Photosynthetic Synthetic Biology: Current Status and Future Development Strategies Postprint

Authors: Zhu Xinguang, Xiong Yan, Ruan Meihua, Liu Xiao, Xu Jian, Zhong Chao

Date: 2023-03-19T00:00:00+00:00

Abstract

First, the current research status of photosynthesis both internationally and domestically is introduced, followed by a brief overview of photosynthetic synthetic biology as an emerging discipline, its principal research scope, and recent advances. It is proposed that China's research in photosynthetic synthetic biology currently faces needs to enhance its systematic nature, more closely integrate with practical demands, and increase support. Given the strategic importance of photosynthesis for future food security, energy security, and sustainable ecological maintenance, its future development should focus on research directions including optimization of existing photosynthetic systems, coordination between photosynthetic systems and photosynthate utilization pathways, interspecies reconstruction of photosynthetic systems, construction of novel photosynthetic pathways, and coupling of photosynthetic systems with biomaterials.

Full Text

Research Status and Future Development Strategies of Synthetic Biology in Photosynthesis

ZHU Xinguang[1]*, XIONG Yan[2], RUAN Meihua[2], LIU Xiao[2], XU Jian[3], ZHONG Chao[4]

[1]CAS Center for Excellence in Molecular Plant Sciences, National Key Laboratory of Plant Molecular Genetics, Institute of Plant Physiology and Ecology, Chinese Academy of Sciences, Shanghai 200032, China
[2]Shanghai Institute of Nutrition and Health, Shanghai Institutes for Biological Sciences, Chinese Academy of Sciences, Shanghai 200031, China
[3]Qingdao Institute of Bioenergy and Bioprocess Technology, Chinese Academy of Sciences, Qingdao 266101, China
[4]ShanghaiTech University, Shanghai 201210, China

*Corresponding author

Abstract

This perspective first introduces the current status of photosynthesis research internationally and domestically, followed by a brief overview of the major research scope and progress of photosynthesis synthetic biology as an emerging discipline. We identify that photosynthesis synthetic biology research in China currently faces challenges including fragmented research efforts, weak integration with practical applications, and insufficient funding support. Given the strategic importance of photosynthesis for future global food security, energy security, and sustainable ecological environment maintenance, future development should focus on five key research directions: optimization of existing photosynthetic systems, coordination between photosystems and photosynthate utilization pathways, cross-species reconstruction of photosynthetic systems, construction of novel photosynthetic pathways, and coupling of photosynthetic systems with biomaterials. To effectively promote photosynthesis synthetic biology research, we propose establishing a series of technical platforms, theoretical frameworks, and supporting policies.

Keywords: photosynthesis, breeding, energy security, synthetic biology, environment, food security

---

1. Current Status of Photosynthesis Synthetic Biology Research in China and Internationally

Photosynthesis is a biophysical and biochemical process in which plants utilize solar energy to synthesize carbohydrates from CO_2 and water. This process provides food and energy for humanity while serving as a critical component of Earth's ecosystem carbon and water cycles. The fundamental importance of photosynthesis to human society has positioned its research and application at the forefront of humanity's exploration and transformation of nature. Currently, rapid developments in genomics, genome editing and synthesis technologies, and computational capabilities are fostering a new synthetic biology research paradigm. On one hand, this enables the design and construction of novel metabolic, structural, and regulatory patterns to create new biological functions; on the other hand, it provides new research materials and perspectives for fundamental life science research, thereby testing current biological theories and hypotheses. Within this multidisciplinary context, photosynthesis synthetic biology has emerged as a distinct field. Its essence lies in applying fundamental photosynthesis principles, integrating multidisciplinary theories and technical methods, and employing theoretical design, engineering modification, and artificial evolution to create novel photosynthetic systems that can provide better supplies of food, energy, and ecosystem services for society, while offering new materials and resources for photosynthesis research and enhancing humanity's capacity to understand and utilize photosynthesis.

Historically, China has made significant contributions to fundamental photosynthesis research. As early as the 1960s–1970s, Chinese scientists conducted concentrated studies on the mechanism of photosynthetic phosphorylation, proposing that high-energy states are required during ATP synthesis and supporting the electrochemical potential gradient theory of ATP synthesis [1]. Concurrently, Yin Hongzhang and colleagues at the Institute of Plant Physiology, Chinese Academy of Sciences, recognized in the 1960s that canopy photosynthetic efficiency makes major contributions to crop yield and systematically initiated quantitative research on this topic. In recent years, China has achieved substantial progress in photosynthetic reaction center pigment-protein complex structure and function [2–4], C_4 photosynthesis [5,6], Rubisco structure and function [7], and photosystem regulation and assembly [8,9]. However, overall, China's photosynthesis research still lags behind the United States in both scale and level. A statistical analysis of SCI papers on photosynthesis-related research from 1997–2017 reveals that the United States leads the world in both quantity and quality: its 10-year publication count reached 22,312, accounting for 26.04% of the global total; its ESI highly-cited papers numbered 521, representing 43.38% of the 1,201 highly-cited papers worldwide; and its publications in Nature, Science, and Cell (CNS) totaled 247, comprising 61.29% of all CNS papers (403) in the field. While China's patent applications in photosynthesis (12,102) surpassed the United States (4,288) during 1997–2017, ranking first globally, the number of high-strength patents (score $ $5) was highest in the United States (1,025) compared to China (654) .

In the field of photosynthesis synthetic biology, international research teams have advanced considerably in recent years. Notably, supported by the Bill & Melinda Gates Foundation, the international C_4 Rice Project and the RIPE project (Realizing Increased Photosynthetic Efficiency) focusing on C_3 improvement have established multiple international research hubs for photosynthesis synthetic biology. These initiatives have created highly collaborative international research teams and developed critical tools and platforms for photosynthesis synthetic biology research, achieving major progress [10]. Meanwhile, the Weizmann Institute of Science has made substantial advances in creating autotrophic *E. coli*, achieving self-sustaining growth using pyruvate [11], representing a substantial step toward establishing autotrophic industrial microorganisms.

Chinese scientists have also, through years of effort, achieved international leadership or parity in several research areas. First, with support from national funding, particularly the Chinese Academy of Sciences' Strategic Priority Research Program, China has established a series of photosynthesis system models spanning molecules, organelles, cells, leaves, canopies, and whole organisms [12], which support the modification of C_3, C_4, and novel photosynthetic pathways.

Recently, Chinese researchers, together with international colleagues, founded the specialized academic journal *in silico Plants*, establishing a foundation for China to continue leading international research and setting standards in this field. Additionally, China has conducted research on photorespiratory bypass modification [13,14], phycobilisome reconstruction [15,16], and photosynthesis-specific gene modification [17,18].

Furthermore, Chinese researchers have established research systems and platforms using single-celled cyanobacteria and algae as chassis for producing various energy and high-value molecules [19–22], establishing the industrial microalga *Nannochloropsis* as a model species for synthetic biology [23–27] and creating an international research cooperation network for energy microalgae synthetic biology. This work lays the foundation for deeply understanding the network regulatory mechanisms of photosynthesis and for designing and constructing efficient, low-cost, scalable photosynthetic cell factories. Meanwhile, integrating chemistry, materials science, and synthetic biology, the international community is developing organic/inorganic artificial photosynthetic composite catalytic systems, representing a research hotspot in artificial photosynthesis. These promising artificial photosynthesis systems combine the catalytic specificity of biological systems with the high photoelectric conversion efficiency of inorganic nanomaterials. Two common approaches are protein-nanomaterial systems and living cell-nanomaterial systems. In the latter, the system cleverly combines bacterial metabolic pathways with reductive power provided by inorganic materials to produce high-value products by mimicking photosynthesis. For example, Japanese scientists demonstrated that light can cause specific semiconductor nanomaterials to generate electrons that, via methyl viologen-mediated transmembrane electron transfer, drive hydrogenase-containing bacteria to continuously produce hydrogen [28]. American scientists achieved in-situ deposition of CdS quantum dots on bacterial surfaces: under illumination, electrons are transferred into bacterial cells to provide reductive power for the Wood-Ljungdahl cycle, ultimately enabling direct conversion of CO_2 to acetate and achieving light-to-chemical energy conversion and storage [29,30].

2. Weaknesses in China's Photosynthesis Synthetic Biology Research

Despite progress in related areas, China's photosynthesis synthetic biology research exhibits notable weaknesses. First, photosynthesis-related research remains fragmented. Although China has achieved international discourse power in specific domains such as photosynthesis systems biology and macromolecular structure and function, the overall level remains low, and national-level research platforms have yet to be established—disproportionate to the major strategic significance of photosynthesis for societal development. In contrast, multiple developed countries have competitively established large photosynthesis research teams and platforms, which have shifted from previous competitive relationships to form tightly collaborative international photosynthesis research communities, currently dominating the discourse in photosynthesis synthetic biology.

Second, the distance between China's photosynthesis synthetic biology research and practical applications remains substantial. From an application perspective, although China's National Basic Research Program ("973") deployed an "Artificial Leaf" project and the National High-tech R&D Program ("863") Synthetic Biology Major Project included a topic on "Construction and Application of Photosynthetic Artificial Cell Factories," these studies primarily focused on basic research and generic technology development without integration with practical molecular breeding needs for large-scale biofuel production. Similarly, the "973" project "Scientific Basis for Large-scale Microalgae Energy Production" deployed during the 12th Five-Year Plan focused on demonstration of the entire microalgae biodiesel production process, with minimal content on microalgae photosynthesis research. In the past decade, the National Natural Science Foundation of China's major projects and key R&D programs have included photosynthesis, mineral nutrition metabolism, developmental biology, and stress biology, yet photosynthesis-related research has received the least funding among these areas. In various crop breeding programs, although high photosynthetic efficiency is recognized as crucial for substantial yield improvement, photosynthesis improvement research receives relatively limited support, with similar issues existing in bioenergy research. How to effectively promote integration between basic and applied research through policy and funding support represents a key challenge for ensuring the long-term development of photosynthesis synthetic biology.

Third, funding support for photosynthesis research in China remains insufficient. This is evident in the fact that, compared to historical achievements in photosynthetic phosphorylation—such as the discovery at the Shanghai Institute of Plant Physiology and Ecology in the 1980s that spraying sodium bisulfite could effectively enhance cyclic electron transport and ATP supply, thereby improving canopy photosynthetic efficiency and crop yield [31]—current research in practical domains like food and energy remains limited. Only 2,718 studies (22.70% of China's total photosynthesis papers) simultaneously address "photosynthesis" and "energy" or "breeding" in their abstracts. This issue is also reflected in the design and deployment of national large-scale research projects.

3. Strategic Supporting Role of Photosynthesis in Modern and Future Society

Improving photosynthetic efficiency will play a critical role in future food production. Over the past 50 years, crop yields have increased substantially through dwarf breeding, hybrid breeding, and molecular marker-assisted breeding [32]. Consequently, despite world population growing from 3 billion in 1960 to 7.5 billion in 2018 (a 1.5-fold increase) [33], global food security has not faced major threats. However, population growth in Asia, Africa, and Latin America continues at near or above 1% annually, while the annual rate of grain yield increase is gradually slowing, making food security concerns increasingly prominent. Multiple projections indicate that grain production must increase by 0.85-fold by 2050 to maintain current per capita consumption [34]. With crop harvest indices already approaching or exceeding 0.5, substantial further improvement is unlikely. Additionally, urbanization has eliminated the possibility of large-scale expansion of cultivated land, making improved light use efficiency the important and perhaps only viable pathway for substantially increasing crop yield potential [35]. Notably, while improving crop stress resistance is also crucial for enhancing light use efficiency, numerous studies demonstrate that improving light use efficiency can simultaneously increase crop yields under stress conditions [36].

Bioenergy based on photosynthesis will become an important alternative energy form. As Earth's non-renewable fossil fuels are depleted, humanity faces an urgent task to seek new alternative energy sources. Photosynthesis-based bioenergy, alongside nuclear, wind, and solar energy, represents a major future energy option. Compared to other alternatives, photosynthesis-based bioenergy offers numerous advantages including high efficiency, easy maintenance, low energy consumption for efficient operation, storability, high safety, and no greenhouse gas emissions. Furthermore, algae-based biomass energy production is increasingly important due to its advantages of not competing with farmland and achieving high rates of light-to-biomass energy conversion. The United States has established four bioenergy research centers, and its Renewable Fuel Standard mandates that biofuel blending in annual fuel supplies reach 36 billion gallons by 2022 . Brazil's National Energy Plan 2030 targets annual production of 66 billion gallons of bioethanol and 18.5 billion gallons of biodiesel by 2030. The U.S. 2015–2020 Strategic Research Report aims for biomass energy to account for 25–33% of total energy consumption by 2050 [37].

Improving light use efficiency is key to creating green, efficient agriculture and future ecological civilization. By the 1990s, eutrophication affected 77% of China's lakes [38]. Enhancing light use efficiency to create high-yield, efficient crops while reducing fertilizer use is critical for developing green, sustainable agriculture and constitutes an important component of national ecological civilization construction. Moreover, the two most important factors in current global climate change—increasing atmospheric CO_2 concentration and rising temperature—are both major factors affecting photosynthesis [39]. How to modify and optimize current photosynthetic systems to maintain optimal light conversion efficiency under global climate change is a major challenge in contemporary agriculture.

4. Major Future Research Directions in Photosynthesis Synthetic Biology

Photosynthesis synthetic biology is currently facing a valuable strategic opportunity period. Although international development in this field began earlier, the discipline remains in its infancy when viewed historically. While China's research exhibits weaknesses including fragmentation and weak connections to practical applications, China possesses unique advantages for large-scale photosynthesis synthetic biology research. First, China's large population and collective memory of recent major famines provide strong political foundation and public support. Second, China has internationally first-class research teams in plant genetics, crop genomics, and synthetic biology, providing key technological and platform foundations [40–42]. Additionally, current re-evaluation of photosynthetic efficiency provides powerful theoretical justification for large-scale research. Photosynthesis requires CO_2, water, and light, with efficiency profoundly influenced by environmental factors like temperature. Historically, plants evolved current photosynthetic systems adapted to specific environmental conditions. Current global CO_2 concentration has reached 405 µL/L, nearly double the average over the past 400,000 years [43]. Under the RCP8.5 scenario, the IPCC projects CO_2 concentrations of 550 and 950 µL/L by 2050 and 2100, respectively [39]. The current plant photosynthetic system (including light reactions and carbon metabolism) must be adjusted and modified to adapt to this new environment. Furthermore, natural selection has evolved plant traits primarily to maximize genetic information transmission rather than photosynthetic efficiency. Finally, during evolution and artificial selection, plants could only utilize existing genetic resources and tools, preventing evolution of a maximally optimized light-to-chemical energy conversion system [35,44]. All these factors indicate that current plant photosynthetic systems are far from achieving optimal light use efficiency, and that synthetic biology technologies can artificially intervene to optimize and engineer photosynthetic systems for better food and energy provision.

Currently, photosynthesis synthetic biology research is gradually coalescing around five major directions (Table 1):

Synthetic biology modification and optimization of natural variation in existing photosynthetic pathways. The near-term goal is to utilize existing natural photosynthetic systems, identify modification and optimization targets, and employ synthetic biology approaches to engineer and optimize current systems for improved light use efficiency. Key targets for systematic improvement include: Rubisco kinetic parameters, ATP synthase structure and function, antenna system size and composition, carbon metabolic enzyme content and regulation, leaf structure, utilization capacity under high, low, and dynamic light conditions, and photosynthetic function under high and low temperatures.

Coordination between photosynthetic systems and photosynthate utilization pathways. Directed regulation of photosynthate consumption processes through synthetic biology will not only improve light use efficiency and crop yield but also provide novel approaches for producing high-energy, high-value raw materials in "plant factories." Urgent research areas include: modifying plant source-sink-translocation systems to optimize photosynthate transport, storage, partitioning, and utilization; optimizing root photosynthate storage; improving source-sink-translocation interactions to enhance light use efficiency across the entire growth period; modifying plant hormone regulation of photosynthesis to unlock photosynthetic potential; and engineering photosynthetic systems and basic metabolic pathways to increase growth rates while simultaneously enhancing lipid synthesis.

Cross-species reconstruction of naturally existing high-efficiency photosynthetic pathways. Introducing high-efficiency photosynthetic systems into current crops through effective reconstruction can substantially improve light, water, and nitrogen use efficiency. These pathways include: implementing C_4 photosynthesis engineering in C_3 plants, carboxysome reconstruction, pyranoid reconstruction, and introducing crassulacean acid metabolism (CAM) into C_3 plants to improve drought resistance.

Construction of novel photosynthetic systems. Based on molecular mechanisms of photosynthetic system operation, constructing entirely new photosynthetic systems not existing in nature can expand energy utilization channels and provide tremendous potential for expanding food and energy production. Fundamental and applied research in this area includes: constructing novel CO_2 fixation pathways independent of Rubisco for more efficient carbon fixation; creating autotrophic *E. coli* as a novel industrial microbial chassis; establishing novel photosynthetic metabolic pathways that directly utilize cellulose-based biomass as energy to efficiently produce industrial sugars like starch and sucrose; and developing novel metabolic pathways that use energy sources other than light (e.g., reducing power) for CO_2 fixation.

Creation of photosynthetic system-biomaterial hybrids. Based on photosynthetic molecular mechanisms, creating novel photosynthetic system-material integrated systems can efficiently produce high-value products like O_2, H_2, and electricity. Research directions include: establishing artificial photosynthetic systems for O_2, electricity, and hydrogen production; constructing artificial photosynthetic "leaves" through organic integration of natural photosynthesis with smart materials (e.g., establishing waxy layers on leaf surfaces to improve drought resistance by increasing reflectance, or implanting novel materials with CO_2 absorption/release capacity to create high CO_2 concentration zones in substomatal chambers). Additionally, to address limitations of current artificial photosynthesis systems (e.g., hole-induced damage to organic systems from inorganic materials and mismatched catalytic activities), rational design strategies using self-assembly can precisely organize enzymes and inorganic nanomaterials required for photocatalysis, improving charge transport and catalytic efficiency while reducing photodamage to biological systems, thereby facilitating practical applications of artificial photosynthesis.

5. Potential for Improving Light Use Efficiency Through Photosynthesis Engineering

**** Potential for improving light use efficiency through photosynthesis engineering, key technical challenges, and projected industrialization timelines

Important Research Topics	Key Technical Challenges	Expected Improvement in Light Use Efficiency	Timeline for Industrial Application	Primary Technologies Required
Rubisco kinetic parameters	Chloroplast transformation	15–25%	8–12 years	Chloroplast transformation
ATP synthase structure and function	Chloroplast transformation	10–20%	8–12 years	Chloroplast transformation
Canopy photosynthesis improvement	Genetic control factors for leaf structure	20–30%	10–15 years	Optimization of source-sink-translocation systems
Antenna system size	Clarifying genetic control factors for canopy photosynthesis; improving nitrogen use efficiency	10–15%	8–12 years	Chloroplast transformation
Carbon metabolic enzyme content	Optimizing source-sink-translocation; reducing feedback inhibition of photosynthetic apparatus by photosynthates	15–25%	8–12 years	Chloroplast transformation

Important Research Topics	Key Technical Challenges	Expected Improvement in Light Use Efficiency	Timeline for Industrial Application	Primary Technologies Required
Utilization under fluctuating light conditions	Clarifying regulatory factors for photosynthetic inhibition during later growth stages	10–20%	8–12 years	Chloroplast transformation
Hormone regulation of photosynthetic apparatus	Identifying key regulatory elements controlling photosynthetic efficiency by hormones	15–25%	8–12 years	Chloroplast transformation
Integration of photosynthesis and basic metabolism	Discovering optimal regulatory patterns for photosynthesis and lipid synthesis	20–30%	8–12 years	Chloroplast transformation
Pyranoid reconstruction	Clarifying key protein components of pyranoids; chloroplast transformation	Not evaluated, water use efficiency improvement	10–15 years	Chloroplast transformation

Important Research Topics	Key Technical Challenges	Expected Improvement in Light Use Efficiency	Timeline for Industrial Application	Primary Technologies Required
CAM pathway introduction	Identifying key regulatory factors for Kranz anatomy	30–50%	15–20 years	Chloroplast transformation, large vector construction
Carboxysome reconstruction	Clarifying key protein components of carboxysomes; chloroplast transformation	Not evaluated	10–15 years	Chloroplast transformation
Phycobilisome establishment	Clarifying minimal phycobilisome unit composition	Not evaluated, expanded spectral absorption	8–12 years	Chloroplast transformation
Chlorophyll *d* and *f* reconstruction	Clarifying synthetic pathways for chlorophyll *d* and *f*	Not evaluated, expanded spectral absorption	8–12 years	Chloroplast transformation
Photorespiratory bypass construction	Designing optimal photorespiratory bypasses and integrating with existing metabolic pathways	15–30%	8–12 years	Chloroplast transformation, large vector construction

Important Research Topics	Key Technical Challenges	Expected Improvement in Light Use Efficiency	Timeline for Industrial Application	Primary Technologies Required
Autotrophic *E. coli* construction	Establishing novel autotrophic industrial microbial chassis	Not evaluated	10–15 years	Metabolic pathway design and evolutionary strategies
Novel photosynthetic metabolic pathways	Utilizing cellulose as energy source to produce starch, sucrose, etc.; greatly improving harvest index	Not evaluated	15–20 years	Metabolic pathway design and evolutionary strategies
Artificial photosynthesis for H_2/O_2/electricity	Utilizing photosynthetic principles to produce O_2, H_2, and electricity	Not evaluated	10–15 years	Novel material composites
Photosynthetic system-biomaterial hybrids	Improving leaf drought resistance; establishing high CO_2 concentration zones inside leaves	Not evaluated	10–15 years	Novel material composites

References

1. Shen YK, Shen GM. The high-energy state of chloroplasts as an intermediate step of photophosphorylation. *Scientia Sinica*, 1962, II-8: 1087-1106.
2. Qian M, Wei XP, Su XD, et al. Structure of spinach photosystem II-LHCII supercomplex at 3.2 Å resolution. *Nature*, 2016, 534: 69-74.
3. Pan XW, Ma J, Su XD, et al. Structure of the maize photosystem I supercomplex with light-harvesting complexes I and II. *Science*, 2018, 360: 1109-1113.
4. Liu J, Yang HX, Lu QT, et al. PsbP-domain protein1, a nuclear-encoded thylakoid lumenal protein, is essential for photosystem I assembly in *Arabidopsis*. *Plant Cell*, 2012, 24: 4992-5006.
5. Wang Y, Bräutigam A, Weber APM, et al. Three distinct biochemical subtypes of C_4 photosynthesis? A modelling analysis. *Journal of Experimental Botany*, 2014, 65: 3567-3578.
6. Gao X, Hong H, Li WC, et al. Down-regulation of Rubisco activity by non-enzymatic acetylation of RbcL. *Molecular Plant*, 2016, 9: 1018-1027.
7. Xiao Y, Chang TG, Song QF, et al. ePlant for quantitative and predictive plant science research in the big data era – Lay the foundation for the future model guided crop breeding, engineering and agronomy. *Quantitative Biology*, 2017, 5: 260-271.
8. Kebeish R, Niessen M, Thiruveedhi K, et al. Chloroplastic photorespiratory bypass increases photosynthesis and biomass production in *Arabidopsis thaliana*. *Nature Biotechnology*, 2007, 25: 593-599.
9. Shen B-R, Wang L-M, Lin X-L, et al. Engineering a new chloroplastic photorespiratory bypass to increase photosynthetic efficiency and productivity in rice. *Molecular Plant*, 2019, 12: 199-214.
10. Kromdijk J, Głowacka K, Leonelli L, et al. Improving photosynthesis and crop productivity by accelerating recovery from photoprotection. *Science*, 2016, 354: 857-861.
11. Antonovsky N, Gleizer S, Noor E, et al. Sugar synthesis from CO_2 in *Escherichia coli*. *Cell*, 2016, 166: 115-125.
12. Song QF, Wang Y, Qu M, et al. The impact of modifying photosystem antenna size on canopy photosynthetic efficiency. *Plant, Cell & Environment*, 2017, 40: 2946-2957.
13. Tang K, Ding W-L, Höppner A, et al. The terminal phycobilisome emitter, LCM: a light-harvesting pigment with a phytochrome chromophore. *PNAS*, 2015, 112(52): 15880-15885.

14. Liu H, Zhang H, Niedzwiedzki DM, et al. Phycobilisomes supply excitations to both photosystems in a megacomplex in cyanobacteria. *Science*, 2013, 342: 1104-1107.
15. Liu H, Frankenberg-Dinkel N. A new pathway for phycobilin biosynthesis in cyanobacteria and its application in *Arabidopsis*. *Plant Physiology*, 2016, 171: 1685-1695.
16. Wlodarczyk A, Selão TT, Norling B, et al. Proteomic analysis of the model cyanobacterium *Synechocystis* sp. PCC 6803 reveals major proteome changes during optimized biofuel production. *Metabolic Engineering*, 2016, 38: 217-227.
17. Sun T, Li S, Song X, et al. Toolboxes for cyanobacteria: Recent advances and future direction. *Biotechnology Advances*, 2018, 36(4): 1293-1307.
18. Luan G, Lu X. Tailoring cyanobacterial cell factory for improved industrial properties. *Biotechnology Advances*, 2018, 36(2): 430-442.
19. Zhang H, Liu Y, Nie X, et al. The cyanobacterial ornithine-ammonia cycle involves an arginine dihydrolase. *Nature Chemical Biology*, 2018, 14: 575-581.
20. Wang D, Ning K, Li J, et al. *Nannochloropsis* genomes reveal evolution of microalgal oleaginous traits. *PLoS Genetics*, 2014, 10: e1004094.
21. Li J, Han D, Wang D, et al. Choreography of transcriptomes and lipidomes of *Nannochloropsis* reveals the mechanisms of oil synthesis in microalgae. *Plant Cell*, 2014, 26(4): 1645-1665.
22. Xin Y, Lu Y, Lee YY, et al. Producing designer oils in industrial microalgae by rational modulation of co-evolving type-2 diacylglycerol acyltransferases. *Molecular Plant*, 2017, 10(12): 1524-1536.
23. Honda Y, Hagiwara H, Ida S, et al. Application to photocatalytic H_2 production of a whole-cell reaction by recombinant *Escherichia coli* cells expressing [FeFe]-hydrogenase and maturases genes. *Angewandte Chemie International Edition*, 2016, 55: 8045-8048.
24. Sakimoto KK, Wong AB, Yang P. Self-photosensitization of nonphotosynthetic bacteria for solar-to-chemical production. *Science*, 2016, 351: 74-77.
25. Zhang H, Liu H, Yang P, et al. Bacteria photosensitized by intracellular gold nanoclusters for solar fuel production. *Nature Nanotechnology*, 2018, 13: 900-905.
26. Zhu XG, Portis AR Jr, Long SP. Would transformation of C_3 crop plants with foreign Rubisco increase productivity? A computational analysis extrapolating from kinetic properties to canopy photosynthesis. *Plant, Cell & Environment*, 2004, 27: 155-165.

27. Zhu XG, de Sturler E, Long SP. Optimizing the distribution of resources between enzymes of carbon metabolism can dramatically increase photosynthetic rate: A numerical simulation using an evolutionary algorithm. *Plant Physiology*, 2007, 145: 513-526.

28. Xiao Y, Zhu XG. Component of mesophyll resistance and their environmental responses. *Plant, Cell & Environment*, 2017, 40: 1019-1032.

29. McGrath JM, Long SP. Can the cyanobacterial carbon-concentrating mechanism increase photosynthesis in crop species? A theoretical analysis. *Plant Physiology*, 2014, 164: 2247-2261.

30. Blankenship RE, Chen M. Spectral expansion and antenna reduction can enhance photosynthesis for energy production. *Current Opinion in Chemical Biology*, 2013, 17: 457-461.

31. Qian Q, Guo L, Smith SM, et al. Breeding high-yield superior quality hybrid super rice by rational design. *National Science Review*, 2016, 3: 283-294.

32. United Nations, Department of Economic and Social Affairs, Population Division. *World Population Prospects: The 2017 Revision, Volume I: Comprehensive Tables* (ST/ESA/SER.A/399). https://population.un.org/wpp/Publications/Files/WPP2017_{Volume}-I_{Comprehensive}-Tables.pdf.

33. Ray DK, Mueller ND, West PC, et al. Yield trends are insufficient to double global crop production by 2050. *PLoS ONE*, 2013, 8: e66428.

34. Long SP, Marshall-Colon A, Zhu XG. Meeting the global food demand of the future by engineering crop photosynthesis and yield potential. *Cell*, 2015, 161: 56-66.

35. Zhu XG, Long SP, Ort DR. Improving photosynthetic efficiency for greater yield. *Annual Review of Plant Biology*, 2010, 61: 235-261.

36. Bauen A, Berndes G, Junginger M, et al. Bioenergy: a sustainable and reliable energy source. A review of status and prospects. Netherlands: International Energy Agency Bioenergy, 2009.

37. Jin GD. Research status of lake eutrophication in China. *Modern Agricultural Science and Technology*, 2008, 16: 334-336.

38. IPCC. *Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Geneva, Switzerland: IPCC, 2014.

39. Barnola JM, Raynaud D, Lorius C, et al. Historical CO_2 record from the Vostok ice core. In *Trends: a Compendium of Data on Global Change*. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory: Department of Energy, Oak Ridge, 2003.

40. Shao Y, Lu N, Wu Z, et al. Creating a functional single-chromosome yeast. *Nature*, 2018, 560: 331-335.

41. Song QF, Wang Y, Qu M, et al. The impact of modifying photosystem antenna size on canopy photosynthetic efficiency. *Plant, Cell & Environment*, 2017, 40: 2946-2957.

42. Xiao Y, Chang TG, Song QF, et al. ePlant for quantitative and predictive plant science research in the big data era – Lay the foundation for the future model guided crop breeding, engineering and agronomy. *Quantitative Biology*, 2017, 5: 260-271.

Author Biography

ZHU Xinguang is a Principle Investigator at the National Key Laboratory of Plant Molecular Genetics, Institute of Plant Physiology and Ecology, Chinese Academy of Sciences. In 2013, Dr. Zhu received the Melvin Calvin-Andrew Benson Award from the International Society of Photosynthesis Research for discovering new pathways to improve photosynthetic efficiency. He serves on editorial boards of *Plant Cell and Environment*, *Frontiers in Plant Physiology*, *Royal Society Open Science*, and *Frontiers in Plant Systems Biology.* He co-founded the journal *in silico Plants*, which is a member of F1000Prime. He has published over 110 papers with more than 7,600 citations. E-mail: zhuxg@sippe.ac.cn

Responsible Editor: Yue Lingsheng

Note: Figure translations are in progress. See original paper for figures.