

## Inorganic carbon utilization by aquatic photoautotrophs and potential usages of algal primary production

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This special issue is a collection of invited reviews and peer-reviewed articles submitted by some of the keynote speakers at *The Seventh International Symposium on Inorganic Carbon Utilization by Aquatic Photosynthetic Organisms (CCM7)*, which was held at Awaji Yumebutai International Conference Center, Awaji City, Hyogo, Japan, from August 29 to September 2, 2010. The meeting was attended by 72 delegates from nine countries in Asia, North America, Europe, and Oceania, and the attendees spent substantially 3 days on the latest studies on CO<sub>2</sub> concentrating mechanisms (CCMs), CO<sub>2</sub> sensing, and its ecophysiological aspects in cyanobacteria, eukaryotic microalgae, and macrophytes from freshwater and marine environments. In the CCM7, two sessions were organized which dealt with topics of particular current interest: carbon-flow controls across chloroplasts; and biofuel synthesis as outputs of algal CCMs. The meeting was sponsored by Ogasawara Foundation for the Promotion of Science & Engineering, Grants from the Suntory Institute for Bioorganic Research, and Hyogo International Association. Yusuke Matsuda (Kwansei Gakuin University, Japan) and Hideya Fukuzawa (Kyoto University, Japan) were the chief organizers of the meeting with assistance from the local organizing committee comprising: Akiho Yokota (NAIST, Japan), Yoshihiro Shiraiwa (Tsukuba University, Japan), Tatsuo Omata (Nagoya University, Japan), and Mitsue Miyao (NIAS, Japan). The international committee included George Espie (University of Toronto, Canada), Brian Colman (York University, Canada), Murray Badger (ANU,

Australia), Dean Price (ANU), Mario Giordano (Università Politecnica delle Marche, Italy), Aaron Kaplan (University of Hebrew, Israel), Stephen Maberly (Lancaster Environment Centre, UK), James Moroney (Louisiana State University, USA), Tatsuo Omata (Nagoya University, Japan), Martin Spalding (Iowa State University, USA), and Philippe Tortell (University of British Columbia, Canada). The plans and the organizations of the meeting and that of the special issue have benefited from advice provided by George Espie, Brian Colman, and Dean Price.

The first “CCM” meeting was held at Asilomer, USA in 1984 soon after the discovery of direct accumulation systems of inorganic carbon in cyanobacteria and green algae. The original aim was to promote the study on acquisition systems of inorganic carbon by aquatic photoautotrophs and to shed light on the importance of carbon fixation in aquatic environments. Five subsequent meetings were held at Kingston, Canada (1990), Vancouver, Canada (1997), Cairns, Australia (2001), St. Sauveur, Canada (2004), and Malaga, Spain (2007), while this seventh symposium, CCM7, was the first to be held in Asia. Special issues of all past meetings have been published (Lucas and Berry 1985; Colman 1991, 1998; Price and Badger 2002; Espie and Colman 2005; Gordillo 2008) and this issue of the *Photosynthesis Research* is the collection of papers representing the seventh milestone in the developments of our knowledge, both basic and applied, of CO<sub>2</sub> concentrating mechanism and CO<sub>2</sub> responses in aquatic photoautotrophs. Three decades of research have demonstrated the general occurrences of CCMs in a wide range of bacteria and algae living in freshwater and seawater, and ecophysiological impacts of aquatic photoautotrophs. Moreover, the establishment of genome databases in model systems of cyanobacteria, green algae, and diatoms, together with reverse genetic approaches are providing molecular details of the

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factors controlling the uptakes and flow of inorganic carbon. These findings allow us to consider that algal primary production can be adapted to provide a crucial source of renewable energy and that some components of algal CCMs might be transferred by gene manipulation to higher plants in order to improve crop yield.

The symposium was initiated by the plenary talk of one of the pioneers of this research field, Shigetoh Miyachi (Professor Emeritus, University of Tokyo). He described his 60 years of research on algal physiology. Sessions started with talks on molecular studies of the CCM in cyanobacteria, *Chlamydomonas* and marine diatoms, followed by more physiological works in haptophytes and marine macrophytes. Topics then changed to metabolic controls in chloroplasts including studies aiming at biofuel productions and then moved on to eco- and geo-scale studies of algal physiology and diatom genomics. In the middle of the meeting an excursion was arranged to the Naruto Channel Whirlpool, which is located between Awaji Island and Shikoku Island and is known to be one of the fastest currents in the world.

Studies of the CCM in cyanobacteria have led the field and have revealed a whole set of CCM components that fully account for the performance of the CCM in representative species of cyanobacteria. These studies have recently focused on the relationship between biochemical functions and the crystallographic structures of the carboxysome, a focal point for the CCM. Espie and Kimber (2011) and Kinney et al. (2011) reviewed the role of carboxysomes in CO<sub>2</sub> fixation in relationship to packaging topology of CsoS1/CcmK proteins and CsoS4/CcmL proteins; respectively, these proteins form shell facets and vertices of the icosahedral body of  $\alpha$ - and  $\beta$ -carboxysomes. This review also addressed key components of intracarboxysomal CO<sub>2</sub> formation by carbonic anhydrases and the interior organization of the carboxysome by CcmM/CsoSCA. Kinney et al. (2011) further illustrated the dynamism of the shell forming protein hexamers and pentamers and discussed that the possible small substrate molecules may pass through the pores of these protein complex units with diameters and electrostatic charges of pore interiors. Long et al. (2011) reported the structural adjustment of the  $\beta$ -carboxysome in response to changes in CO<sub>2</sub> concentration by demonstrating the tight correlation between the content of CcmM M58 and the carboxysomal CA, CcaA. Under limited CO<sub>2</sub>, CcmM M58 slightly increased over the other form M35 and concomitantly CcaA levels increased to flexibly optimize the CA content in the carboxysome.

Also elucidated during the last decade is the participation of unique proteins components and their molecular mechanisms in the acquisition of dissolved inorganic carbon (DIC) by cyanobacteria. Price (2011) thoroughly summarized the current knowledge in his review

describing the three plasma membrane-localized HCO<sub>3</sub><sup>-</sup> transporters (CmpABCD, BicA, and SbtA) and the two CO<sub>2</sub> converting systems of Ndh-Chp complexes that are located in the thylakoid membranes and possibly in the plasmalemma. Price's (2011) review also illustrated the membrane topology of the 12 and 10 transmembrane helix domains of BicA and SbtA, respectively; this review will stimulate future study leading to an understanding of the fine regulatory mechanisms that control transporter activities in concert with environmental fluctuations. A highly efficient CCM system, "especially active in  $\beta$ -cyanobacteria," possibly contributed to the evolutionary adaptations of  $\alpha$ -cyanobacteria as these organisms shifted habitation from a marine/oligotrophic environment to a coastal/freshwater environment (Rae et al. 2011). Rae et al. (2011) reported the interesting case of a "hybrid" CCM in the  $\alpha$ -cyanobacterium, *Synechococcus* sp. WH5701. This organism possesses transcriptionally CO<sub>2</sub>-responsive  $\beta$ -type-Ci-transporters. Rae et al. (2011) also provided phylogenetic analyses which suggested that  $\beta$ -type CCM components were acquired by horizontal gene transfer events.

CCM is intimately related to many fundamental metabolisms neighboring photosynthesis, and thus CO<sub>2</sub> availability and the extent of CCM operation would influence these significantly. Kranz et al. (2011) reviewed the effect of *p*CO<sub>2</sub> increase on the bloom-forming marine cyanobacterium, *Trichodesmium erythraeum*. This diazotrophic, filamentous cyanobacterium exhibits extraordinary stimulation of growth and primary production, including N<sub>2</sub> fixation, in response to increase in *p*CO<sub>2</sub>. Stimulation of nitrogenase under light and subsequent higher N<sub>2</sub> fixation occurred concomitantly with the down-regulation of the HCO<sub>3</sub><sup>-</sup> transport under high CO<sub>2</sub>. This environmentally relevant phenomenon in a cyanobacterium is ascribed to a transition of energy supply from DIC uptake to N fixation rather than an increase in gross energy production.

Unlike the C<sub>4</sub> type biochemical CCM which captures CO<sub>2</sub> in an organic acid, the algal biophysical CCM maintains inorganic carbon as bicarbonate, throughout the process of uptake to its fixation by Rubisco and thus, any free CO<sub>2</sub> formed in the process, can readily leak out of cells, short-circuiting the flow of DIC. Araujo et al. (2011) demonstrated experimentally that, in the filamentous cyanobacterium, *Leptolyngbya* sp. CPCC696, originally obtained from Lake Erie, DIC transport increased as a function of light energy; after saturation, however, excess light excitation pressure seemed to be dissipated by DIC recycling both internally and at the plasma membrane. The dissipation of excess light energy due to the "short circuit" between uptake and leakage indicated a role for the biophysical CCM in short-term light acclimation.

Kern et al. (2011) reviewed the evolutionary origins of photorespiratory pathway in higher plants and concluded

that the chloroplastic and peroxysomal components of the pathway were most probably derived from a cyanobacterial endosymbiosis whereas the mitochondrial components were likely of proteobacterial lineage.

Molecular studies on the eukaryotic CCM still lag well behind those on cyanobacteria. The green alga, *Chlamydomonas reinhardtii*, is the most extensively studied eukaryote and recent accomplishment of genome sequencing, together with the establishment of an RNA sequence database and reverse genetics tools, enables this organism to be a model organism for the study of the green algal CCM. Wang et al. (2011) reviewed the recent progress in the study of the *C. reinhardtii* CCM and gave an analysis of the role of putative CCM components based upon transcriptome data. Key components, which have been found recently, for a pyrenoid-based CCM, LCIB/C, were described and a CO<sub>2</sub> recapturing hypothesis by LCIB/C complex surrounding the pyrenoid was proposed in the review. Also, candidate HCO<sub>3</sub><sup>-</sup> transporter proteins, required for transport across the plasma membrane, chloroplast envelope, and the thylakoid membranes, and a possible CO<sub>2</sub> channel, the Rhesus factor, HLA, were described (one of those, LCII, has now been shown to be HCO<sub>3</sub><sup>-</sup> transporter; Ohnishi et al. 2010).

The pyrenoid forming factor LCIB/C was found by the analysis of *pmp1* and *ad1* mutants of *C. reinhardtii*, which are unable to grow at air-level CO<sub>2</sub> but able to grow under very low CO<sub>2</sub> conditions. Duanmu and Spalding (2011) tried to isolated suppressor mutants for *pmp1* and *ad1*, which complement the “air-dying” phenotype of *pmp1* and *ad1*, and successfully obtained four lines of mutants. From physiological analyses of photosynthetic parameters of these mutants, the complex modes of the CCM, which require or are independent of LCIB, were revealed. Such complex modes of the CCM in *C. reinhardtii* and in other eukaryotic algae are tightly related to carbonic anhydrases (CAs), which probably function as DIC-flow controllers at specific subcellular locations. Moroney et al. (2011) reviewed the possible functions of multiple subtypes of CAs in *C. reinhardtii* based upon their localizations and expression profiles. In the review, the occurrence of a cryptic component of extracellular CA, CAH8, which might be a critical component to form CO<sub>2</sub> on the outside surface of the plasmalemma, was discussed. There were also two interesting hypotheses proposed in the review on the function of stromal CA, CAH6 as a barrier to CO<sub>2</sub> leaking from the chloroplast, and on the putative mitochondrial  $\gamma$ -CA moiety, which may be associated with the NADH dehydrogenase and function as a CO<sub>2</sub> converter analogous to the cyanobacterial system.

Mechanisms regulating the CCM in response to environmental CO<sub>2</sub> are an intriguing aspect of this research field. Yamano et al. (2011) reported the function of the

master regulator of CO<sub>2</sub>-responsive transcription of the CCM, in the green alga *Volvox carteri*, a multicellular alga closely related to *C. reinhardtii* indicated that *Volvox* possesses a CO<sub>2</sub>-inducible CCM. A putative master regulator gene for *Volvox* CCM, *Volvox CCM1*, was identified and sequence characteristics strongly suggested the function of this gene product is analogous to that in *C. reinhardtii*. CO<sub>2</sub> may also affect physiological states other than CCM. Dillard et al. (2011) tested an effect of low CO<sub>2</sub> acclimation on the cell-division cycle in *C. reinhardtii* and demonstrated that low CO<sub>2</sub> treatment caused an apparent arrest of ongoing cell division and that the cells were transiently synchronized, thus revealing a potentially new aspect of CO<sub>2</sub> response in eukaryotic algae. Baba et al. (2011) dissected the structure–function relationship of the promoter region of the H43/Fea1 protein gene, which is known to be stimulated at the transcriptional levels by both increments of *p*CO<sub>2</sub> and iron limitation under cadmium enriched condition. Loss-of-function assay of the promoter conjugated with an aryl-sulfatase reporter gene revealed that the promoter is multifunctional and possesses both CO<sub>2</sub> and iron responsive regions, which were regulated by each signal independently. Spijkerman (2011) reported on CCM regulation in the extremophilic green alga, *Chlamydomonas acidophila* under extremely acidic conditions (pH 2.4) with changing phosphorous and iron concentrations and demonstrated that the size of the internal DIC pool was related to maximum photosynthesis, and became significantly higher with a high phosphorous quota.

Primary production by marine eukaryotic algae has been shown to be a vital part of global primary production as revealed by extensive biogeochemical research over the last one and half decades, aided by recent developments of the remote-sensing technique. Diatoms are a predominant component of the marine phytoplankton and have been estimated to be responsible for one-fifth of global primary production. CCMs appear to be distributed widely among Chromoalveolates, which is the super group of eukaryotes that arose from secondary endosymbiosis and which includes diatoms. The increased awareness of the importance of diatoms in the global carbon cycle has greatly stimulated studies of the ultra-structure and molecular biology of diatoms in the last decade. Matsuda et al. (2011) reviewed recent progress on CCM study in marine diatoms. There is a significant body of physiological evidence that both CO<sub>2</sub> and HCO<sub>3</sub><sup>-</sup> are taken up by diatom cells from the surrounding seawater, but metabolic processes to deliver accumulated DIC to Rubisco is not clear and no molecular evidence exists at present. In this respect, it was proposed that CO<sub>2</sub> acquisition by diatoms may have undergone a significant diversification including the development of a C<sub>4</sub>-like system, which may also be related to a diversification of diatoms' cell size (Matsuda et al. 2011).

Molecular evidence of CAs localization strongly suggests that the function of the four-layered chloroplast membrane is the center of flow control of DIC. The Diatom CCM is also regulated by  $p\text{CO}_2$ , and recent progress in molecular studies on the transcriptional control of CCM components in response to  $p\text{CO}_2$  have revealed that cAMP is a second messenger (Matsuda et al. 2011). There are redundant CA genes in genomes of two model marine diatoms, *Phaeodactylum tricornutum*, and *Thalassiosira pseudonana* (Tachibanal et al. 2011). In *P. tricornutum*, all 5  $\alpha$ -CAs were localized at the four-layered chloroplast membrane system whereas the 2  $\beta$ -CAs were localized in the pyrenoid and one  $\gamma$ -CA in the mitochondria (Tachibanal et al. 2011), which provide a set of data to support the predominant operation of a biophysical CCM in *P. tricornutum*. In *T. pseudonana*, one  $\alpha$ -CA and one  $\zeta$ -CA were localized to the stroma and the periplasm, respectively and these CAs were induced under  $\text{CO}_2$  limitation (Tachibanal et al. 2011).

Diatoms are also one of the most likely candidate sources for biofuels because of their capacity to produce high amounts of triacylglycerols (TAG) and hydrocarbons. A chloroplast genome was determined of a recently isolated pennate, marine diatom *Fistulifera* sp. JPCC CA0580, a strain known for its high production of TAG (Tanaka et al. 2011). The chloroplast genome contained 134,918 bp and the protein-coding region was found to be almost identical to that of *P. tricornutum*. Although no noteworthy clue was found so far in the structure of the chloroplast genome to account for high TAG production in this diatom, the attempt is certainly the first important step for the industrial use of such high-lipid producing algae. In this context, McGinn et al. (2011) extended the discussion in his review on scaling up toward industrial algal biofuel production into account the many realistic practical constraints. Calculated energy density of algae including the diatom, *P. tricornutum* was about half the gasoline/diesel and equivalent to coal. But limitations in land area, sunlight density, and major nutrients (such as N and P) are severe for large scale cultivation. Feasibility to supply these critical factors by remediation technique and so on was proposed in the review (McGinn et al. 2011).

CCMs seem to occur in photoautotrophs belonging to most of the eukaryotic supergroups except unikonta, which does not accommodate photoautotrophs. However, the mode of algal DIC acquisition has undergone significant diversifications during evolution and thus not all photoautotrophs necessarily possess active CCMs. In one subgroup of heterokonta, synurophyte, complete lack of active uptakes of DIC and of development of internal DIC pool under active photosynthesis was reported by Bhatti and Colman (2011). It was also clearly demonstrated that this group of algae exhibit a typical Warburg effect, thus

indicated the occurrence of photorespiration (Bhatti and Colman 2011).

Micro-environments surrounding photoautotrophs in marine ecosystem are also variable and experience the daily and seasonal fluctuations of increase in pH and decrease in  $\text{CO}_2$  to different extents (Mercado and Gordillo 2011). Mercado and Gordillo (2011) proposed that the extent of saturation of algal photosynthesis reflects the physiological characteristics of  $\text{CO}_2$  acquisition machinery of habitat in each micro-environment.

In submerged grass, elodeids and isoetids, DIC uptake via Crassulacean Acid Metabolism (CAM) contributes significantly to the carbon budget (18–55%) and thus is of ecological importance (Klavnsen et al. 2011). In the review, Klavnsen et al. (2011) concluded that CAM is a carbon conserving mechanism for submerged grass enabling  $\text{CO}_2$  accumulation and recycling of respiratory  $\text{CO}_2$  in the night but does not inhibit DIC uptake in daytime.

One of our ultimate goals of algal CCM research is to obtain clues for logical estimates for the fate of algae in natural environment over the next few decades to century under continued climate change. Raven et al. (2011) pointed out in their review that environmental factors currently changing (such as  $p\text{CO}_2$ , temperature, light, nitrogen, phosphorous, iron, UV irradiation) may have direct effects on CCMs although current models of the effects of climate change on global primary productivity do not consider the role of CCMs. CCM is likely a factor, which can alter the primary productivity and incorporation of effect of environmental factors on CCMs into the prediction model thus will modify the conclusions (Raven et al. 2011). In the review, Raven et al. described the unreliability to use molecular clock approach, that is, estimate of CCM effect from organic matter deposit in ocean sediment, for the prediction model of the CCM effect, because of the lack of reliable fossil marker of the CCM and of the unclarity of timing of emergence of the CCM origin.

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