are required for splicing at a downstream A-G. It will be interesting to see whether this analogy will extend further. One difficulty is that A-G has been seen at positions -5, -4 in two vertebrate introns^{13,14}.

A second possibility, advocated by Rosbash's laboratory, is that UACUAAC, present in the mRNA precursor, plays a part in 5' splice-site recognition. They have observed that UACUAAC is itself a site of cleavage. In trying to understand this result they noticed that the 5' end of the U1 RNA, which is proposed to recognize 5' splice sites¹⁵⁻¹⁷, is homologous to UACUAAC (the U1 sequence is UACUUAAC). Thus, they reasoned that UACUAAC might interact with the 5' splice site, the cleavage of UACUAAC resulting in some way from this interaction. This proposal is supported by their observation that UACUAAC cleavage is inhibited in a 5' splice-site mutant.

Whichever possibility is upheld by later results, research on splicing in yeast should elaborate a mechanism of splice-site

recognition that could apply, if only in altered form, to higher organisms. □

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Plant ecology

Photosynthetic pathways in aquatic plants

from Peter D. Moore

THE C_4 and crassulacean acid metabolism (CAM) photosynthetic systems are generally associated with terrestrial plants growing in habitats where water stress and high temperature are frequently encountered¹⁻³. The efficiency of carbon accumulation resulting from the elimination of photorespiration permits these plants the luxury of closer stomatal control leading to lower water losses. In the case of CAM plants, stomata open for gaseous exchange only at night when potential water losses are minimal.

Some C_4 species are known from marine saline habitats such as estuaries and salt marshes, for example *Spartina anglica*⁴, but it is surprising to find that some of the biochemical features associated with this photosynthetic strategy have been described recently in submerged freshwater aquatic plants. One such plant is the Canadian pondweed, *Elodea canadensis*⁵. When *Elodea* was supplied with $^{14}CO_2$, 45 per cent of the label ended up in C_4 acids rather than C_3 compounds.

One possible explanation of the occurrence of such a pathway in an aquatic plant is the diurnal fluctuation in dissolved carbon dioxide in a freshwater body, especially if it contains a high density of aquatic plants. Carbon dioxide concentration would tend to be high during the night and low during the day, when it would be in demand for photosynthetic fixation. A mechanism whereby night fixation of CO_2 could take place (as in CAM plants) could therefore be of considerable selective

value. But although a C_4 mechanism is present, there is no evidence of nocturnal net carbon uptake occurring in *Elodea*.

Work on other aquatic plants, however, has shown that at least some species can enhance their carbon metabolism by nighttime fixation. For example, the North American submerged water plant *Scirpus subterminalis* has been shown to accumulate malate during the dark (at least in part derived from respiratory CO_2) which accounted for 12 per cent of the net photosynthesis⁶.

Whilst working with another aquatic macrophyte, *Hydrilla verticillata*, Holaday and Bowes⁷ found a considerable variation in CO_2 compensation point (the CO_2 concentration below which a plant takes up less CO_2 by photosynthesis than it gives out by respiration), which depended on growth conditions. Winter collections had high compensation points and summer collections low ones. The plants with low compensation points, when provided with $^{14}CO_2$, showed a 60 per cent incorporation of labelled carbon into the C_4 acids malate and aspartate, and a high activity of phosphoenolpyruvate carboxylase, the first enzyme in the C_4 fixation pathway. Clearly these plants have the ability to vary the CO_2 compensation point in response to environmental demands by the facultative assumption of a C_4 fixation system.

Just how widespread C_4 fixation is among water plants is not yet known, but Keeley and Morton⁸ have recently conducted a survey of 30 species of aquatic

plants found in a variety of pools and lakes, ranging from oligotrophic to eutrophic, and have found only two species which showed overnight accumulation of acids. These are *Crassula aquatica*, a plant of the margins of temporary ponds, and the shoreweed, *Littorella uniflora*, found mainly along the gravelly edges of nutrient-poor lakes with fluctuating water levels. The authors interpreted their results as support for the hypothesis that aquatic plants can increase their efficiency of carbon utilization in this way under conditions where carbon availability is likely to be growth limiting.

From a taxonomic and an evolutionary point of view, one of the most interesting groups in which such diurnal acid metabolism has emerged is the fern *Isoetes*. The mechanism seems to be very uncommon among pteridophytes, having previously been reported only in two tropical ferns⁹, and it was first reported in *Isoetes* by Keeley¹⁰. He found an overnight accumulation of malic acid in the leaves of *Isoetes howellii*, which grows in seasonal pools produced by the winter and spring rains of California, which dry out during the summer drought. Keeley has since surveyed 11 other *Isoetes* species¹¹ (the genus contains about 70 species in all) derived from locations as far apart as Guatemala, British Columbia and North Wales. All the species were found to exhibit diurnal acid metabolism, and Keeley has proposed⁸ that it may be present in all members of the genus. Many of the species, like *I. howellii*, become emersed during dry periods and the diurnal variations in leaf acid content then become less marked.

These studies are of interest and importance both in their further demonstration of the taxonomically widespread nature of C_4 and CAM mechanisms of carbon fixation and also in that they indicate another ecological advantage of such a mechanism in an unexpected habitat. In this case, a daytime shortage of dissolved inorganic carbon for use in photosynthesis in aquatic ecosystems has led to the evolutionary selection of a biochemical pathway which has previously been associated largely with arid environments where its value relates to economy in water loss rather than a general scarcity of carbon. □

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