cultivation
Inefficiency of the current algal biorefinery technologies	Develop more efficient algal biorefinery technologies that are capable of coproducing biofuels, biochemicals, heat, and electricity
Uncertainty of algae-based bioenergy and bioproduct market	Expand the market for algae-based bioenergy and bioproducts Government policies such as mandates, incentives, subsidies, soft loans, and project funding

addition, social impact (e.g., employment) should also be considered when considering the commercial applications of algae-based biofuel.

Industrial symbiosis systems ('ecoindustrial parks') are industry clusters that comprise multiple industries in which raw materials (e.g., algae), energy, technology, and even knowledge are shared and utilized between/among the industries of the system [81]. The concept of an industrial symbiosis system can be applied to an algal bioeconomy as part of a greater circular bioeconomy. For example, the output of one industry (e.g., algal biomass) can be the input to another industry (e.g., biofuels, biochemicals, biomaterials, etc.), thus minimizing the cost of logistics and transportation, as well as reducing the carbon footprint. Similarly, the surplus heat and electricity produced can be supplied to others in the system.

Concluding Remarks

The immense potential demonstrated by a algae-based low-carbon circular bioeconomy will play a crucial role as human society evolves in the near future. Algae can not only serve as a feedstock for fuel and bioproducts to fulfill our demand for energy, food, and chemicals but can also play an important role in wastewater phycoremediation, carbon capture, and converting unwanted waste into value-added products, thus minimizing waste generation as well as tackling sustainability and pollution issues. Therefore, significant action should be taken by governments, industries, and researchers to fully explore the potential of algae (see Outstanding Questions). Commercial-scale implementation of an algae-based low-carbon circular bioeconomy can be achieved by overcoming the associated challenges and limitations through government support. With technological innovations and advances, algae can help to decouple economic growth from GHG emissions for a greener and more sustainable future.

Outstanding Questions

How can we produce algae at a feasible cost with minimal environmental impact?

How can the efficiency of current algal biorefinery technologies be improved?

What is the best way to fully utilize waste streams through algae and convert them into valuable products?

Can we further expand the market of algal products?

How can we further integrate algae into the framework of a low-carbon circular bioeconomy (biofuels, bioplastics, biochemicals, etc.)?

Acknowledgments

The authors gratefully acknowledge financial support from the Taiwan Ministry of Science and Technology (grants MOST 109-2221-E-029-004, 109-3116-F-006-016-CC1, 109-2621-M-029-001, and 107-2221-E-006-112-MY3). This work was also supported by the Fundamental Research Grant Scheme, Malaysia (FRGS/1/2019/STG05/UNIM/02/2) and a Malaysia Partnerships and Alliances in Research (MyPAIR) Hubert Curien Partnership (PHC) Hibiscus grant (MyPAIR/1/2020/STG05/UNIM/1).

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