Mechanism of Microalgal Symbiosis

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Microalgae have been considered a promising and sustainable candidate for wastewater treatment and valuable bioproducts, such as feedstocks for food, nutrients, and energy. However, many challenging bottlenecks, such as low biomass productivity, expensive biomass harvesting techniques, and inefficient extraction of biofuels restrict its large-scale commercial production. Symbiotic relationships between microalgae and bacteria, also known as microalgal consortia, have proven to be effective solutions for mitigating technical and economic limitations.

microalgal consortia symbiosis wastewater treatment bioproducts

1. Introduction

Microalgae are prokaryotic (cyanobacteria, which include with microalgae, unless specifically stated otherwise) or eukaryotic photosynthetic phytoplanktonic microorganisms. They are the indisputable primary producers in the aquatic ecosystem and contribute approximately half of the global net primary productivity [1]. Microalgae have higher photosynthetic efficiency when it comes to converting solar energy into biomass than terrestrial plants. Additionally, microalgae can adapt to various environments, require less water, and have a smaller footprint for cultivation, which makes them an attractive and valuable candidate for commercialized production [2][3]. Most microalgae store a large amount (20–50% cell dry weight) of fixed carbon (CO_2) in the form of neutral lipids, with some strains of *Schizochytrium* sp. accumulating 77% of the dry weight of lipids [4]. Microalgae have been considered a sustainable and renewable alternative for bioenergy production coupled with pollutant removal from wastewater.

Although microalgae have been successfully applied in various commercial applications, it is challenging to maintain microalgal monocultures [5]. Furthermore, a series of challenging bottlenecks, such as costly biomass harvesting, low biomass productivity, and energy-intensive extraction methods, limit its large-scale production [6]. Several studies have explored the potential applications of microalgal consortia and their cooperative interactions, especially in the form of microalgal–bacterial symbiosis. In fact, large-scale cultivation of microalgae is often accompanied by other microbes. These microbes often conversely affect algal growth, boost the accumulation of lipids and carbohydrates, facilitate microalgal cell wall disruption, and promote microalgal growth flocculation processes [1]. These cocultures could result in the development of robust systems that can resist a complex environment, thereby promoting the effective degradation of nutrients and improved biomass and bioenergy productivities [7][8].

Microalgal consortia, consisting of photosynthetic microalgae and heterotrophic bacteria (microalgal–bacterial consortia), or photosynthetic microorganisms (microalgal consortia), and microalgal–fungi or yeast, can naturally occur or be artificially generated for a unique application [5][7][9][10]. For example, many diatoms inhabit low-nutrient, open ocean water and have a close association with autotrophic N_2-fixing bacteria (Cyanobacteria) [11]. Watanabe et al. isolated a fungal strain and four bacterial strains from the green algae *Chlorella sorokiniana* IAM C-212 slant culture and found that the fungus *Acremonium*-like hyphomycete KR21-2 and the bacterium *Microbacterium trichotecenolyticum* could promote the growth of *Chlorella*. Interestingly, the chlorophyll content was kept at a high level in the *C*. *sorokiniana* together with symbionts, while it declined dramatically in pure *C*. *sorokiniana* culture [12].

More and more studies have illuminated that algae and bacteria synergistically affect each one's physiology, cytology, and metabolism [13][14], although bacteria have often been considered as a mere contamination of algae cultures during commercialization. In fact, Algae and bacteria have coexisted since the early stages of evolution and interacted with each other in many aspects. In nature, the development of algal blooms is often influenced by many bacteria [15][16][17]. Depending on the specific species and living requirements, the interactions between microalgae and other microorganisms contain a variety of biological relationships, ranging from mutualism/commensalism to competition/parasitism [18].

Many studies have elaborated on the advantages of microalgal consortia in terms of survival, nutrient removal, and biomass production against single organisms [19][20]. In fact, microalgal consortia have recently been used to enhance organics and nutrient removal efficiency from wastewater and the enrichment of microalgal biomass for biofuel and high-value-added products. Microalgal-associated bacteria or fungi were also found to improve the sedimentation of the algae consortia, causing easier harvesting of algal biomass [9][21]. An algal–bacterial symbiosis, composed of wastewater-born filamentous blue-green algae and activated sludge (bacteria), behaved 91.0 ± 7.0% and 93.5% ± 2.5% of nitrogen and phosphorus removal efficiencies with 5:1 (microalgae/sludge) inoculation ratios within 10 days, respectively [22]. On the contrary, the nitrogen, phosphorus, and chemical oxygen demand (COD) removal with only microalgae or activated sludge were much lower than those microalgal consortia with both of them, indicating the importance of synergistic cooperation between microalgae and activated sludge. The highest sedimentation of microalgal biomass was achieved with the assistance of sludge by the 1:5 (microalgae/sludge) cultures. The immobilization of a microalgal bacterial consortium constituted by the genus of *Chlorella* sp., *Scenedesmus* sp., *Stichococcus* sp., *Phormidium* sp., and the actinobacteria *Rhodococcus* sp., *Kibdelosporangium aridum* onto various solid carriers (capron fibers for algae; ceramics, capon, and wood for bacteria) resulted in the formation of a stable consortium during the degradation of the industrial wastewater, thereby preventing them from being washed off. Additionally, this consortium exhibited effective removal efficiency of phenols, heavy metals (copper, nickel, zinc, manganese, and iron), and chemical oxygen demand [23]. The co-pellets produced by *Aspergillus fumigatus* in association with microalgae *Chlorella protothecoides* and *Tetraselmis suecica* have been used to purify anaerobically digested swine wastewater. It showed more than 73.9% and 55.6% removal efficiency of ammonia and phosphates, respectively [9]. The biomass production of both microalgal consortia yields 1.7- and 1.6-fold increases after 48 h of nutrient uptake.

Several studies have reported the oil degradation potential of microbial communities dominated by phototrophic cyanobacteria such as *Microcoleus chthonoplastes*, *Phormidium corium*, *Oscillatoria salina*, *Plectonema terebrans*, and *Aphanocapsa* sp [24][25]. A stable consortium was gained by culturing the oil-tolerant phototrophic cyanobacteria genus of *Phormidium*, *Oscillatoria*, and *Chroococcus* and the oil-degrading β-proteobacterium *Burkholderia cepacia* in bioreactors. This consortium showed several advantages, including efficient total petroleum hydrocarbon removal, no soluble carbon source requirement, and good sedimentation of biosolids [26].

2. Mechanism of Microalgal Symbiosis

2.1. Natural Microalgal Consortia Systems

In nature, most microalgae and cyanobacteria are associated with other aerobic or anaerobic microorganisms (**Table 1**). Even long-term laboratory algal cultures have shown a symbiotic relationship with bacteria [27]. The lichens, which cover more than 6% of the land surface of earth, are a stable, self-supporting, mutualistic natural symbiosis between filamentous fungi and microalgae and/or a cyanobacterium [10][28]. Generally speaking, fungi consume the sugars and nutrients produced by the photosynthetic microalgae and/or cyanobacterium; in return, fungi offer protection to microalgae via retaining water, extending a larger capture region for mineral nutrients [29]. More than one-fifth of the known fungal genus is shown to be lichenized, coexisting in a close (obligate) mutualistic association with photoautotrophic microalgae and/or cyanobacteria [29]. For example, green-algal lichen (*Trebouxia* sp., *Ramalina yasudae*) showed increased tolerance to photoinhibition under drying conditions due to the association of the photobionts with the mycobionts [30]. The detailed interaction mechanisms between fungi and microalgae remain unclear. Still, it is universally accepted that the interaction between oppositely charged surfaces may prompt microalgae to attach to the fungal cell wall [9][31].

Table 1. Some examples of microalgal consortia in nature.

Microalgal Consortia in Nature	Types of Microalgal Consortia	Refence
Lichens	Microalgae–fungi	[32]
Microalgal mats or biofilms: microalgae such as diatoms, cyanobacteria, and anoxygenic phototrophic bacteria and sulfate-reducing bacteria	Microalgae–bacteria	[33]
Algal blooms	Microalgae and microalgae–bacteria	[16][34]
Diatom *Epithemia turgida* and the coccoid cyanobacteria *Rhopalodia gibba*	Microalgae–cyanobacteria	[35]
Diatom *Hemiaulus*, *Rhizosolenia*, *Chaetoceros*, and N_2 fixing cyanobacteria *R. intracellularis* and *C. rhizosoleniae*	Microalgae–cyanobacteria	[11][36][37]

Microalgal Consortia in Nature	Types of Microalgal Consortia	Refernce
Microalgae (*Microcystis aeruginosa*., etc.) and bacteria (*E. coli*, *Pseudomonas* sp., and *Bacillus* sp., etc.): phosphorus transfer	Microalage–bacteria	[38]
Microalgae (*Stichococcus* sp., *Chlorella* sp., and *S. quadricauda*), cyanobacteria (*Phormidium* sp., and *Nostoc* sp.,), and alcanotrophic bacteria	Microalgae/Cyanobacteria–bacteria	[39]

onia, that *Calothrix rhizosoleniae* have been proven to provide nitrogen to several diatom genera with a close symbiotic association [37].

2.2. Interaction between Microalgae and Microalgal–Bacteria Consortia

Although an axenic microalgal culture can be achieved, it is impractical to maintain an aseptic microalgal culture in a large-scale culture system, especially in outdoor open ponds. Nutrient availability, cultivation conditions, and growth phase significantly affect their relationships. Microalgal biofilms, intact or attached to solid surfaces, represent micro-ecosystems with typical photosynthetic microorganisms (green microalgae, diatoms, cyanobacteria) along with some non-photosynthetic microorganisms, especially the bacteria which are almost always present and have been proven essential for microalgal biofilm formation [10][40]. Microalgal biofilms can be found in a wide range of natural environments, including estuaries, lagoons, and sheltered sandy beaches. The majority of those microalgal biofilms secrete a sticky self-produced matrix of extracellular polymeric substance (EPS) adhering to each other and/or to a surface [33]. To some extent, the EPS matrix also acts as a storage compartment for water and other chemicals and protects the cells against harmful chemicals or the environment [33].

Little attention has been paid to the consortia formed by microalgae and other microorganisms, such as other microalgae species, cyanobacteria, fungi, and yeast. Several studies showed that heterotrophic bacteria play a ubiquitous role in algal growth and survival [41][42]. Occasionally, bacteria stimulate algal growth via supplying fixed nitrogen, releasing phytohormones and exogenous sources of thiamin (vitamin B_1), cobalamin (vitamin B_{12}), biotin (vitamin B_7), and siderophores (important chelating agents for microalgal growth under iron deficiency), while microalgae may also release organic sources, such as carbohydrates, that bacteria could utilize as an energy source [7][43][44][45][46][47][48][49]. The microalga *Amphidinium operculatum* was reported to exclusively gain the vitamin cobalamin from the bacteria belonging to the genus *Halomonas* living in microalgal proximity [44]. The green alga *Chlamydomonas reinhardtii* was protected from heat stress with the presence of cobalamin-producing bacteria [46]. It has also been discovered that some genus bacteria can generate antibiotics to protect microalgae against other microorganisms (mutualism/commensalism) or for algal cell lysis (parasitism, regulation of algal blooms) [50]. In addition to direct nutrient exchange, bacteria also produce AHLs (*N*-acyl-homoserine lactones) and indole-3-acetic acid (IAA), specific chemical signals, to become involved in biofilm formation and mediate collective behaviors and ecological functions between microalgae and bacteria cells, such as environmental niche formation, nutrient absorption, and reproduction [1][51].

Interactions between microorganisms in consortia are not well understood. It is widely believed that growing microorganisms in a consortium may cause both cooperative and competitive interactions. Occasionally, some genus algicidal bacteria may generate toxic metabolites, called phycotoxins, inhibiting the growth of microalgae; in turn, some members of microalgae families (*Prasinophyceae* and *Bacillariophyceae*, *etc*) may produce exotoxins (such as various fatty acids, glycosides, chlorellin, terpenes, and chlorophyll α derivatives) to kill bacteria [52][53]. A similar situation also occurs in multiple algal composition consortia. For instance, when growing a microalgal consortium composed of *Pseudokirchneriella subcapitata* and *Chlorella vulgaris*, *P. subcapitata* was significantly inhibited by chlorellin, a fatty acid mixture excreted by the co-cultivated algae *C. vulgaris* [54]. Antagonistic interactions play an essential role in establishing and maintaining the microalgal consortia symbiosis [6].

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