Bulletin du Centre Franco-Japonais d'Histoire des Sciences **(Kitakyushu-Paris), Vol. 14(2): 9-20 (2020)**

日仏科学史資料センター紀要　ISSN 1882-3548 (online), 1882-353X (CD-ROM)

-Mini Review-

Scientific history of cyanobacteria research: Achievements of Roger Stanier (1916-1982) and the mechanisms of inorganic carbon enrichment in cyanobacteria.*

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Abstract

Cyanobacteria (previously known as blue-green algae) are known for prototypic oxygen-evolving photosynthesis functionming in the same manner as plants, appered on Earth ca. 3.8 billion years ago, and they still survive and thrive today. In the history of science, cyanobactera have made a great contributions to the development of photosynthesis research. In 1996, the entire nucleotide sequence of the Pasteur collection strain Synechocystis sp. PCC6803 was determined for the first time among the photosynthetic model organisms. Roger Stanier, who contributed to the Pasteur culture collection of cyanobacteria, was a prominent microbiologist who laid the foundation for cyanobacterial research, including establishing the name Cyanobacteria. This paper briefly describes the history of cyanobacterial research with emphasis to the works of Stanier and the mechanism of inorganic carbon (C_i) enrichment due to which cyanobacterial photosynthesis is efficiently driven.

Keywords: CO_2 concentrating mechanism, cyanobacteria, inorganic carbon (C_i), Institut Pasteur, Pasteur culture collection (of cyanobacteria), Roger Stanier.

Ohkawa, H. (2020) Scientific history of cyanobacteria research: Achievement of Roger Stanier (1916-1982) and the mechanisms of inorganic carbon enrichment in cyanobacteria. Bull. Cent. Fran. Jpn. Hist. Sci. 14(1): 9-20.

***This is a peer-reviewed article** communicated by Prof. T. Kawano (Univ. Kitakyushu). Preliminarily communicated for the concept of article in September, 2019; first complete manuscript received on April 13th; 2020; Revised after comments by reviewers on April 13th, 2020; Accepted for publication on April 14th, 2020.

Introduction

Cyanobacteria are photosynthetic prokaryotes that have been photosynthetic for billions of years on Earth. They have attracted scientists as model organisms for the study of plant biology involving oxygen photosynthesis. While photosynthesis in cyanobacteria is governed by a single set of genomes, that found in higher plants is governed by genetic information encoded by both nucleic and chloroplastic genomes. Obviously, the size of the cyanobacterial genome is much smaller than that of higher plants. Cyanobacteria are also considered as one of potential ancenstors of chloroplasts. Evidence has also been shown from the analysis of genomic information (Martin et al., 2002). Therefore, it is an attractive organism as a chloroplast model not only for microbiologists but also for botanists. In recent years, microalgae including cyanobacteria have gained much attention, because they are important organisms for biotechnologies for producing food additives, bioactive substances, pharmaceutical compounds, biofuels (Abed et al., 2009, Khetkorn et al., 2017). In traditional classifications, morphological distinctions have been used to divide the group into five subsections (Rippka et al. 1979). Recent phylogenic studies based on 16S rRNA have demonstrated further diversity. Therefore, the discussion on their phylogeny as well as the current number of cyanobacterial species are still controversial (Foster et al., 2009, Tomitani et al., 2006).

This short article presents a brief history of cyanobacterial research and short review of the mechanisms of Ci enrichment in the cell.

Blue-green algae (cyanophyceae) or blue-green bacteria (cyanobacteria) ?

Cyanobacteria were originally called blue-green algae. The classical term was derived from alga which looks blue-green by phycocyanin and chlorophyll a. For over a century, cyanobacteria have been considered to belong to the algal group. It was actually classified under the International Botanical Naming Convention (now the International Algae, Fungi and Plant Naming Convention). However, Stanier et al. (1978) has proposed the name cyanobacteria in the ICNP (the International Code of Nomenclature of Prokaryotes), and is the term that has become the most established.

Table 1 compares the popularities of the scientific names/terms for this organism, namely cyanobacteria, blue-green bacteria, cyanophyceae, and blue-green algae, to be used in the titles of scientific publications (papers). Among four names, "blue-green algae" was oldest term given to this orgamnism (Richards, 1901). In the early 1900s, "blue-green algae" was most friquently used term suggesting its popularity among scientific community. Additionally, "cyanophyceae" was temporally used in limited number of publications (tottaly 54) since the first appearance in the work by Lloyd in

1923. However, the term "cyanobacteria", which appeared half century later, was accepted and used in 3648 articles and its overwhelmingly used today.

While the researchers started to use both “cyanobacteria” and “blue-green bacteria” in the 1970s, "cyanobacteria" has been largely favored by majority of the biologists who documented a number of articles throughout the decades since the first appearance of the termup to today. On the other hand, it seems that "blue-green bacteria" did not penetrate into the research community. In the process that “cyanobacteria” gained the popularity ammong the scientific communities, Stanier's constant achievements might have been significant.

Table 1. Comparison of the number of papers using the the related terms (cyanobacteria, blue-green bacteria, cyanophyceae or blue-green algae) in the titles.

	number of articles		
the terms	total number	year 2019	oldest article
cyanobacteria	3648	299	Lemasson, et al. (1973)
blue-green bacteria	21	0	Ingram, et al. (1973)
cyanophyceae	54	1	Lloyd (1923)
blue-green algae	534	4	Richards (1901)

The number of articles with each term was estimated based on the searches with PubMed database.

Roger Stanier and Pasteur culture collection of cyanobacteria

After contributing to the understanding of the microbial world (Stanier R., et al., 1962) at the University of California at Berkeley, Stanier, a world-renowned microbiologist, moved to the Institute of Pasteur in France, where he achieved many research achievements such as the classification of cyanobacteria, and also physiological and morphological studies of cyanobacteria (Kenyon et al., 1970, Stanier, 1971, Pelroy et al., 1972). The cyanobacterial collection at Berkeley (Berkeley strain) has been preserved as the Pasteur culture collection of cyanobacteria (PCC strain) and has contributed to the development of various studies to date.

For the first time as a photosynthetic organism, the entire nucleotide sequence of cyanobacteria was decoded by the Kazusa DNA Research Institute (Kaneko et al., 1996). The cyanobacterium used for this decoding is a unicellular spherical Synechocystis sp. PCC6803 (Fig. 1A). The complete nucleotide sequence of unicellular Synechococcus

elongatus PCC7942 (S. elongatus PCC6301 is the type strain for S. elongatus, Fig. 1B), which was first reported as a strain capable of natural transformation, has been determined.

In this way, the Pasteur culture collection of cyanobacteria contributed by Stanier et al. forms the basis of cyanobacterial research development to date by elucidating the shape and physiological characteristics of cyanobacteria that differ in classification and the complete genome base sequence.

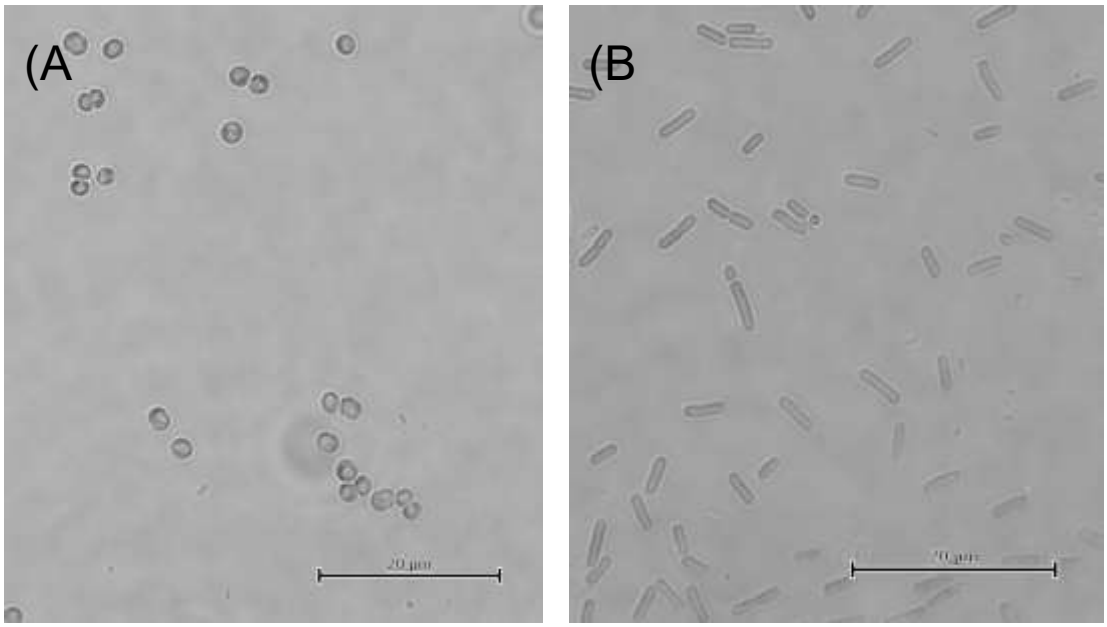

Fig. 1. Microscopic photographs of two different cyanobacterial strains. (A) *Syenchocystis* sp. PCC6803; (B) *Synechococcus elongatus* PCC7942. The scale bars represent 20 μm for both microscopic panels (Olympus BX53, Tokyo)

Carbon fixing in photosynthetic organisms

Plants and other oxygen-generating photosynthetic organisms absorb CO_2 and produce reducing sugars through the Calvin cycle. Ribulose - 1,5 - bisphosphate carboxylase / oxygenase (Rubisco), the initial carbon-fixing enzyme in the circuit, produces two molecules of 3-phosphoglycerate (3-PGA) by a carboxylase reaction that fixes CO_2. On the other hand, it also has oxygenase activity that reacts with O_2, producing 3-PGA and phosphoglycolic acid. Rubisco has a lower affinity for O_2 than that of CO_2, but under current atmospheric conditions (21% O_2, 0.04% CO_2), the Rubisco oxygenase reaction will always work due to the very high O_2 concentration. This oxygenase reaction results in a loss of

energy and organic carbon, reducing the efficiency of CO_2 fixation. Therefore, it can be said that the affinity of Rubisco for CO_2 and O_2 and the ratio of CO_2 to O_2 around Rubisco are the main factors controlling the efficiency of photosynthesis.

However, to overcome these problems, cyanobacteria have a mechanism to increase the CO_2 / O_2 ratio around Rubisco and suppress photorespiration by concentrating Ci in cells (CO_2 - concentrating mechanism: CCM).

Cyanobacterial CCM

Plants and other oxygen-generating photosynthetic organisms absorb CO_2 and produce reducing sugars through the Calvin cycle. Ribulose - 1,5 - bisphosphate carboxylase / oxygenase (Rubisco), the initial carbon-fixing enzyme in the circuit, produces two molecules of 3-phosphoglycerate (3-PGA) by a carboxylase reaction that fixes CO_2. On the other hand, it also has oxygenase activity that reacts with O_2, producing 3-PGA and phosphoglycolic acid. Rubisco has a lower affinity for O_2 than that of CO_2, but under current atmospheric conditions (21% O_2, 0.04% CO_2), the Rubisco oxygenase reaction will always work due to the very high O_2 concentration. This oxygenase reaction results in a loss of energy and organic carbon, reducing the efficiency of CO_2 fixation. Therefore, it can be said that the affinity of Rubisco for CO_2 and O_2 and the ratio of CO_2 to O_2 around Rubisco are the main factors controlling the efficiency of photosynthesis.

Physiological properties of CCM and isolation of HCR mutants:

To elucidate the cyanobacterial Ci transport system, physiological analysis has been performed on the Ci transport characteristics, and the main characteristics have been clarified. (1) Although it has high affinity for CO_2, it has low affinity for bicarbonate ions, about 1/100 of its affinity for CO_2 (Volokita et al., 1984). (2) The requirements for sodium are different (Espie GS. et al., 1988). A high concentration of sodium ions (> 10 mM) is required for bicarbonate transport, whereas a low concentration of sodium ions (> 0.1 mM) is sufficient for CO_2 transport (Miller, AG. and Canvin DT., 1985). For these reasons, it has been thought that CO_2 and bicarbonate ions are transported in separate systems. (3) The ratio of Ci in cells is different. No matter which type of Ci is given, bicarbonate ions are selectively accumulated in the cells.

Subsequently, in order to elucidate these mechanisms at the molecular level, a number of mutants requiring high CO_2 (HCR) that required high concentrations of CO_2 to grow were isolated, and many of the causative genes were carboxysomes and carbonic anhydrase (Friedberg et al., 1989, Schwarz et al., 1992, Ogawa et al., 1987, Kaplan et al., 1991, Fukuzawa et al., 1991). Among them, a mutant lacking the ability to transport CO_2 was first isolated (Ogawa, 1990). This ushered in a

molecular understanding of the Ci transport system. To date, five Ci transport pathways have been identified for cyanobacteria.

Two CO_2 transport routes:

From the analysis of the double mutants, NdhD1/2 is essential for photoheterotrophic and PSI cyclic electron transfer, and NdhD3/4 is involved in CO_2 uptake. The existence of 1 was suggested (Ohkawa et al., 2000). In addition, ndhD4 is constitutively expressed, ndhD3 gene is induced at low CO_2 concentration, and ndhF3, ndhD3 and cupA are co-transcribed, and all mutants show the same phenotype as ndhD3 mutant Therefore, it was suggested that CupA is a constituent subunit of NDH-1 including the ndhD3 subunit (Ohkawa et al., 1998, Ohkawa et al., 2000). On the other hand, ndhF4, ndhD4 and cupB mutants show low CO_2-induced uptake characteristics (Shibata et al., 2001, Shibata et al., 2002). In other words, high-affinity CO_2 uptake via NDH-1 containing NdhD3, ndhF3 and cupA (later NDH-1MS or NDH-13) and NDH-1 containing ndhD4, ndhF4 and cupB (later NDH-1MS 'or NDH-14).

Three HCO_3^- transport routes:

The transport of bicarbonate ion, another substrate, is a pathway that is taken up into cells by transporters located in the cell membrane, but three types of transporters have been known so far. BCT1 (Bicarbonate transporter) was first identified as a low CO_2-inducible cell membrane protein CmpA of *Synechococcus* 7942 (later, a substrate-binding subunit of BCT1) (Omata et al., 1986, Omata et al., 1999). Subsequently, analysis using a constantly expressed strain proved physiologically the first time to be a high-affinity bicarbonate ion transporter BCT1. Next, a sodium-dependent high-affinity bicarbonate ion transporter (SbtA) was isolated from *Synechocystis* 6803 (Shibata et al., 2002). This is a low CO_2 inducible type, and if the CO_2 transport ability is deficient, it is essential in a low CO_2 growth environment at alkaline pH, and plays an important role in the acquisition of Ci in a CO_2 restricted environment. The third transporter (BicA) is a sodium-dependent low-affinity transporter isolated from the marine cyanobacterium *Synechococcus* PCC7002. It belongs to the SulP/SLC26 family, which is widely conserved from prokaryotes to eukaryotes, and BicA homologs exist in any group of cyanobacteria (Shelden et al., 2010).

Different Ci transport systems depending on carboxysome type:

The evolutionary comparison of CCM has been made based on the comparison of various cyanobacterial genome information. It has been proposed that cyanobacterial carboxysomes be divided into two types based on the differences in the constituent Rubiscos (Badger et al., 2002). Those having Form-1B Rubisco, ccm-type carboxysome (β-carboxysome) are β-cyanobacteria, and those of

Form-1A Rubisco, cso-type carboxysome (α-carboxysome) are α-cyanobacteria. Comparing the numbers of Ci transporters between these types, many freshwater β-cyanobacteria possess all five of the above pathways (Fig. 2), while α-cyanobacteria have a number of Ci transport pathways. And the number is often missing or partially missing (Ogawa et al., 2007).

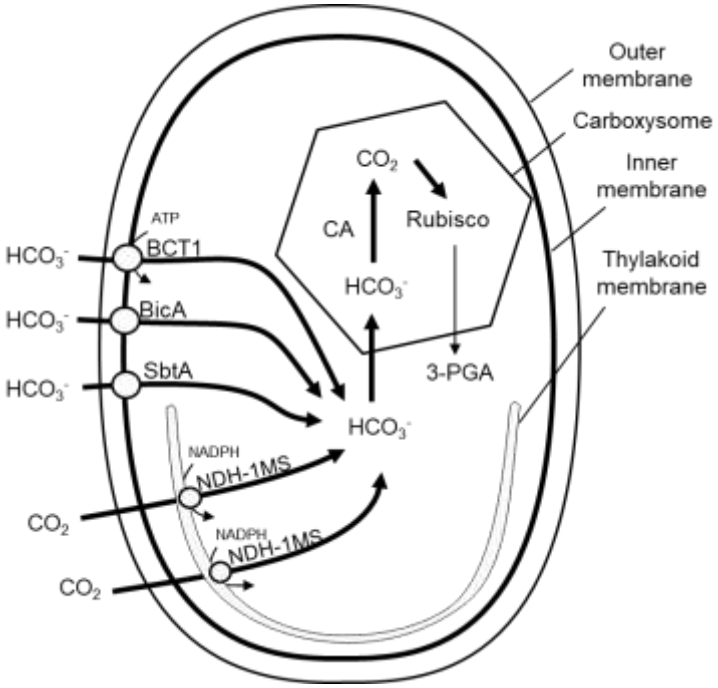

Fig. 2. Cyanobacterial CCM model. This figure shows a typical freshwater ß-cyanobacterial model. There are five inorganic transport systems, namely, three types of HCO_3^- transporting systems and two types of CO_2 transport systems as shown in this figure. Note that α-cyanobacteria lack BCT1 and NDH-1MS.

Conclusion

This short review described the history of Cyanobacteria research. The study of Stanier and co-workers of the Institut Pasteur in France would be a great achievement to be commended for the taxonomic status of cyanobacteria and the research-based cyanobacterial strain collection. In recent years, attempts have been made to isolate microalgae including cyanobacteria, and various reports have been made indicating that the microalgae have characteristic properties as compared with their homologous strains (Yu et al., 2015, Nitanai et al., 2015, Nguyen et al., 2017, Ohta et al., 2018,

Konstantinou et al., 2018). It has been suggested that Ci transport is carried out by various pathways, and that the transport pathway of Ci differs depending on the classification of carboxysome, which is a place for carbon fixation. More than 40 years after the initial research, the elucidation of cyanobacterial CCM has greatly advanced.

As with Stanier's pioneering research approach, understanding the differences in morphological, physiological, and chemical properties associated with various cyanobacteria will continue to be better understood.

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シアノバクテリア研究の科学史：Roger Stanier（1916-1982）の功績とシアノバクテリアにおける無機炭素濃縮機構

要約

植物と同様に酸素発生型の光合成を行うシアノバクテリアは、光合成研究の発展に大きく貢献してきた生物材料である。1996 年、光合成モデル生物として初めて、パスツールコレクション *Synechocystis* sp. PCC6803 株の全ヌクレオチド配列が明らかにされた。このコレクションの「構築に貢献した Stanier は著名な微生物学者であり、シアノバクテリアという用語の確立を含め、シアノバクテリアの研究の基礎を築いた。本論文では、Stanier の功績をはじめとしたシアノバクテリア研究の歴史と、シアノバクテリアの光合成において重要な役割を果たす無機炭素（C_i）濃縮のメカニズムについて簡単に解説する。