PLANT BIOCHEMISTRY

Mutant Alga Blurs Classic Picture of Photosynthesis

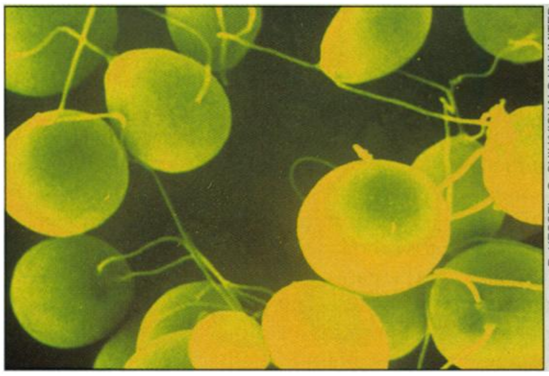
As perhaps the most important reaction in biology, photosynthesis has long been a target of study by plant biochemists. Indeed, for nearly 3 decades researchers have been fairly confident that they understand how the photosynthetic machinery uses light energy to manufacture both oxygen and the sugars and other carbohydrates that ultimately feed all living organisms. But work reported on page 364 by biochemist Elias Greenbaum of Oak Ridge National Laboratory in Tennessee and his colleagues is now challenging one of the longest standing tenets of photosynthesis.

The classic view of photosynthesis, developed in the 1960s, holds that the reaction requires the cooperation of two protein-pigment complexes, known as photosystems I and II (PSI and PSII). In the first step of this process, called the "Z scheme" because of the zigzag way the reactions are written, photons strike pigments, such as chlorophyll, in PSII, which use their energy to split water molecules, releasing molecular oxygen, hydrogen ions, and electrons. The electrons thus freed are then transferred to PSI, where, with energy from more photons, they chemically reduce the molecule nicotinamide adenine dinucleotide phosphate ($NADP^+$). The reduced $NADP^+$ is needed to convert carbon dioxide into sugars and other carbohydrates.

But the Oak Ridge team has studied mutants of a single-celled alga called *Chlamydomonas reinhardtii* in which PSI is disabled and found that the organism still thrives in normal conditions. This result suggests that the mutants can carry out photosynthesis with just PSII. While not all researchers are yet ready to accept that idea, if the Oak Ridge team turns out to be right, the results may force researchers to consider the possibility that there may be alternatives to the Z scheme. The result may also throw light on the evolution of photosynthesis. "It's one of the most significant stories to emerge in recent years," says biochemist Gregory Schmidt of the University of Georgia, Atlanta.

Greenbaum and his team are not the first to consider alternatives to the Z scheme. Daniel Arnon of the University of California, Berkeley, a distinguished photosynthesis expert who died last year, had long argued that photosynthesis could be driven by PSII, independent of PSI. Indeed, there were hints from earlier work that PSII might be able to both split water and reduce $NADP^+$. But few researchers were convinced by the results: The yields of reduced $NADP^+$ were very low and the work was done with plant extracts, raising the possibility that the $NADP^+$ reduction was an artifact, brought about by a reaction that is not important in intact organisms.

Last summer, however, Greenbaum and his colleagues reported in *Nature* that intact cells of a strain of *C. reinhardtii*, which they selected from a library of experimental mutants and found to be lacking in PSI, were able to assimilate carbon dioxide and split water molecules when exposed to light in culture. But while that finding suggested that photosynthesis was taking place in the absence of PSI, an organic nutrient, which might have provided an alternate energy source, was present in the cultures. The response of the research community was accordingly cautious: At the triennial congress on photosynthesis, held last year in Montpellier, France, "there was skepticism among many researchers" about the result, says biochemist Bertil Andersson of the University of Stockholm.



R. KESSEL, G. SHIH/VISUALS UNLIMITED

Is one enough? The *C. reinhardtii* cells shown here may be able to photosynthesize with just PSII.

But Greenbaum's team has now found the same signs of photosynthesis when the mutant cells were cultured in either aerobic or anaerobic conditions, with normal light levels, but without organic nutrients. Not only that, but they survived for long periods and the patterns of growth were similar in mutant cells in anaerobic or aerobic conditions, which suggests that other respiration activities, occurring only in aerobic conditions, were not responsible for the observed growth. The implication is that in these cells PSII does the whole job, splitting water and reducing $NADP^+$, and using only half the number of photons envisaged in the Z scheme. "It was really unexpected," says Greenbaum.

The team's new results have received cautious welcome from some researchers. "Last year I was hesitant about the work, but now I feel much more comfortable," says biochemist Himadri Pakrasi of Washington University in St. Louis. But others remain skeptical. They note that Greenbaum's team has not demonstrated directly that the PSI system has been lost, raising concerns that the mutant cells retain undetected PSI activity. "It's vital to get genetic evidence that the PSI genes are deleted or inactivated," says Andersson.

In response, Greenbaum notes that he and his colleagues were unable to find a key PSI protein in the mutant cells either before or after the period of growth. They also checked for PSI function by examining whether light of the wavelengths PSI is normally sensitive to was in fact being absorbed by the mutant cells, but they saw no evidence that it was. "Statistical error suggests that there may be up to 3% of the normal activity of PSI in the mutant cells, but that would not be enough to explain our results," Greenbaum maintains. The mutant cells, he says, are not totally normal, but are larger and multiply at 60% to 70% of the rate of wild-type cells. In spite of this evidence, some researchers are also anxious for quantitative measurements of photon uptake and details of how electron transfer takes place in the mutant cells. Many would also like to see the finding confirmed in other organisms.

Still, there is no doubt that researchers are now having to take notice of these uncomfortable results, says Andersson, and they may lead research in new directions. For example, the work has implications for the evolution of photosynthesis: PSII may have evolved first under the more anaerobic conditions that existed before photosynthesis caused oxygen to accumulate in the atmosphere. The PSI scheme may therefore have evolved to stabilize PSII under changing atmospheric conditions, Greenbaum speculates: "The Z scheme may turn out to be nothing more than a specialist adaptation to provide a protective mechanism for cells in an oxygen atmosphere."

So will the next photosynthesis congress be buzzing with the new work? Greenbaum points out that the new results are not challenging the existence of the Z scheme, but do suggest that it might be short-circuited under certain conditions. "It's just that there may be an alternative," he says. But he faces a substantial task in convincing his colleagues. "The scientific community puts a heavy demand on this kind of claim," says Andersson. "We'll have to wait and see."

–Nigel Williams