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Photosynthesis in the Open Ocean

Jonathan P. Zehr, *et al.*

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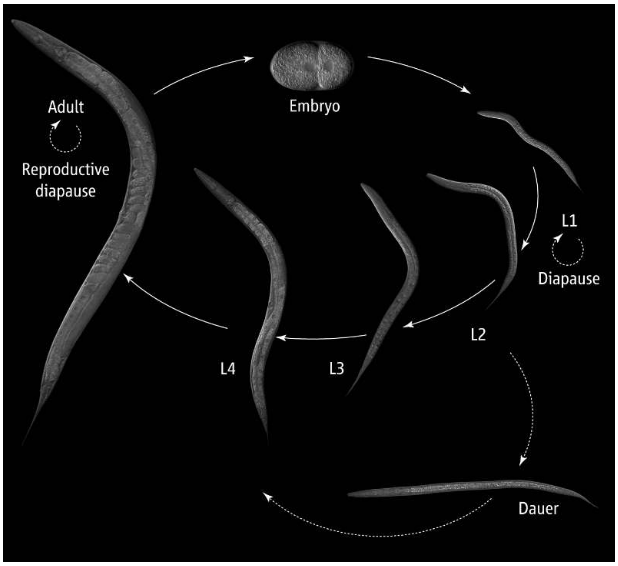

A worm's life. Self-fertilizing *C. elegans* lay eggs that complete embryogenesis in 14 hours (25°C). Four larval stages (L1 to L4) follow before a worm becomes an adult. Under stress conditions, young larvae enter the dauer stage, an arrested long-living dispersal stage. Young larvae can also arrest at the L1 stage, and adults can enter reproductive diapause.

The dauer stage of *C. elegans* is not only a survival strategy; it also helps dispersal of the organism by facilitating association with invertebrates. This phenomenon is thought to represent an evolutionary trend toward parasitism (*10*). Indeed, experimental support for a conserved endocrine mechanism that controls the formation of dauer and infective larvae in nematodes (*11*, *12*) indicates that a more detailed understanding of *C. elegans* dauer regulation might result in long-term practical applications.

Despite the long-standing interest in dauer development, *C. elegans* researchers have focused little on other survival strategies. This is surprising, as the dauer stage is an option to escape unfavorable conditions only for young larvae. Animals in other stages must find different means to cope with the environment. Angelo and Van Gilst describe an additional survival strategy of adult *C. elegans*. Starvation induces adult reproductive diapause, a delay of reproduction that results in increased longevity and protection of germ stem cells. By contrast, most other germ cells undergo programmed cell death (apoptosis), possibly providing nutrition (through resorption) required for survival. The gene *nhr-49*, which encodes a nuclear hormone receptor, controls adult reproductive diapause entry and exit, whereas the gene *daf-12* encodes another nuclear hormone receptor that controls dauer formation (*13*). These similarities strongly illustrate the importance of endocrine signaling in nematode survival strategies.

These two studies further establish nematodes as a unique model for studying animal survival strategies and the environmental regulation of life histories. One interesting aspect is that the genes involved in dauer pheromone sensing and adult reproductive diapause both belong to gene families that have undergone recent gene duplication (*14*, *15*). Such duplicated genes are believed to supply building blocks for new features without affecting preexisting biological systems. However, the function of duplicated genes is often hidden by redundancy, leaving open the possibility that the full complexity of environmental regulation escapes genetic analysis.

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OCEAN SCIENCE

Photosynthesis in the Open Ocean

A little-understood electron flow pathway helps cyanobacteria to adapt to high-light, low-nutrient ocean environments.

Jonathan P. Zehr and Raphael M. Kudela

Global primary productivity (the fixation of carbon dioxide, CO_2, into organic matter) fuels food production on land and in the sea. About half of this CO_2 fixation occurs in the sea, mainly by a type of phytoplankton called cyanobacteria (*1*). Recent reports (*2*–*4*) have shown that a key characteristic of oxygenic photosynthesis—the electron flux through photosynthetic reaction centers coupled to oxygen (O_2) evolution—is variable, thus uncoupling oxygen cycling from CO_2 fixation. This insight has implications for how phytoplankton have adapted to the marine environment and for how we measure the productivity of the oceans.

During oxygenic photosynthesis, energy is captured by linear electron transfer through two multiprotein reaction centers, or photosystems, coupled with reduction of CO_2 to sugars in the Calvin cycle. In a perfect world, the coordinated linear electron flow reactions (see the figure, panel A) would stoichiometrically couple O_2 production with CO_2 fixation, without a need for alternate pathways, and measurements of O_2 production or CO_2 fixation would estimate primary productivity, whereas fluctuations in fluorescence intensities would directly represent electron transport rates between photosystems (*5*). However, although linear electron flow from water to carbon is the most important pathway, because it results in CO_2 fixation, other pathways become important under suboptimal growth conditions, allowing photosynthetic organisms to balance input of light energy with production of adenosine triphosphate (ATP) and reductant.

Well-known examples of such pathways include the Mehler reaction, in which electrons are cycled around the photosystem I (PSI) complex, and the use of cytochrome oxidase to reduce O_2, forming water and ATP. Previously reported light-stimulated oxidation of photosynthetic electron carriers, or chlororespiration (*6*), was found to at least partially involve a third pathway using plastoquinol oxidase (PTOX). Recent papers (*2*, *3*) suggest that this pathway (see the figure, panel B) may be more widespread in open

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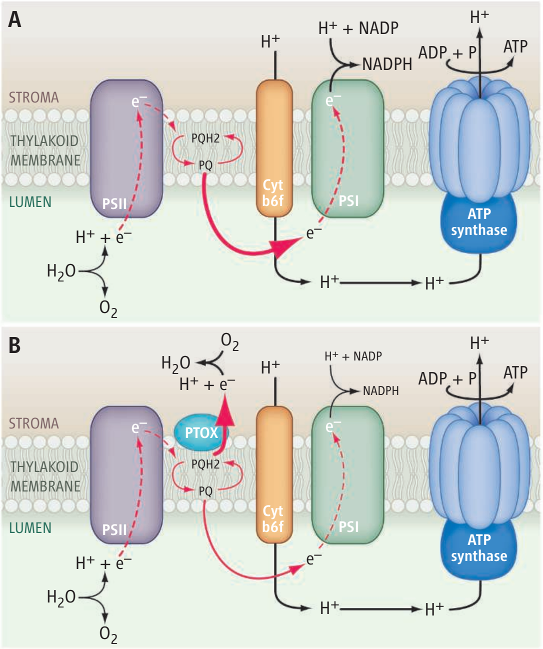

Photosynthesis with a difference. Light harvesting leads to linear electron transport through photosystems PSI and PSII. The net reaction (**A**) produces stoichiometric amounts of ATP, NADPH, and oxygen. When the PTOX electron valve is activated (**B**), electrons are siphoned away from PSI to PTOX, mediating the reduction of oxygen back to water. The result is dissipation of light energy with reduced O_2 and NADPH production and reduced CO_2 consumption while maintaining ATP production.

ocean cyanobacteria than previously recognized. The PTOX pathway provides an electron valve after PSII, allowing the cell to avoid photoinhibition and photosystem damage while producing ATP. This electron valve bypasses PSI, uncoupling PSII and PSI activities and thus changing the stoichiometry of O_2 production and CO_2 fixation.

Photosynthesis is affected by various environmental factors. In the sea, temperature, light quality and quantity, and nutrient availability are the main variables that determine the ability or efficiency of organisms to transform light energy into chemical energy and fixed carbon. Nutrients and trace elements, especially iron, are at vanishingly low concentrations in much of the open ocean, and iron limits photosynthetic production over large regions of the ocean (*7*). In these regions, the ratio of PSII to iron-rich PSI is lower than it is in iron-replete regions (*8*).

To maximize efficiency, the rate of light harvesting at PSII has to equal the rates of electron transfer from water to the PSI reaction center. If electrons are not transferred fast enough, the gateway between light harvesting and electron transfer in PSII is closed or reduced; given that single-celled algae cannot easily escape high light intensities, photodamage occurs if the electrons are not shunted to another acceptor. Various organisms take advantage of PTOX as an electron valve between PSII and PSI (*2*–*4*). PTOX only requires 2 iron molecules (compared with 6 for cytochrome b6f and 12 for PSI), allowing the cells to survive in low-iron environments. When necessary, linear electron flow is reduced, and the electrons are transferred from PSII through PTOX back to O_2 in a closed loop, reducing the electron flux to the Calvin cycle and consuming O_2.

These alternate electron flows provide ecological advantages for organisms in the high-light, low-nutrient environment of the open ocean. O_2 cycling around the photosystems does not change the fundamental operation of light energy harvesting and carbon fixation; its importance lies mainly in enabling phytoplankton to adapt to variable light environments. However, these seemingly minor molecular-scale changes can also have implications on ocean basin scales, because they affect the efficiency of photosynthesis and provide a mechanism for protecting the photosynthetic apparatus, while also impacting measurements of oceanic production.

The PTOX pathway may have implications for photosynthesis rate measurements. Although the pathway provides an ecological advantage, measured changes in O_2 concentrations should still be correlated with CO_2 fixation, because electrons simply cycle through PTOX (with no net change in O_2 and no CO_2 fixation). Carbon fixation is associated with linear electron flow, which produces stoichiometric amounts of O_2. Thus, the net change in O_2 should still be correlated with net CO_2 fixation.

Chlorophyll fluorescence data have been widely used to measure the rate of energy transfer from photosynthetic pigments to the reaction centers, allowing electrons to be tracked directly. These data are generally well correlated with O_2 evolution. By keeping PSII oxidized, the PTOX electron shunt effectively decouples fluorescence from oxygenic photosynthesis. Even though the PTOX pathway thus complicates primary productivity rate measurements using fluorescence, it appears that at global scales, fluorescence measurements remain a robust proxy for assessing phytoplankton physiology and productivity (*9*).

Both prokaryotic (*2*, *3*) and eukaryotic (*4*) algae can generate ATP from the PTOX pathway without producing reductant. This source of ATP could be physiologically advantageous to support processes such as active transport of ions (especially nutrients), synthesis of macromolecules, nitrogen fixation, and activation of metabolic pathways.

Ultimately, NADPH is needed for both carbon and nitrogen assimilation, and it remains unclear how the cell uses the excess ATP to maintain chemical and energy balance. The ratio of electron transfer and oxygen production to carbon fixation is flexible, ranging from O_2 production to CO_2 fixation ratios of ~1 to 1.6 or greater (*10*); this highlights the many uses for ATP and reductant in the cell besides CO_2 fixation (*11*). Fluorescence measurements track the total electron flow, not the number of electrons diverted to PTOX, and fluorescence exceeds measured CO_2 fixation rates by a factor of five or more, with a surprisingly diverse rates and ratios among algal species (*10*). Taken together, the recent reports (*2*–*4*, *10*) provide a mechanistic basis for deviations between electron transfer and CO_2 fixation and highlight the need to think carefully about how these measurements relate to CO_2 fixation.

The PTOX pathway may be a ubiquitous feature of high-light, low-nutrient ocean regimes, but many details remain elusive. Which organisms use alternate electron pathways, and how often do they do so? Is this process restricted to well-lit surface waters and mainly cyanobacteria, and does this change our interpretation of vertical profiles of photosynthetic processes, or satellite-derived proxies? Does iron limitation really lead to reduced PSII:PSI ratios in natural populations of cyanobacteria that are limited by other nutrients as well as iron? Intriguing possibilities for the PTOX pathway include mitigation of chronic iron limitation, enhanced nitrogen fixation, or acquisition of scarce macro- and micronutrients. These adaptations should be considered in any scenario of how the ocean's biogeochemical cycles are likely to operate in the near future.

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