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Inorganic Carbon Concentrating Mechanisms

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This special issue provides an exciting update on the long standing question: how can algae and some photosynthetic bacteria be so effective in acquiring CO₂ from the environment? In the 1970s, the fact that Rubisco catalyzed the oxygenation of RuBP as well as its carboxylation was well understood (Jensen and Barr, 1977). In addition, all Rubisco appeared to have a fairly low affinity for its substrate CO₂. However, the high rates of photosynthesis measured with many algae and cyanobacteria at low CO₂ concentrations was in apparent contradiction to what we knew about Rubisco kinetics (Kaplan et al., 1980). In addition, most algae do not perform C₄-type photosynthesis – the only mechanism known at that time to concentrate CO₂ for photosynthesis.

To answer this question Joe Berry and Bill Lucas hosted, in 1984, a meeting at Asilomar, CA (Lucas and Berry, 1986; Kaplan, 2017) that turned out to be the starting point for a series of subsequent meetings on this topic. What was established at the time was the concept that most aquatic photosynthetic organisms had the ability to concentrate CO₂ for Rubisco, thus increasing the photosynthetic rate of algae and cyanobacteria at low CO₂ concentrations (Badger et al., 1980). This metabolic pathway became known as the CO₂ concentrating mechanism or CCM. Over time, C₄ photosynthesis was included in the CCM terminology, with C₄ photosynthesis involving a “biochemical CO₂ concentrating system” where CO₂ is first fixed into a C₄ organic acid, while most algae use a “biophysical CO₂ concentrating system” where inorganic carbon ($C_i = CO_2 + HCO_3^-$) is physically transported across cellular compartments and concentrated prior to fixation by Rubisco. Over the next few decades, our understanding of algal and bacterial CCMs grew immensely (Badger and Price, 2003; Giordano et al., 2005; Moroney and Ynalvez, 2007). We now understand that there are many types of CCMs, as most of the algal lineages diverged before CO₂ in the atmosphere was drawn down below the $K_m(CO_2)$ of Rubisco (Badger and Price, 2003; Iñiguez et al. 2020). While researchers have largely deciphered the CCMs of cyanobacteria and the green alga *Chlamydomonas reinhardtii*, more recently studies have elucidated the CCM of model diatoms (Tsuji et al., 2017). With that said, there are still many other photosynthetic organisms in which the CCM has not been greatly studied. Researchers also understand the ecological importance of the CCM. Almost 50% of the world’s photosynthesis is carried out by aquatic organisms (Field

et al., 1998). As such, the CCM plays a central role in the carbon cycle in all aquatic environments.

The articles in this special issue are largely based on presentations and discussions at the tenth International Conference on Inorganic Carbon Acquisition by Aquatic Photosynthetic Organisms, better known as CCM10, which was held in Princeton, NJ on July 6-9, 2022. The meeting was hosted by Martin Jonikas with help from Alistair McCormick and Luke Mackinder. The meeting was supported, in part, by the International Society of Photosynthesis Researchers.. CCM10 covered important topics such as the biogenesis of β -carboxysomes, the environmental and evolutionary context of CCMs, α and β -carboxysomes, the *Chlamydomonas* CCM, other Eukaryotic CCMs, including diatoms, and the engineering of CCMs to increase crop yields. Indeed, the potential for incorporating CCM components into crop plants to improve photosynthesis has resulted in increased publicity and funding for CCM research worldwide.

The papers assembled in this special issue reflect this diversity of CCM research. The *Chlamydomonas* CCM is the topic of two papers. Shimamura et al. (<https://doi.org/10.1007/s11120-022-00996-7>) investigate the regulatory factor CAS1 and convincingly show that the localization of the CAS1 protein to the thylakoid tubules is essential to its function. If the thylakoid tubules are not formed correctly, CAS1 cannot localize correctly and the CCM genes it controls are not regulated properly. The other *Chlamydomonas* contribution is from Kasili et al. (<https://doi.org/10.1007/s11120-023-01005-1>). They demonstrate that LCIB is an active carbonic anhydrase and can complement carbonic anhydrase knockout strains in both yeast and Arabidopsis.

Diatom CCM research is also the topic of two papers. Li and Young (<https://doi.org/10.1007/s11120-023-01004-2>) document how temperature affects the CCM in the *Phaeodactylum tricornutum*. In another contribution, Nawaly et al. (<https://doi.org/10.1007/s11120-023-01007-z>) study the θ carbonic anhydrases in *Thalassiosira pseudonana*. This same group first reported on this new class of carbonic anhydrases, the θ class, at the last CCM meeting, highlighting the impressive variety of carbonic anhydrase types present in algae.

Two more papers study the CCM in extremophiles. Aguiló-Nicolau et al. (<https://doi.org/10.1007/s11120-023-01008-y>) studies how the cyanobacteria

Chroococciopsis thermalis adapts to extremely high temperatures. Steensma et al. (<https://doi.org/10.1007/s11120-023-01000-6>) studies the extremophilic red algae *Cyanidioschyzon merolae* and how it acquires CO₂ under low pH and high temperature conditions. These contributions point to the emergence of novel CCM functionality in diverse environments.

Finally, there is a paper by Nguyen et al. (<https://doi.org/10.1007/s11120-023-01009-x>) describing novel carboxysome engineering approaches. This report discusses the potential to generate a hybrid carboxysome using a fast Form IB Rubisco in a genetically simple alpha carboxysome which could then be used to form a synthetic CCM in plants for improved photosynthesis. This ambitious project is part of an even larger effort to introduce a functional carboxysome-based CCM into crop plants (Long et al. 2018). Multiple groups around the world are working to introduce algal CCM components into plants and most of the present attempts are using either a carboxysome-based pyrenoid-based approach (Hennacy and Jonikas, 2020). This is partly because the CCMs from cyanobacteria and *Chlamydomonas* are best understood. One conclusion from the papers in this special issue and the presentations at CCM10 is that there are a wide variety of CCMs in nature and that more is to be mined to inform us of their potential applications. The more we study CCM diversity, the better we will be able to rationally design CCMs in crop plants.

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