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Carbon Fixation and Concentrating Mechanisms[1]

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OVERVIEW

The objective of the workshop was to identify and discuss dissolved inorganic carbon (DIC) concentrating mechanisms as they affect inorganic carbon uptake characteristics and growth of submerged freshwater and marine macrophytes. However, it was not anticipated that the discussion would reach any consensus. Rather, it was hoped that the discussion would inspire the participants in their research and help them to identify important new problems to be investigated.

Each of the topics addressed was briefly introduced by a presenter and then discussed by the workshop participants for about 15 min. The topics included the following areas.

WHAT IS A CONCENTRATING MECHANISM?

A concentrating mechanism was defined as a mechanism which increases the CO_2 concentration around the rubisco (ribulose bisphosphate carboxylase-oxygenase) carboxylation site to levels above that in the bathing medium. The rationale for choosing CO_2 as the concentrating carbon species was that it is the species used by rubisco. Concentrating mechanisms generally involve an active process; passive uptake of CO_2 only leads to a higher DIC pool in the cells (providing the pH of the bulk medium is lower than pH of the cytosol), not a higher CO_2 concentration *per se*.

METHODS FOR MEASURING INTERNAL CO_2

The methods which have been used so far to measure internal CO_2 in submerged macrophytes were described, and their advantages and limitations were identified. The methods are based either on measurements of oxygen release into CO_2-free water or on ^{14}C labeling and subsequent extraction of the inorganic carbon from the plant tissue with strong acid. None of these methods measures internal CO_2 directly. It must be calculated from measured (or estimated) internal pH. The ^{14}C method was considered preferable, as it gives a direct measure of internal DIC and also allows for the use of inhibitors to probe the system. The drawbacks are that it is destructive and very time-consuming. For both methods, the uncertainties surrounding measurements of internal pH, especially in regard to specific pH values in the various intracellular compartments, adds a significant degree of uncertainty to the estimation of internal free CO_2 from the DIC actually measured.

PHYSIOLOGICAL ASPECTS: C_4-LIKE SYSTEMS. HOW DO THEY WORK AND WHERE DO THEY CONCENTRATE?

Submerged macrophytes do not have Kranz anatomy or other anatomical features which could separate the C_3 and C_4 carboxylation processes spatially. It was agreed that an intracellular separation between the two carboxylation events is required for the operation of a C_4-type system, and it was suggested that the separation of these processes between cytosolic and chloroplastic components may be the answer. The discussion then focused on mechanisms by which the plants could maintain high internal CO_2 and avoid or counterbalance backflux. Finally, the need for studies of carbon uptake kinetics on isolated chloroplasts and protoplasts, which could give valuable information on the site of concentrating, and techniques to isolate chloroplasts/protoplasts were debated.

PHYSIOLOGICAL ASPECTS: HCO_3^- / CO_2 UPTAKE. HOW DOES IT WORK?

The widely accepted models for HCO_3^- uptake based either on (a) acidification of the cell wall/boundary layer via an ATP-driven pump and subsequent passive uptake of CO_2 derived from conversion of HCO_3^- or (b) a H^+/ HCO_3^- symport mechanism were described. Bicarbonate pumps may not be confined to the plasmalemma, but may also be located at the chloroplast envelope. The possible role of facilitated diffusion of HCO_3^- mediated by anion exchange proteins was discussed. It was agreed that such a passive mechanism could concentrate CO_2 internally only if the pH in the compartment where CO_2 is concentrated is lower than the pH of the bathing medium.

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COST EFFICIENCY OF DIC CONCENTRATING MECHANISMS

A theoretical balance sheet for inorganic carbon concentrating mechanisms was outlined. The balance sheet must include costs associated with synthesis, maintenance, and running of the carbon acquisition apparatus in plants with inorganic carbon concentrating systems relative to plants without such a system.

The cost efficiency will change within a canopy, and it is therefore important that the whole organism be taken into consideration when the cost efficiency of inorganic carbon mechanisms are evaluated.

ECOLOGICAL ROLE(S) OF INORGANIC CARBON CONCENTRATING MECHANISMS

The ecophysiological functions of inorganic carbon concentrating mechanisms were defined as the means to (a) reduce the $[O_2]/[CO_2]$ ratio at the site of fixation by rubisco, thus allowing it to operate closer to its maximum; (b) maintain the flux of inorganic carbon into the cell at low external DIC concentrations; and (c) minimize the loss of photorespiratory CO_2. Consequently, species possessing a concentrating system would be expected to have a competitive advantage in (a) habitats low in DIC; (b) habitats with substantial depletion of CO_2 and HCO_3^- during the day due to photosynthetic activity; and (c) dense mats where photosynthetic depletion of carbon is common. The carbon concentrating systems in submerged macrophytes are inducible systems which are activated/induced only under certain environmental conditions and are not always operative. The environmental parameters responsible are not fully elucidated, but the concentration of DIC may play a key triggering-role, as carbon concentrating systems can be induced under carbon limitation or stress. Finally, management implications of the invasion of species with efficient carbon concentrating systems, such as *Hydrilla verticillata* and *Myriophyllum spicatum*, were discussed. Although no consensus was reached, it was suggested that the degree to which this characteristic adds to the weed potential of certain aquatic plants needs to have more attention paid to it.