



Versatility of algae—exploring the potential of algae for nutrient circulation

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Abstract For feeding the world in 2100, the global agriculture, the entire food chain, as well as the behavior of all consumers must be change fundamentally. Essential resources needed to intensify agriculture and use barren land, such as phosphorus, water, and fossil fuels, are becoming increasingly scarce and expensive. An ecological form of agriculture that uses these resources more responsibly requires more land for the same yields. Therefore, new concepts for food and feed production have to be developed, in which nutrients are recycled beyond these areas. A possible starting point could be bioreactors, since these are enormously efficient and enable resource-efficient land use. Wastewater treatment as a means of nutrient recycling will be one of the most important tasks in the future. Hereby, not only the heterotrophic bioreactors currently used for this purpose but also autotrophic photobioreactors show great potential, especially if these two reactor types would be combined. Because of the ability to use inorganic nitrogen and phosphorus for their growth as well as the ability to produce a wide range of metabolites, microalgae offer an integrated approach. This review provides an overview of the potential of microalgae as components of a sustainable, circular agricultural system for feed and food production.

Keywords Microalgae · Photosynthetic efficiency · Nutrient circulation · Photosynthetic storage products · Photobioreactor

Introduction

Today agriculture is based on the primary production of terrestrial plants. With the notable exception of most fish (etc.), almost every calorie a human consumes was produced in the leaf of a relatively large, soil-based vascular plant. Eukaryotic in water living organisms which operate photosynthesis are called algae. The number of species can only be estimated, but they are the major contributors of biodiversity and present in salt-, brackish- or freshwater (Graham et al. 2009; Metting 1996). On the basis of their size, a distinction is made between microalgae and macroalgae. Microalgae are single-celled organism, and they can be found individually, in chains, or groups with a size ranging from a few micrometers to a few hundred micrometers. Responsible for roughly 70% of the oxygen in the atmosphere, these single-celled algae and cyanobacteria (together referred to as microalgae) dominate in aquatic ecosystems. These organisms have long been viewed by scientists as having great potential for the agricultural system, especially with regard to biofuel but also for food, feed, and fertilizer production. The main reasons for this optimism are very high photosynthetic efficiency of microalgae and the possibility of using waste water for their cultivation, as well as flue gases, which can be fed into photobioreactors to increase

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productivity and mitigate CO₂. However, the “hype” (Posten 2009; Walker et al. 2005) around the potential of microalgae cultivation has not yet been accompanied by large-scale success of photobioreactors.

The individual algae classes (divisions), Fig. 1, are distinguished primarily by the composition of their photosynthetic pigments and products. The microalgae diatoms (Bacillariophyceae) can be found in the oceans, freshwater, brackish water, and soils of the world. The green algae (Chlorophyceae) are abundant, especially in freshwater and have the same photosynthetic pigments (chlorophyll a and b), the same set of carotenoids (alpha, beta, and gamma carotene; lutein; zeaxanthin; violaxanthin; etc.), the same reserve substance (starch), and the same framework substance of the cell wall (cellulose) as green plants. Euglenophyta (Euglenophyceae) are predominating in freshwater, especially in eutrophic waters. Their frequent occurrence can cause a water bloom. The golden algae (Chrysophyceae) are a large group of algae, found mostly in freshwater. The dinoflagellates (Pyrrophyta) belong to the class of Dinophyceae with more than 1000 species, many of which live parasitic. Dinoflagellates occur in salt- and freshwater. In the sea, they are the second most important group of phytoplankton after diatoms. In

warm waters, biodiversity is high with low numbers of individuals. In cold climates, few species with high numbers of individuals predominate. At regular intervals, mass developments of certain species occur in which the water turns red or orange (red tide) because of the large amount of carotenoids formed (Algen 1996–2004). The red algae (Rhodophyta, Rhodophyceae) are a division of algae, which are colored red by the phycobilin that is involved in photosynthesis. Beside Glaucophyta and Chloroplastida, the red algae form one of the three groups of Archaeplastida. Red algae occur in the majority in the littoral zone of the sea and some species also in freshwater and in moist soil.

The brown algae (Phaeophyceae) are a large group of multicellular algae mostly living in marine environments, and they are important for food and as habitat. The blue green algae (Cyanophyceae; Cyanobacteria, prokaryotes) are an excellent source of biologically active natural products including vitamin, protein, fine chemicals, and renewable fuel. They are largely unexplored and offer a great opportunity to discover new compounds, among others, biologically active compounds like antibacterial, antiviral, antifungal, algacide, therapeutic agents, and cytotoxic activities (El Abed et al. 2008; van den Hoek and Jahns 1995).

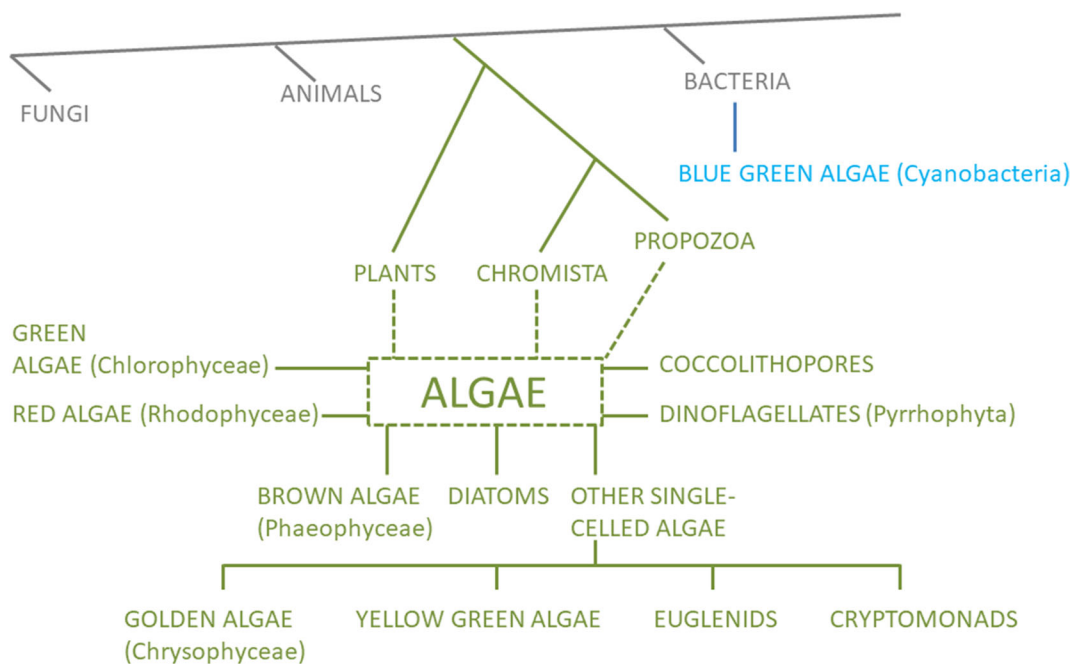


Fig. 1 Simplified taxonomy of single-celled algae and cyanobacteria, modified after (Enamala et al. 2018; Fondriest Environmental 2014); dashed line: classification under debate

Microalgae are a large, unexplored group of organisms, and only a few of the 30,000 known species are currently of commercial significance (Table 1). Even though they can be used to produce a wide range of metabolites like proteins, lipids, carbohydrates, carotenoids, and vitamins for health, food and feed additives, cosmetics, and for energy production. Microalgae can enhance the nutritional value of food and feed and play a crucial role in aquaculture (polyunsaturated fatty acids, PUFA). Three key points of microalgae can be converted into technical and commercial advantages:

- Genetically very diverse with a wide range of physiological and biochemical characteristics
- Cost-effectively incorporate the stable isotopes ^{13}C , ^{15}N , and ^2H into their biomass
- A large, unexplored group of organisms which offer an untapped source for products (Chew et al. 2017; Priyadarshani and Rath 2012; Vanthoor-Koopmans et al. 2013)

Nevertheless, the positive aspects of using microalgae also have downsides or rather challenges. High yields can only be achieved by high energy expenditure. Light energy is an important factor, therefore, either artificial lighting costs have to be borne or the strong dependence of sunlight has to be accepted. Currently, the use of algae as an alternative to fuels is not competitive (Hannon et al. 2010; Lehr and Posten 2009; Razzak et al. 2013; Richardson et al. 2012).

Technological improvements and economic changes, as well as a gradual cost reduction when photobioreactors become more established, could lead to more large-scale operations in the coming years. However, it is not clear

yet how microalgae cultivation can best be integrated into the agricultural system as a whole. Here we analyze the potential of microalgae cultivation with regard to photosynthetic and areal efficiency, as well as resource use and nutrient circulation.

Photosynthetic efficiency

Photosynthetic efficiency (PE), sometimes also referred to as photon conversion efficiency, is the conversion rate from solar energy (photons) to chemical energy (biomass), usually given as a percentage in relation to the light that hits a certain surface area. The basis of photosynthesis is the quantum-mechanical process of light absorption, which takes place at the thylakoid membranes in chloroplasts. In this process, energy is transferred from photons to pigments, which are part of large protein-pigment complexes. These either form antenna, meant exclusively for light harvesting, or reaction centers, which also absorb light but are most important for passing on the energy, to power the chemical reactions which ultimately cumulate in the production of glucose from CO_2 and H_2O . These pigments can only absorb light in a certain bandwidth. Most higher plants use light in the range from 400 to 700 nm, which means that 51.3% of solar energy is unavailable to them (Zhu et al. 2008). Chlorophylls are the most important pigments for photosynthesis. Different types of chlorophylls have different absorption characteristics, but in general, they absorb light in the red and blue range, leaving a “green gap” between roughly 500 and 600 nm. Microalgae and cyanobacteria have different types of chlorophyll, which enable them to absorb light above 700 nm and below 400 nm (Zhu et al. 2010). To

Table 1 Major microalgae commercialized for human nutrition, adapted from (Priyadarshani and Rath 2012)

Major Producers	Microalgae	Products
Hainan Simai Pharmacy Co. (China); Earthrise Nutritionals (California, USA); Cyanotech Corp. (Hawaii, USA); Myanmar Spirulina factory (Myanmar)	<i>Spirulina (Arthrospira)</i>	Powders, extracts tablets, beverages, chips, pasta, and liquid extract
Taiwan Chlorella Manufacturing Co. (Taiwan); Roquette Klötze GmbH & Co. KG (Germany)	<i>Chlorella</i>	Tablets, nectar, noodles, and powders
Cognis Nutrition and Health (Australia)	<i>Dunaliella salina</i>	Powders and b-carotene
Blue Green Foods (USA) Vision (USA)	<i>Aphanizomenon flos-aquae</i>	Capsules, crystals, and powder

fill the green gap, different pigments, such as the bacterial phycobilins, are used (Zhu et al. 2010). The use of a wider range of pigments is one of the reasons why microalgae usually have higher PE than vascular plants. However, too much light can be harmful and lead to photosynthetic stress and the creation of toxic reactive oxygen species (ROS). To react to this, plants and microalgae can change the interactions between pigments through conformational changes of the proteins, or they can use pigments such as carotenoids, xanthophyll, and zeaxanthin as protection. These pigments emit the energy from light absorption as heat rather than passing it on to the reaction centers (Zhu et al. 2010).

Photosynthesis also depends on a light-independent chain of reactions: the Calvin cycle. Here, one of the main factors affecting PE is the functioning of the enzyme RuBisCO. This enzyme is responsible for fixating CO₂ but also has an affinity to O₂. When O₂ concentrations are high, usually due to oxygen production in the light-dependent reaction of photosynthesis, electrons will be transferred to O₂ more frequently, which leads to energy loss. Many higher plants solve this problem by separating the light-dependent and independent reactions in space, by letting them take place in different compartments (C4-plants), or by separating them in time, letting the light-independent reaction take place at night (CAM-plants). Microalgae cannot use these strategies and are thus dependent on protection from light stress through the use of protective pigments and antioxidants. However, while higher plants will regularly experience high oxygen concentrations in their leaves when closing the stomata, the level of photorespiration in microalgae is mostly dependent on the oxygen concentration in the surrounding substrate. While this might mean that microalgae are experiencing less photorespiration than higher plants in most natural environments, in photobioreactors it represents one of the central problems and challenges, since it means that the cultivation process is only effective when oxygen concentrations are sufficiently low and CO₂ concentrations are sufficiently high. In most reactor types, this requires constant gas exchange. An advantage of this circumstance is, however, that the productivity (and thus PE) can be increased through feeding excess CO₂ from industrial or agricultural activities (e.g., biogas plants) into the photobioreactors. This has the added benefit of CO₂ mitigation.

PE is not only affected by molecular differences, such as described above, but also by morphological

traits. Microalgae, for example, have a lower surface to volume ratio, which is beneficial. Also, microalgae do not have to grow and support non-photosynthetic tissues. While a tree has to form roots, stems, fruits, etc. and keep up nutrient and water flow between these different body parts to complete its life cycle, microalgae will simply duplicate once their single cell has reached sufficient size and accumulated enough energy. It is important to note for microalgae cultivation that electric energy is needed to fulfill many of the functions that a higher plant takes care of itself: gas exchange, nutrient and water flow, as well as temperature control (Sayre 2010). To determine the PE of a photobioreactor, it is necessary to take these energy inputs into account. Sometimes it is not clear whether this was done when researchers give PE values for photobioreactors.

Estimations of the PE of different organisms vary widely, but the general consensus is that microalgae have much higher PE than higher plants. It is however difficult to pinpoint the magnitude of this difference from literature. Sometimes PE is given as a theoretical maximum, sometimes as a “realistic estimate” and very occasionally as a value that has actually been measured. Another difficulty is that some estimates of PE refer to the whole spectrum of sunlight, while others refer only to the spectrum of light available to plants.

The theoretical maximum of PE is generally higher for C4 plants than for C3 plants, with 6% compared with 4.6% (Zhu et al. 2010). In the “real world,” however, PE of higher plants is typically below 1% in temperate and tropical climates (Blankenship et al. 2011). Microalgae are said to have theoretical maximum PE of more than 20% (Janssen et al. 2003), based on photosynthetically available light, which would amount to about 10% PE and thus roughly twice as much as higher plants. In reality, the PE of photobioreactors is also way below the theoretical maximum. A PE of above 5% can however be seen as realistic according to most sources (Schenk et al. 2008; Janssen et al. 2003; Wijffels and Barbosa 2010). All in all, the energy yield of photobioreactors is lower than that of photovoltaic solar panels (Blankenship et al. 2011) but very high compared with crops. Solar panels take advantage of a larger spectrum of light, by stacking different light-absorbing layers above each other (Blankenship et al. 2011). It would be possible to do the same with photobioreactors, for example, by positioning two flat-panel bioreactors with two different species that make use of different

wavelengths of light, in front of each other. Researchers are also looking at ways of improving energy yield of photosynthesis by genetically altering organisms and for example making RuBisCO less prone to photorespiration or modifying the pigment-protein complexes (Zhu et al. 2010).

Algae for nutrient circulation

Microalgae mainly consist of proteins, carbohydrates, and lipids with varying composition depending on the microalgae species. The carbohydrate fraction (starch, sugars, glucose, and other polysaccharides) is found to be up to 64% in microalgae biomass, the protein fraction up to 71%, and the lipid fraction up to 22% of cell dry weight (Becker 2007; Razzak et al. 2013). The content is highly specific to species and depending on growth conditions (Weyer et al. 2009). Under stress conditions like low nitrogen content or in the presence of supplemental reductants like sugar or glycerol, some species, e.g., *Nannochloropsis* sp. F&M-M24, accumulate energy-dense storage compounds such as lipids, with a content up to 60% per gram of dry weight (Rodolfi et al. 2009; Sayre 2010). Of course, to build up biomass, microalgae need a carbon source, water, temperature control, and light but also minerals like nitrogen, phosphorus, and other essential nutrients like sulfur, iron, and magnesium (Graham et al. 2009). Therefore algae are well suited to grow on wastewater that naturally includes high amounts of nutrients (Arashiro et al. 2019; Razzak et al. 2013).

Carbon source

Microalgae are capable of using carbon in the form of carbon dioxide from the atmosphere as well as emission from industrial power plants; inorganic carbon like NaHCO_3 and Na_2CO_3 ; and organic carbon in form of sodium acetate, glucose, and glycerol. Since the beginning of the industrialization, the well-balanced ecosystem, including carbon capture from photosynthesis, carbon deposition in soil and oceans, and carbon release from biological and geological sources, is out of balance. The atmospheric CO_2 concentration increased from 295 to 380 ppm over the last century, which is one of the main driving factors of global warming and climate change (Sayre 2010). According to Razzak et al. (2013), producing 100 t of algal biomass fixes about

183 t of CO_2 . The nongaseous form of CO_2 , which occurs in water at a ratio over 50% at pH values between 6.4 and 10.3, is bicarbonate which can be transported and concentrated in algae. Inside the cell, the bicarbonate is reconverted to CO_2 and can be fixed to RuBisCO. After several reactions these molecules are substrates for starch and oil production (Huertas et al. 2001; Sayre 2010). According to literature, flue gas can be used as a carbon source for the production of microalgae (Demirbas 2011; Doucha et al. 2005; Holdmann and Schmid-Staiger 2016; Kadam 2002). Doucha et al. provided a combined biotechnological process scheme where agricultural wastes are anaerobically digested, the produced biogas is combusted in a boiler, and, following this, the flue gases are decarbonized by microalgae (Doucha et al. 2005). In addition to autotrophic microalgae, which mainly use CO_2 as a carbon source, there are several mixotrophic and heterotrophic species which can access carbon from a range of different substrates. In the cultivation of these species, light energy is not an absolutely limiting factor (Kong et al. 2013). According to Cheng et al., the algae *Chlorella protothecoides* achieved an oil content of 53% by cell dry weight during a heterotrophic cultivation in a media containing sugar cane juice as an alternative carbon source (Cheng et al. 2009). This strain is also able to use glycerol, crude glycerol, and a glucose/glycerol mixture as carbon sources (Kamjunke et al. 2008; O'Grady and Morgan 2011).

Nitrogen and phosphorus

Nitrogen and phosphorus are essential to all organisms. Therefore, not only the environmental burdens resulting from excessive use should be considered but also the overuse of a finite resource. Nitrogen is the essential element of proteins and DNA and therefore also the building block of all enzymes that control plant, animal, and human metabolism. Nitrogen and hydrogen can be taken from the ambient air to synthesize ammonia (Haber-Bosch process). Among other things, ammonia is used to produce urea, ammonium nitrate, ammonium sulfate, and ammonium phosphates, which are used as fertilizers and contribute to the nutrition of a large part of the world's population. Also compounds of phosphorus are essential for all living organisms and involved in the structure and function of organisms in key areas, such as DNA and the cellular energy supply (ADP/ATP). Phosphorus is naturally present in minerals, most commonly

apatite. These minerals are mined in places with high phosphate content and, after appropriate treatment, used as mineral fertilizer, thus entering the phosphate cycle. Phosphorus, with increasing annual degradation, is about to reach the peak, where production reaches its maximum. It is estimated that the world's reserves will cover the need for about 100 years (BMEL 2011), and other sources calculate shorter periods of time out (White and Cordell 2008).

Through traditional technologies for wastewater treatment, nitrogen, phosphorus, carbon, and other nutrients are not completely utilized and recycled (Abdel-Raouf et al. 2012; Han et al. 2019). In order to guarantee an environmentally friendly supply of these essential nutrients, continued work on economic recovery and recycling of these resources is necessary.

Microalgae offer the opportunity for the treatment of wastewater due to their ability to use inorganic nitrogen and phosphorus to build up biomass (Abdel-Raouf et al. 2012; Zhao et al. 2019). Sources of nitrogen are inorganic nitrogen sources like nitrate, nitrite, ammonia, and urea (Li et al. 2008; Xiong et al. 2008) and for some algae species also organic nitrogen sources like glycine and yeast extract (Xiong et al. 2008). Algae take up nitrate and ammonium ions directly from the surrounding water, with ammonium being preferred to build up cellular nitrogen compounds. Using the enzyme nitrate reductase, algae are able to convert nitrate to ammonium (Graham et al. 2009).

Phosphorus in the form of orthophosphate (PO_4^{3-}) is the preferred uptake form of algae.

After aerobic or anaerobic biological degradation of wastewater, the content of inorganic components like nitrate, ammonium, and phosphate ions is sufficient for eutrophication of water environment. Microalgae show high capacity to take up these components and use inorganic nitrogen and phosphorus for their growth (Abdel-Raouf et al. 2012; Zhao et al. 2019).

Other nutrients

Elements like sulfur, iron, magnesium, and others are required as trace elements. Indeed, iron acts as a cofactor for several enzymes like ferredoxin, catalase, cytochromes, glutamate synthetase, nitrogenase, nitrate, and nitrite reductase (Graham et al. 2009). Sulfur is usually taken up and assimilated as sulfate and is essential for the incorporation into a variety of sulfur-containing compounds critical for protein, lipid, and

polysaccharide synthesis, as well as signaling molecules (Giordano et al. 2008; Shibagaki and Grossman 2008). Magnesium also serves as a cofactor of several enzymes and is required for the biosynthesis of chlorophyll (Brzezowski et al. 2015; Graham et al. 2009). Beside the requirement of trace elements, algae are also known for their ability to absorb and accumulate heavy metals and compounds like organochlorides intracellularly. Additionally the secretion of extracellular esterase, which degrades Deltamethrin (insecticide), and the ability to degrade a range of hydrocarbons (found in oily wastes) are known for some species of microalgae (Abdel-Raouf et al. 2012; Arunakumara and Xuecheng 2008; Worms et al. 2010).

Potential of microalgae

Due to the biodiversity, the composition of the biomass depending on the nutrient availability, use of different nutrients, and the production of different substances, microalgae show great potential for a wide variety of applications (Metting 1996).

Microalgae-assisted aquaculture is known for live feed for larvae, fish species, and zooplankton (Brown et al. 1997), as food additive to supply basic nutrients, enhance the color of salmonids or for other biological activities (Muller-Feuga 2000), stabilization and improvement of quality of culture medium (Chuntapa et al. 2003), stimulation of immune systems (Spolaore et al. 2006) as well as probiotic effects (Irianto and Austin 2002; Han et al. 2019; Roy and Pal 2014). The most used species are *Spirulina*, *Chlorella*, *Scenedesmus*, *Dunaliella*, *Tetraselmis*, *Isochrysis*, *Pavlova*, *Skeletonema*, *Chaetoceros*, *Phaeodactylum*, *Nitzschia*, and *Thalassiosira* (Beal et al. 2018; Brown et al. 1997; Han et al. 2019).

Next to the potential of microalgae in aquaculture, the potential is also given in the area of implementing an eco-friendly system using microalgae in form of, e.g., wastewater treatment and nitrogen removal (Abdel-Raouf et al. 2012; Arashiro et al. 2019; Di Termini et al. 2011; Ledda et al. 2015b; Razzak et al. 2013; Wang et al. 2019; Yu et al. 2019), treatment of heavily polluted meat processing wastewater as primary or secondary treatment option (Hu et al. 2019), recycling of animal wastewater and manure (Kim et al. 2007; Ledda et al. 2015a; Pizarro et al. 2002), and flue gas (Doucha et al. 2005; Nagase et al. 1997; Yoo et al. 2010).

The potential of microalgae in generating biofuels has been of major interest over the last decades (Chew et al. 2017; Hussian 2018; Vanthoor-Koopmans et al. 2013). The usage of algae components like carbohydrates, mainly consisting of glucose, starch, cellulose as well as polysaccharides, show potential too (Chew et al. 2017). Microalgae are able to generate a wide variety of photosynthetic storage products including α -(1-4)-linked glucans (starches), β -(1-3)-glucans, fructans, low molecular weight carbohydrates, and fats and oils. Different types of starches are produced by different divisions of algae, e.g., red algae are known to synthesize floridean starch (amylopectin subunits), whereas blue-green algae synthesize myxophycean starch (amylopectin or glycogen-like subunits). Some species of green algae synthesize a cross-linked amylose-amylopectin starch and fructosans (inulin-like fructose oligosaccharides), which are comparable with starch in land plants. Cryptophytes and dinoflagellates generate α -(1-4)-linked glucans. Chrysophytes store oils or chrysophycean starch, a water-soluble β -(1-3) glucopyranoside (Metting 1996). According to literature, starch contents up to 60% of dry weight are achieved with *Chlorella vulgaris* (Branyikova et al. 2011; Dragone et al. 2011; Pruvost et al. 2011) and *Tetraselmis subcordiformis* (Yao et al. 2012) and up to 50% of dry weight with *Phaeodactylum tricornutum* (Jakob et al. 2007).

Hence, investigations (beside the usage for biofuel or as a source of bioactive compounds and pharmaceuticals, health foods, or cosmetic additives) could be of high interest maybe to yield starch (produced without the need of arable land) or fermentable monosaccharides to receive an ecological and sustainable bioresource (Chew et al. 2017; Reisky et al. 2019).

Conclusion

The versatility of algae and therefore their potential for nutrient circulation, biomitigation of carbons must be of increasing interest in the future due to existing problems including global warming, discharge of wastes, supply of nutrients (nitrogen, phosphorus), or toxic chemicals.

The possibility given through these highly diverse microalgae, capable to grow photoautotroph, heterotroph, and mixotroph on barren land, and the ability of CO₂ fixation must be investigated more intensively. An ideal algae strain for tropical climates should be able to

produce biomass at high solar radiance and high oxygen levels.

The challenge will be to have this ideal strain in the right place and in a perfect, yet simple combination of wastewater treatment, CO₂ biomitigation and nutrient recycling to create new concepts for food and feed production in bioreactors. The implementation must be technically simple, long-term stable, and easy to handle and to care for. In order to have enough purified water, food, and feed to supply the world in 2100, the integrated usage of microalgae could be an opportunity for the global agriculture.

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Code availability Not applicable.

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Compliance with ethical standards

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Consent to participate I consent.

Consent for publication I consent.

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