ORIGINAL ARTICLE

Mechanisms of strengthening energy and mass transfer in microbial conversion of flue-gas-derived CO₂ to biodiesel and biogas fuels

Jun Cheng^{*} and Kefa Cen

Abstract

The goals of national energy security and sustainable development necessitate the role of renewable energy, of which biomass energy is an essential choice for realizing the strategic energy diversification and building a low-carbon energy system. Microbial conversion of flue-gas-derived CO₂ for producing biodiesel and biogas has been considered a significant technology in new energy development. Microalgae carbon sequestration is a hot research direction for researchers. However, three fundamental problems relating to energy/mass transfer and conversion remain as follows: (1) contradictory relationship between high resistance of cell membrane micropores and high flux of flue-gas-derived CO₂ limits mass transfer rate of CO₂ molecules across cell membrane; (2) low biocatalytic activity of intracellular enzymes with high-concentration CO₂ results in difficulties in directional carbon/hydrogen conversion; (3) competition between multiple intracellular reaction pathways and high energy barriers of target products hinder the desirable cascade energy transfer. Therefore, key scientific issues of microbial energy conversion lie in the understanding on directional carbon/hydrogen conversion and desirable cascade energy transfer. Multiple researches have established a theoretical foundation of microbial energy conversion which strengthens energy/mass transfer in microbial cells. The innovative results in previous studies have been obtained as follows: (1) Reveal mass transfer mechanism of vortex flow across cell membrane micropores. (2) Propose a strategy that directionally regulates enzyme activity. (3) Establish chain reaction pathways coupled with step changes.

Keywords: Microalgal conversion, Energy and mass transfer, Flue gas, CO₂, Biodiesel, Biogas fuels

1 Introduction

The report of 19th National Congress states that "A beautiful China needs a clean and low-carbon energy system". The goals of international energy security and sustainable development necessitate the role of renewable energy, of which biomass energy is an essential choice for realizing the strategic energy diversification. Microbial conversion of flue-gas-derived CO_2 for producing biodiesel and biogas has been considered a significant technology in many industries, such as energy conservation, environmental

* Correspondence: juncheng@zju.edu.cn

State Key Laboratory of Clean Energy Utilization, Zhejiang University, Hangzhou 310027, China

© The Author(s). 2022 **Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

protection, new energy development, and low-carbon circular economy. The *Outline of the National Program for Long- and Medium-Term Scientific and Technological Development* and the 13th Five-Year Plan For Renewable Energy Development clearly point out that it is necessary to vigorously develop new energy, such as biomass energy and hydrogen energy, to achieve the targets in which 2 million tons of biodiesel and 44 billion cubic meters of biogas should be produced by 2020. Prestigious peer-review journals such as *Nature* and *Cell* have pointed out that microbial energy is one of the hottest research frontiers. However, there are still three basic problems in energy/ mass transfer and conversion in the process of microbial

Open Access





conversion of flue-gas-derived CO2 to biodiesel and biogas fuels, the first is the mass transfer of CO₂ across cell membrane, the research of Prof. Ned Wingreen showed that the growth rate and CO_2 fixation efficiency of microalgae under air conditions were seriously limited by CO2 diffusion rate [1], Khoo et al. found that the contradictory relationship between high resistance of cell membrane micropores and high flux of flue-gas-derived CO₂ limited mass transfer rate of CO₂ molecules across cell membrane [2]. The second is the intracellular enzyme activity of microalgae. Prof. Martin jonikas has proved that the low biological catalytic activity of enzymes in cells with high concentration of CO₂ leads to the difficulty of directional carbon/hydrogen conversion [3], how to improve the activity of key enzymes is still a key problem in the process of microalgae carbon sequestration [4]. The third is problem of competitive intracellular reaction pathways. Many researchers have found that nitrogen starvation was able to promote the synthesis and accumulation of oil in microalgae cells, but reduce the photosynthetic activity of microalgae cells. There is a conflict between CO_2 fixation and lipid accumulation [5, 6]. The competition between multiple intracellular reaction pathways and high energy barriers of target products hinder the desirable cascade energy transfer. Prof. Heinz kopetz proposed that the catalytic reaction of direct conversion of carbon dioxide to lipids is the key to the production of lipids by microalgae [7]. Therefore, key scientific issues of microbial energy conversion lie in the understanding on directional carbon conversion and desirable cascade energy transfer. Facing to those key problems, multiple researcheres haveconducted a long-term research on the topic of microbial conversion of flue-gasderived CO₂ for producing biodiesel and biogas, which established a theoretical foundation of microbial energy conversion and broke the bottlenecks of strengthening energy/mass transfer in microbial cells. Through those studies, they have revealed the mass transfer mechanism of vortex flow across cell membrane micropores, proposed a strategy that directionally regulated enzyme activity, and established the chain reaction pathways coupled with step changes. Therefore, a series of innovative results through long-term research have been obtained as follows:

1. Mass transfer mechanism of vortex flow across cell membrane micropores has been revealed. It was comprehensively discussed that the scientific problem of limited mass transfer at the microporous interface of cell membrane from the perspective of photon conversion during photosynthesis [8–10]. The mechanism explained the behaviors of hydrodynamic mass transfer in terms of vortex enhanced intracellular photon transformation, and further solved the problem of low CO_2 transport rate across the micropore-interface of cell membrane.

2. A strategy that directionally regulates enzyme activity has been proposed. A scientific issue of improving biocatalytic activity from the electron transfer perspective has been issued and the approach coupling gradient flue-gas-derived CO_2 domestication with mutagenesis of enzymes to enhance electron transfer was proposed [10]. Besides, they also developed an approach to regulate active sites of CO_2 fixation enzymes, thus significantly improving the key enzyme activity [11].

3. A chain reaction pathways coupled with step changes has been established. It was identified that high energy barrier was the obstacle of cascade energy transfer, and chemical chain reaction model combining the functions of CO_2 fixation enzymes and lipid synthesis enzymes wasestablished [12]. The energy barrier step pathways of $C1 \rightarrow C6 \rightarrow C18$ chain elongation was revealed, thus developing principles of cascade energy transfer to solve trade-off relationship between CO_2 biofixation and lipid-synthesis [13, 14].

2 Research progress on strengthening energy and mass transfer in microbial conversion of flue-gasderived CO₂ to biodiesel and biogas fuels

As shown in Figs. 1, 3 main problems in microalgal research limited the CO_2 conversion to biogas and biofuels, including the mass transfer rate limitation, low biocatalytic activity of intracellular energy for directional carbon conversion and high energy barriers of target products. Therefore, we planned to make a breakthrough in 3 aspects including CO_2 transport, directional carbon conversion and lipid/gas products.

2.1 A method of high CO_2 flux using flue gas with vortex formation

In the context of the huge emissions of flue gas from coal-fired power plants and the high CO₂ content (up to 15%), fixation and conversion of flue-gas-derived CO_2 to gas and oil fuels using microalgae has been a research hotspot in the research field of energy. Wingreen et al. [1] proved that the growth rate and CO_2 fixation efficiency of microalgae under air conditions are seriously limited by CO₂ diffusion rate. Due to the complex process: (1) the low concentration (400 ppm) of CO_2 molecules (2.4 Å) must first be dissolved in water as the inorganic carbon form of HCO_3^- (3.1 Å); (2) then HCO_3^- combined with transport proteins go across cell membrane into cell; (3) finally CO_2 will be released with the catalysis of carbonic anhydrase. This theory has been widely accepted by researchers in this area, but only limited advances have been achieved in terms of improving the overall reaction rate of microalgal CO₂ fixation. In recent years, many researchers began to explore the scientific problem of limited mass transfer at the microporous interface of cell membrane from the perspective of photon conversion in photosynthetic process. Hu et al. found that making full use of microalgae flash effect, making algal cells



periodically exposed to light/dark conditions was able to effectively promote microalgae growth [15]. Due to the different types of reactors, microalgae varieties and breeding environment, there is no unified understanding of the optimal flash frequency of microalgae photosynthetic reactor, but they all agree that the flash effect can effectively improve the growth rate of microalgae [16]. Some scholars have studied the effect of flash frequency on the growth of microalgae at the millisecond level [17], however, most of these studies were carried out in the laboratory by changing the artificial light frequency or periodically shielding some reactors [18, 19]. In the natural state, realizing the millisecond flash cycle need strong mixing flow, which will greatly increase the breeding system in energy consumption. A case study on comparison of life cycle analyses of microalgal biomass production has been reported by Prof. Jorquera [20]. The authors have reported the net energy ratio (NER) for both the processes for microalgae production, e.g. tubular and flat bed reactors as well as raceway ponds. The NER of a system has been defined as the ratio of the total energy produced (energy content of the oil and residual biomass) over the energy content of photobioreactor construction and material plus the energy required for all plant operations: NER = NetEnergyRatio = Σ Energyproduced(lipidorbiomass) Σ Energyrequirements. The results indicate that the use of horizontal tubular photobioreactors (PBRs) is not economically feasible due to negative NER values. The NER values for flat bed PBRs and raceway ponds are found to be positive. The research of Dasan et al. [21] shows that at present, the dehydration and oil extraction of microalgae biomass require high energy input, accounting for nearly 21% - 30% and 39% - 57% of the total energy demand respectively. The research of Morweiser et al. [22] shows that in terms of energy efficiency, the best reactor (such as different 'water bed' designs) has now entered the range of 50% auxiliary energy demand related to the collected solar energy (or 2 w/m² and 0.04 m³/m²) by reducing the auxiliary energy to 50 w/m^3 .

Therefore, more advanced photobioreactors and lowcost downstream processing technologies were sought to achieve a more feasible microalgae biofuels production system [23]. Based on continuous illumination conditions, the photosynthetic reactor with second flash cycles through turbulence to enhance the turbulent flow of culture medium is more suitable for industrial scale aquaculture. Zhang et al. [24] developed a spiral static mixer, which accelerated the mixing and light dark cycle of the column photoreactor, thereby increasing the biomass yield by 37.26%. Chen et al. [25] introduced six half moon blade static mixers into the column photoreactor and found that the mixer improved the turbulent kinetic energy and light dark cycle frequency. Zhao et al. [26] proposed a multi-scale bubble combined inlet method to strengthen the multiphase mixing and mass transfer process of Chlorella by using millimeter bubbles with strong turbulence characteristics. With large contact area and long residence time, microbubbles can significantly improve the gas retention rate, light utilization efficiency and growth rate of small particle microalgae in microalgae photosynthetic reactor. Ye et al. [8] used the nozzle to generate vortex to enhance the photochemical efficiency of microalgae photosynthetic column reactor. However, due to the small vortex radius and mainly concentrated at the bottom of the reactor, most areas in the upper part of the reactor are little affected by the vortex.

The photobioreactor designed by Prof. Cheng of Zhejiang University based on the theory of hydrodynamics produced alternating clockwise and counterclockwise vortex flow fields, strengthened the flash effect of rapid flow of algae cells in light and dark areas (Fig. 2), increased the gas-liquid two-phase mass transfer coefficient by 25%, and increased the biomass yield by 32.6% [9]. Aiming at the new problems about flow and mass transfer with microbial photosynthesis, they revealed the phenomenon that vortex strengthens the photosynthesis process of microalgal cells [27]. Prof. Dubinsky evaluated that "the novel system" proposed in this research "sequentially generate clockwise and anticlockwise liquid vortexes", "increased the mass transfer coefficient", and "enhanced flashing-light effect" [16]. Professor Simon Judd evaluated this finding and believed that 'HD removal rate was achievable' [28]. Professor Cheng Jun's team of Zhejiang University proposed to use a groundbreaking mechanism of " flashing light effect of vortex flow", which advanced the conventional understanding on transmembrane transport of CO₂ molecules with HCO₃⁻ as the intermediate, so as to reveal the hydrodynamic mass transfer mechanism of vortex, thereby enhancing intracellular photon conversion efficiency [10].

2.2 A flue-gas-derived CO₂ domestication strategy that directionally regulates enzyme activity

The CO_2 concentration of 15% in flue gas from coalfired power plant is about 300 times the atmospheric CO_2 concentration. Although high CO_2 concentration from flue gas improves diffusion and transfer of CO_2 molecules across cell membrane of microalgae, the biological catalytic activity of key CO_2 fixation enzymes in original microalgal cells is severely suppressed under such a high CO_2 concentration condition. Thus, how to efficiently improve the activity of key CO_2 fixation enzymes in microalgal cells is an international research hotspot. Martin Jonikas [3] proved in that traditional biological enzymes have low catalytic activity in the process of microbial energy conversion, resulting in difficulties in directional carbon/hydrogen conversion. Therefore, how to improve the activity of key enzymes



from the perspective of quality/energy transfer of basic reactions in multiple cells is still a bottleneck in the process of microbial biomass hydrogen production. Xu et al. [29] established a model to help understand the changes of cell fluid flux, volume and media molar concentration caused by osmotic pressure. Assuming that cells were submerged in the CPAs, the water flux across the cell membrane (Jw) was given as.

$$J_{W} = L_{p} \triangle P - L_{p} \sigma_{s} R T^{\Delta} c,$$

$$P^{i} - P^{e} = E \frac{V - V_{0}}{V_{0}} + P_{0}^{i} - P_{0}^{e}$$

$$\frac{dV_{w}}{dt} = J_{w} A$$

where L_p (m³ N⁻¹ s⁻¹) indicated the membrane hydraulic conductivity; σ_s was the membrane reflection coefficient of media; R (J mol⁻¹ K⁻¹) was the universal gas constant; T (K) was the temperature; c (M) was the concentration of media; A (m²) was the cell surface area; E (Pa) was the cellular elastic modulus; and V_w (m³) was the water volume of cells. In addition, superscripts i and e in the above equations denoted the intracellular and extracellular regions, respectively. Next, the media flux (J_c) was expressed as

$$J_c = (1 - \sigma_s) c_{up} J_w + \omega RT \Delta c$$
$$\frac{dV_c}{dt} = J_c A$$

where $\omega \pmod{N^{-1} s^{-1}}$ and $\exp(M)$ were the membrane permeability of media and the upstream concentration of media, respectively. Huang et al. [14] found that when a higher concentration of CO₂ was continuously injected into the aqueous solution for microalgae growth, the dissolved CO₂ concentration in the solution increased significantly. Transcriptome sequencing showed that carbonic anhydrase was almost not expressed at this time, indicating that CO₂ directly penetrated into microalgae cells by osmotic pressure to participate in Calvin cycle reaction. This process reduces the active transport of HCO3⁻, saves more energy and improves the efficiency of photosynthesis. The results showed that the cultivation of microalgae with high concentration of CO₂ was able to promote the growth, carbon sequestration rate and biomass yield of microalgae [30].

Hussain et al. [31] found that the two microalgae plants growth was slow under high CO_2 concentration (20% CO_2). However, in step wise CO_2 feeding, the growth of microalgae improved considerably and up to 0.9 and 0.97 (g/L) biomasses were recorded, respectively. According to the professor Ghosh's research results, *Scenedesmus* sp. could effectively exploit high CO_2 concentration (15%) for longer duration under high concentration of glucose supplementation (9 g/L) producing a biomass of 635.24 $+/-39.9 \ \mu g \ /mL$ with a high total fatty acid methyl ester (FAME) content of 71.29 +/- 4.2 μ g /mg [32]. Yun et al. [33] during the growth of *Chlorella vulgaris*, the CO_2 concentration in the gas gradually increased from 5% to 30% with the culture time (about every 43 h, the CO₂ concentration increased by 5% or 10%), and the maximum CO₂ fixation rate was 0.936 g / (L•D). Fulke et al. [34] in India screened a strain of Chlorella sp. from carbonate rich areas. After domestication with low carbon source and high temperature culture, the obtained Chlorella sp. can withstand 15% CO₂ environment. Although some articles believe that overexpression of C4 gene in C3 plants cannot significantly improve the photosynthetic capacity of plants [35]. The research of Liu et al. [36] proposed that carbon fixation is carried out through the combination of C3 and C4 pathways and carbonic anhydrase, and the enhancement of C4 pathway by high CO₂ concentration may provide a variety of carbon fixation pathways for C3 microalgae and finally improve its CO₂ fixation capacity. Anjos et al. found that CO_2 with volume fraction of 6% is most suitable for microalgae growth, but the volume fraction of CO_2 in power plant flue gas is about $12\% \sim 15\%$. Through nuclear mutation, screening and domestication, cultivate algae species resistant to high volume fraction CO_2 and apply it directly to industrial aquaculture [37]. Nuclear mutagenesis induces recombination and improvement of key genes relating to CO2 fixation enzymes and lipid synthesis enzymes in microalgae cells, thus significantly enhancing the activities of CO₂ fixation enzymes (e.g., photosynthetic pigment enzymes, ATP synthase, etc) and lipid synthesis enzymes (e.g., acetyl-CoA carboxylase and glycerol transferase) (as shown in Fig. 3). Vigeolas et al. [38] mutated Chlorella sorokiniana by ultraviolet radiation, screened 2000 single plants after mutation by Nile red fluorescence method, and successfully selected 4 Chlorella mutants with increased oil content. Tanadul et al. mutated Chlorella sp. by EMS, and the mutant obtained has higher biomass yield and oil yield [39].

Prof. Cheng Jun of Zhejiang University proposed a mutagenesis method that uses nuclear radiation to modify the genes relating to key enzymes for catalytic activity enhancement, thus promoting the energy and mass transfer with internal and external collaboration during electron transfer between key enzymes [11]. The research results of Prof. Cheng's research group showed that the photosynthetic pigment enzymes and ATP synthase of the nuclear mutagenized strain increased by 6.8 times and 8.0 times, respectively, as compared to the conventional microalgal strains for CO_2 fixation, thus simultaneously increasing the growth, CO_2 fixation, and lipid accumulation rates of microalgal cells [12]. A 15fold activity up-regulation of key CO_2 domestication was



recorded [40]. This approach significantly improved the key enzyme activity and selectively enabled the promotion of elementary reactions of CO_2 fixation towards efficient C3 pathway rather than inefficient C4 pathway, thus addressing the issue of low catalytic activity of conventional biological enzymes. Ren et al. [41] evaluated these studies and considered that a major breakthrough had been made in the transformation of microalgae strains to produce carbon dioxide and lipids by nuclear mutagenesis. Sachs and others can directionally promote lipid synthesis in microalgae cells by studying gene mutation to enhance the activity of lipid synthase [42].

2.3 Established chain reaction pathways coupling the reaction energy barrier step with chemical chain of enzymes to regulate competitive reaction pathways for biodiesel and biogas production

The ability of microalgae to fix CO₂ and accumulate lipids depends on the growth rate and lipids content in microalgal cells. Because the energy density of lipids is twice as much as those of proteins and carbohydrates, the high energy barrier of direct conversion from CO_2 to lipid causes low reaction rate. The research of Heinz Kopetz showd that the catalytic reactions of direct conversion from CO₂ to lipids was key to lipid production in microalgae [7]. However, there is a conflict between microalgal CO₂ fixation and lipid accumulation. Most microalgal species start to accumulate significant amounts of lipid under stress or unfavorable growth conditions [5]. Seo et al. [6] found that the lack of nitrogen salt in the solution would promote the synthesis and accumulation of oil in microalgae cells. However, nitrogen starvation significantly reduced the photosynthetic activities of algal cells and thus the overall productivity of algal biomass. Also, at the industrial level, nitrogen removal is time-consuming and costly [5]. Therefore, researchers seeking a versatile alternative method for practical induction of lipid accumulation remain active in the field of microalgal biotechnology [43]. Srivastava and Goud [44] investigated the effects of various salt stresses (NaCl, KCl, MgCl₂ and CaCl₂) on lipid accumulation in both Chlorella. sorokiniana CG12 and Desmodesmus GS12 strains, and obtained significant enhancements of lipid contents, up to 40-45% (w/w) under optimal CaCl₂ conditions. Kang et al. [45] investigated the usefulness of oxidative stress by TiO₂ nanoparticles, a well-known photocatalyst, to the induction of lipid accumulation in Chlorella Vulgaris UTEX 265. They observed a slight increase of Chlorella vulgaris under TiO2/UV-A conditions, though a high dosage of TiO_2 (0.1 g/L) and 2-day incubation were required. Praveenkumar et al. [46] reported a new pressure-based stress method for induction of neutral lipid (e.g. TAG) of *Chlorella* spp. by 2 h treatment under mild pressurization conditions (10-15 bar). Compared with the untreated control, this method produced a 55% improvement.

 CO_2 is the only carbon source for photosynthetic autotrophic microalgae. When CO₂ concentration increases, the content of fatty acids in microalgae will increase, and the content of polyunsaturated fatty acids in eukaryotic algae cells will decrease. This is because the increase of CO_2 concentration will cause the excess of carbon source, which will cause the relative lack of nitrogen and phosphorus nutrients, thus affecting the synthesis of enzymes related to extension reaction and desaturation reaction. Cheng et al. found that the content of oil in a single cell increases when nitrogen and phosphorus are deficient, and the decrease of nitrogen and phosphorus nutrient content in the solution would affect the synthesis of enzymes related to prolongation reaction and desaturation reaction, and finally reduce the content of polyunsaturated fatty acids in the oil components of microalgae cells [12]. Yu et al. [47] evaluated the effect of plant hormone Gibberellin on the accumulation of lipid and docosahexaenoic acid (DHA) accumulation in Aurantiochytrium sp. YLH70. Metabolic

								[-
Table	1	Comparison	of	different	t induction	methods to	promote microbial	production of	biodiesel and biogas fuel	

Microalgal species	Induction method	Effects	Refs.
Green microalga Acutodesmus dimorphus	Nitrogen starvation	Promoted the biosynthesis of abscisic acid (ABA) and indole-3 acetic acid (IAA)	Chokshi et al. [51] (2017)
Chlorella spp.	Very short time mild pressure induction (10–15 bar).	The increase of cytoplasmic tag particles and rapid lipid remodeling/transformation	Praveenkumar et al. [46] (2016)
Chlorella sorokiniana CG12 and Desmodesmus GS12	Salt stresses (NaCl, KCl, MgCl ₂ 和 CaCl ₂)	Increased lipid content, up to 40–45% (w/w)	Srivastava et al. [44] (2017)
Scenedesmus sp. LX1	Two auxins (indole-3-acetic acid (IAA) and 2,4-dichlorophenoxyacetic acid (2,4-D)	Enhanced microalgal growth and FAMEs accumulation	Dao et al. [52] (2018)
Haematococcus pluvialis	Butylated hydroxytoluene (BHT), high-light and nitrogen-deficiency conditions	The astaxanthin and lipid contents of <i>H. pluvialis</i> were increased by 71.13% and 10.71%	Zhao et al. [53] (2018)
Aurantiochytrium sp. YLH70.	Phytohormone gibberellin	Metabolites in fatty acid biosynthesis and mevalonate pathway increased, metabolites in glycolysis and TCA cycle decreased	Yu et al. [47] (2016)



pathway analysis showed that gibberellin accelerated the rate of utilization of glucose, and metabolites in fatty acids biosynthesis and mevalonate pathway were increased, while metabolites in glycolysis and TCA cycle were decreased in Aurantiochytrium sp. YLH70. Costa and Ge et al. also found that high concentration of CO_2 is conducive to the synthesis of fatty acids in grape brown algae 765 and other algae species, and also inhibits the extension reaction and desaturation reaction of carbon chain [48, 49]. The results of Tang et al. Showed that both Scenedesmus obliquus sjtu-3 and Chlorella pyrenoidosa sjtu-2 grew fastest at 10% CO₂ concentration, while the oil content continued to increase when the CO₂ concentration increased to 30-50% [50]. Table 1 summarizes the different induction methods for promoting microbial production of biodiesel and biogas fuel, and compares the induction effects.

The novel chain reaction pathways coupled with biocatalyst in microalgae are capable of reducing the energy barrier during direct conversion of CO₂ to lipids. Prof. Cheng Jun of Zhejiang University analyzed CO₂ fixation and lipid accumulation in microalgal cells from the view of energy barrier in intracellular REDOX reactions. Prof. Cheng established the chemical chain reaction model combining the functions of CO₂ fixation enzymes and lipid synthesis enzymes, and broke the bottleneck of high energy barrier in the direct conversion of small molecular CO_2 to high molecular lipids [13]. This leads to the development of the chemical chain reaction model $(CO_2 + C5 \rightarrow 2C3\uparrow \rightarrow C_6H_{12}O_6 \rightarrow (RCOO)_2C_3H_6O\uparrow \rightarrow (RCOO)_2C_3H_6O\land \rightarrow (RCOO)_2O\land \rightarrow (RC$ $RCOO_{3}C_{3}H_{5}\uparrow$), which combines the functions of CO_{2} fixation enzymes and lipid synthesis enzymes. The model reveals the energy barrier step pathways of cell REDOX reactions, including the pathways of $C1 \rightarrow$ $C6 \rightarrow C18$ chain elongation (Fig. 4). The research regulated the multiple intracellular competitive reactions of lipid synthesis, leading to the establishment of general principles for cascade energy transfer [12, 14].

3 Conclusion

Through the research on the microbial conversion of flue gas CO_2 into biodiesel and biogas, the mass transfer mechanism of vortex flow across cell membrane micropores was revealed, a strategy that directionally regulates enzyme activity was proposed, and the chain reaction pathways coupled with step changes was established. Those researches have served as the theoretical foundation for strengthening energy and mass transfer in microbial conversion of flue-gas-derived CO_2 into oil and gas fuels, driven forward the development of engineering thermophysics, and made significant contributions to the development of biomass energy industry and the establishment of clean and low-carbon energy system.

Abbreviations

acetyl-CoA: Acetoacetyl coenzyme A; ATP: Adenosine triphosphate; C3: A CO₂ fixation pathway that CO₂ is directly fixed by five carbon compounds in Calvin cycle, and the initial product is three carbon compounds; C4: In addition to the Calvin cycle, CO₂ combines with phosphoenolpyruvate in the dark reaction of photosynthesis, with oxaloacetic acid as the initial product; C₆H₁₂O₆: Glucose; CH₃CH₂CH₂COOH: n-butyric acid; CH₃CH₂OH: Ethyl alcohol; CH₃COOH: Acetic acid; CO₂: Carbon dioxide; H₂: Hydrogen; HCO₃⁻⁻: Bicarbonate; IF: Impact Factor; SCI: Science Citation Index; TAG: Triglyceride

Acknowledgements

This research was supported by National key research and development program-China (2016YFB0601000) and National Key Research and Development Program-China (2017YFE0122800).

Code availability

Not applicable.

Authors' contributions

JC carried out conceptualization, methodology, formal analysis, writing and visualization. KC carried out conceptualization, writing - review & editing and supervision. The authors read and approved the final manuscript.

Funding

This research was supported by National key research and development program-China (2016YFB0601000) and National Key Research and Development Program-China (2017YFE0122800).

Availability of data and materials

Not applicable.

Declarations

Ethics approval and consent to participate Not applicable.

Consent for publication

We give our consent for information mentioned in this manuscript to be published in Carbon Neutrality. We have been offered the opportunity to read the article.

This consent form will be submitted with the article and will be treated confidentially.

Competing interests

There is no conflict of interest.

Received: 12 October 2021 Accepted: 9 February 2022 Published online: 19 April 2022

References

- Freeman Rosenzweig ES, Xu B, Kuhn Cuellar L et al (2017) The eukaryotic CO2-concentrating organelle is liquid-like and exhibits dynamic reorganization. Cell 171(1):148–162.e19
- Khoo CG, Lam MK, Lee KT (2016) Pilot-scale semi-continuous cultivation of microalgae Chlorella vulgaris in bubble column photobioreactor (BC-PBR): hydrodynamics and gas-liquid mass transfer study. Algal Res 15:65–76. https://doi.org/10.1016/j.algal.2016.02.001
- Mackinder LCM, Chen C, Leib RD et al (2017) A spatial interactome reveals the protein organization of the algal CO2-concentrating mechanism. Cell 171(1):133-+
- Kassim MA, Adnan MFIM, Tan KM et al (2020) Carbonic anhydrase (CA) activity byChlorella sp. in immobilised matrix under carbon dioxide rich cultivation condition. IOP Conf Ser Mater Sci Eng 716:012015
- Kim H, An J, Lee Y et al (2015) Overexpression, purification, crystallization and preliminary X-ray crystallographic analysis of SF173 from Shigella flexneri. Acta Crystallogr F 71(1):54–56. https://doi.org/10.1107/S2053230X14 025941
- Seo JY, Jeon H, Kim JW et al (2018) Simulated-sunlight-driven cell lysis of magnetophoretically separated microalgae using ZnFe2O4 octahedrons. Ind Eng Chem Res 57(5):1655–1661

- Kopetz H (2013) Build a biomass energy market. Nature. 494(7435):29–31. https://doi.org/10.1038/494029a
- Ye Q, Cheng J, Lai X, An Y, Chu F, Zhou J, Cen K (2019) Promoting photochemical efficiency of chlorella PY-ZU1 with enhanced velocity field and turbulent kinetics in a novel tangential spiral-flow column photobioreactor. ACS Sustain Chem Eng 7(1):384–393. https://doi.org/10.1 021/acssuschemeng.8b03718
- Cheng J, Yang Z, Ye Q, Zhou J, Cen K (2015) Enhanced flashing light effect with up- down chute baffles to improve microalgal growth in a raceway pond. Bioresour Technol 190:29–35. https://doi.org/10.1016/j.biortech.2015. 04.050
- Ye Q, Cheng J, Yang Z, Yang W, Zhou J, Cen K (2018) Improving microalgal growth by strengthening the flashing light effect simulated with computational fluid dynamics in a panel bioreactor with horizontal baffles. RSC Adv 8(34):18828–18836. https://doi.org/10.1039/C8RA02863J
- Cheng J, Lu H, He X, Yang W, Zhou J, Cen K (2017) Mutation of Spirulina sp by nuclear irradiation to improve growth rate under 15% carbon dioxide in flue gas. Bioresour Technol 238:650–656. https://doi.org/10.1016/j.biortech.2 017.04.107
- Cheng J, Lu H, Huang Y, Li K, Huang R, Zhou J, Cen K (2016) Enhancing growth rate and lipid yield of Chlorella with nuclear irradiation under high salt and CO2 stress. Bioresour Technol 203:220–227. https://doi.org/10.1016/ j.biortech.2015.12.032
- Huang Y, Cheng J, Lu H, Huang R, Zhou J, Cen K (2015) Simultaneous enhancement of microalgae biomass growth and lipid accumulation under continuous aeration with 15% CO2. RSC Adv 5(63):50851–50858. https://doi. org/10.1039/C5RA08401F
- Huang Y, Cheng J, Lu H et al (2017) Transcriptome and key genes expression related to carbon fixation pathways in Chlorella PY-ZU1 cells and their growth under high concentrations of CO2. Biotechnol Biofuels 10:181
- Hu J, Sato T (2017) A photobioreactor for microalgae cultivation with internal illumination considering flashing light effect and optimized lightsource arrangement. Energ Convers Manage 133:558–565
- Abu-Ghosh S, Fixler D, Dubinsky Z, Iluz D (2016) Flashing light in microalgae biotechnology. Bioresour Technol 203:357–363. https://doi.org/10.1016/j. biortech.2015.12.057
- Iluz D, Abu-Ghosh S (2016) A novel photobioreactor creating fluctuating light from solar energy for a higher light-to-biomass conversion efficiency. Energ Convers Manage 126:767–773
- Lima S, Villanova V, Grisafi F, Brucato A, Scargiali F (2020) Combined effect of nutrient and flashing light frequency for a biochemical composition shift in Nannochloropsis gaditana grown in a quasi-isoactinic reactor. Can J Chem Eng 98(9):1944–1954. https://doi.org/10.1002/cjce.23776
- Abu-Ghosh S, Fixler D, Dubinsky Z, Iluz D (2015) Continuous background light significantly increases flashing-light enhancement of photosynthesis and growth of microalgae. Bioresour Technol 187:144–148. https://doi.org/1 0.1016/j.biortech.2015.03.119
- Jorquera O, Kiperstok A, Sales EA, Embiruçu M, Ghirardi ML (2010) Comparative energy life-cycle analyses of microalgal biomass production in open ponds and photobioreactors. Bioresour Technol 101(4):1406–1413. https://doi.org/10.1016/j.biortech.2009.09.038
- Dasan YK, Lam MK, Yusup S, Lim JW, Lee KT (2019) Life cycle evaluation of microalgae biofuels production: effect of cultivation system on energy, carbon emission and cost balance analysis. Sci Total Environ 688:112–128. https://doi.org/10.1016/j.scitotenv.2019.06.181
- Morweiser M, Kruse O, Hankamer B, Posten C (2010) Developments and perspectives of photobioreactors for biofuel production. Appl Microbiol Biot 87(4):1291–1301. https://doi.org/10.1007/s00253-010-2697-x
- Medipally SR, Yusoff FM, Banerjee S et al (2015) Microalgae as sustainable renewable energy feedstock for biofuel production. Biomed Res Int 2015;519513
- Zhang Q, Wu X, Xue S, Liang K, Cong W (2013) Study of hydrodynamic characteristics in tubular photobioreactors. Bioprocess Biosyst Eng 36(2): 143–150. https://doi.org/10.1007/s00449-012-0769-2
- Cheng W, Huang J, Chen J (2016) Computational fluid dynamics simulation of mixing characteristics and light regime in tubular photobioreactors with novel static mixers. J Chem Technol Biot 91(2):327–335. https://doi.org/10.1 002/jctb.4560
- Zhao L, Lv M, Tang Z, Tang T, Shan Y, Pan Z, Sun Y (2018) Enhanced photo bio-reaction by multiscale bubbles. Chem Eng J 354:304–313. https://doi. org/10.1016/j.cej.2018.06.019

- Cheng J, Zhou JH, Liu JZ, Zhou Z, Huang Z, Cao X, Zhao X, Cen K (2003) Sulfur removal at high temperature during coal combustion in furnaces: a review. Prog Energ Combust 29(5):381–405. https://doi.org/10.1016/S03 60-1285(03)00030-3
- Judd S, van den Broeke LJP, Shurair M, Kuti Y, Znad H (2015) Algal remediation of CO2 and nutrient discharges: a review. Water Res 87:356– 366. https://doi.org/10.1016/j.watres.2015.08.021
- Xu F, Moon S, Zhang X et al (2010) Multi-scale heat and mass transfer modelling of cell and tissue cryopreservation. Philos T R Soc A 368(1912): 561–583
- 30. Lam MK, Lee KT, Mohamed AR (2012) Current status and challenges on microalgae-based carbon capture. Int J Greenh Gas Con 10:456–469. https://doi.org/10.1016/j.ijggc.2012.07.010
- Hussain F, Shah SZ, Zhou W, Iqbal M (2017) Microalgae screening under CO2 stress: growth and micro-nutrients removal efficiency. J Photoch Photobio B 170:91–98. https://doi.org/10.1016/j.jphotobiol.201 7.03.021
- Ghosh A, Samadhiya K, Kiran B (2022) Multi-objective tailored optimization deciphering carbon partitioning and metabolomic tuning in response to elevated CO2 levels, organic carbon and sparging period. Environ Res 204(B):112137. https://doi.org/10.1016/j.envres.2021.112137
- Kao C, Chiu S, Huang T et al (2012) A mutant strain of microalga Chlorella sp for the carbon dioxide capture from biogas. Biomass Bioenergy 36:132– 140. https://doi.org/10.1016/j.biombioe.2011.10.046
- Fulke AB, Mudliar SN, Yadav R et al (2010) Bio-mitigation of CO2, calcite formation and simultaneous biodiesel precursors production using Chlorella sp. Bioresource Technol 101(21):8473–8476
- Senda T, Yamada T, Sakurai N, Kubota M, Nishizaki T, Masai E, Fukuda M, Mitsui Y (2000) Crystal structure of NADH-dependent ferredoxin reductase component in biphenyl dioxygenase. J Mol Biol 304(3):397–410. https://doi. org/10.1006/jmbi.2000.4200
- Liu D, Ma Q, Valiela I, Anderson DM, Keesing JK, Gao K, Zhen Y, Sun X, Wang Y (2020) Role of C-4 carbon fixation in Ulva prolifera, the macroalga responsible for the world's largest green tides. Commun Biol 3(1):494. https://doi.org/10.1038/s42003-020-01225-4
- Anjos M, Fernandes BD, Vicente AA, Teixeira JA, Dragone G (2013) Optimization of CO2 bio-mitigation by Chlorella vulgaris. Bioresour Technol 139:149–154. https://doi.org/10.1016/j.biortech.2013.04.032
- Vigeolas H, Duby F, Kaymak E et al (2012) Isolation and partial characterization of mutants with elevated lipid content in Chlorella sorokiniana and Scenedesmus obliquus. J Biotechnol 162(15l):3–12
- Tanadul O, Noochanong W, Jirakranwong P et al (2018) EMS-induced mutation followed by quizalofop-screening increased lipid productivity in Chlorella sp. Bioproc Biosyst Eng 41(5):613–619
- Cheng J, Yang Z, Huang Y, Huang L, Hu L, Xu D, Zhou J, Cen K (2015) Improving growth rate of microalgae in a 1191 m(2) raceway pond to fix CO2 from flue gas in a coal-fired power plant. Bioresour Technol 190:235– 241. https://doi.org/10.1016/j.biortech.2015.04.085
- Liu B, Ma C, Xiao R, Xing D, Ren H, Ren N (2015) The screening of microalgae mutant strain Scenedesmus sp. Z-4 with a rich lipid content obtained by 60Co γ-ray mutation. RSC Adv 5(5):52057–52061. https://doi. org/10.1039/C5RA07263H
- Sachs JP, Maloney AE, Gregersen J, Paschall C (2016) Effect of salinity on H-2/H-1 fractionation in lipids from continuous cultures of the coccolithophorid Emiliania huxleyi. Geochim Cosmochim Ac 189:96–109. https://doi.org/10.1016/j.gca.2016.05.041
- Church J, Hwang J, Kim K et al (2017) Effect of salt type and concentration on the growth and lipid content of Chlorella vulgaris in synthetic saline wastewater for biofuel production. Bioresour Technol 243:147–153. https://doi.org/10.1016/j.biortech.2017.06.081
- Srivastava G, Nishchal GVV (2017) Salinity induced lipid production in microalgae and cluster analysis (ICCB 16-BR_047). Bioresource Technol 242(SI):244–252
- Kang NK, Lee B, Choi G et al (2014) Enhancing lipid productivity of Chlorella vulgaris using oxidative stress by TiO2 nanoparticles. Korean J Chem Eng 31(5):861–867. https://doi.org/10.1007/s11814-013-0258-6
- Praveenkumar R, Kim B, Lee J, Vijayan D, Lee K, Nam B, Jeon SG, Kim DM, Oh YK (2016) Mild pressure induces rapid accumulation of neutral lipid (triacylglycerol) in Chlorella spp. Bioresour Technol 220:661–665. https://doi. org/10.1016/j.biortech.2016.09.025

- Yu X, Sun J, Sun Y et al (2016) Metabolomics analysis of phytohormone gibberellin improving lipid and DHA accumulation in Aurantiochytrium sp. Biochem Eng J 112:258–268. https://doi.org/10.1016/j.bej.2016.05.002
- Vieira Costa JA, de Morais MG(2011) The role of biochemical engineering in the production of biofuels from microalgae. Bioresource Technol. 102(1SI):2-9
- Ge Y, Liu J, Tian G (2011) Growth characteristics of Botryococcus braunii 765 under high CO2 concentration in photobioreactor. Bioresource Technol 102(1SI):130–134
- Tang D, Han W, Li P et al (2011) CO2 biofixation and fatty acid composition of Scenedesmus obliquus and Chlorella pyrenoidosa in response to different CO2 levels. Bioresource Technol 102(3):3071–3076
- Chokshi K, Pancha I, Ghosh A, Mishra S (2017) Nitrogen starvation-induced cellular crosstalk of ROS-scavenging antioxidants and phytohormone enhanced the biofuel potential of green microalga Acutodesmus dimorphus. Biotechnol Biofuels 10(1):10. https://doi.org/10.1186/s13068-017-0747-7
- Dao G, Wu G, Wang X et al (2018) Enhanced growth and fatty acid accumulation of microalgae Scenedesmus sp LX1 by two types of auxin. Bioresour Technol 247:561–567. https://doi.org/10.1016/j.biortech.2017.09.079
- Zhao Y, Yue C, Ding W, Li T, Xu JW, Zhao P, Ma H, Yu X (2018) Butylated hydroxytoluene induces astaxanthin and lipid production in Haematococcus pluvialis under high-light and nitrogen-deficiency conditions. Bioresour Technol 266:315–321. https://doi.org/10.1016/j. biortech.2018.06.111

Publisher's Note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.