PHOTOSYNTHESIS

The simplicity of robust light harvesting

A universal design principle underlies photosynthetic antenna systems

By Christopher D. P. Duffy

Photovoltaic light harvesting can achieve a quantum efficiency that approaches 100% (that is, the conversion of 100 photons of light into 100 chemically available electrons), and yet it displays notable robustness in the face of ever-changing external light conditions. Although light harvesting varies in structure and composition across the range of photosynthetic life, there is an ongoing effort to uncover a set of common “design” principles for these systems. On page 1490 of this issue, Arp et al. (1) have revealed the first hints of a simple, seemingly universal set of rules that define the robustness of natural light harvesters. These rules should inform the design of future solar technology.

The main challenge facing early photosynthetic life was the paucity of light that was characteristic of marine environments. This led to the evolution of the light-harvesting “antenna”—a large modular assembly of various pigment-binding proteins that absorbs and delivers energy to the photosynthetic reaction centers (2). Despite major structural and compositional differences, it has become apparent that antenna systems share several common features (3, 4). Each antenna harbors more than one type of pigment. For example, light-harvesting complex II (LHCII), the major antenna protein of plants, binds chlorophyll a and b and several carotenoids. This allows broader coverage of the solar spectrum, which is further enhanced by the fine-tuning of each pigment by its local protein environment. A mixture of pigments is bound at a high density but with specific relative distances and orientations, resulting in energy transfer that is fast and directional. The distribution of different pigments and their specific interactions with the protein ensures irreversibility, with energy flowing downhill to the photosynthetic reaction center rather than lingering in the antenna. It has been argued that these systems owe their efficiency to nontrivial quantum effects (5), although this has been recently challenged (6). Regardless, photosynthetic light harvesting is considered to be a biological mechanism that is finely tuned for efficiency.

Efficiency, however, can be detrimental under strong light conditions. A mismatch between an antenna’s ability to deliver energy and the finite maximum working rate of reaction centers can result in oxidative damage called photoc pituation (7). Although effective repair mechanisms exist, they are slow and metabolically costly. Therefore, a suite of reg-

**REFERENCES AND NOTES**

2. S. Daly, F. Rossu, V. Gabeleca, Science 368, 1465 (2020).

10.1126/science.abc1294

Photosynthetic antenna that handles the noise

An antenna binding at least two different types of pigments, whose absolute and relative absorption wavelengths are finely tuned, can convert a fluctuating (i.e., noisy) input into a consistent (i.e., quiet) output.
ulotary and protective processes is in place to minimize damage. The fastest regulators activate within minutes and relax on a similar time scale when light returns to normal (8), but these arguably still lag behind the fastest fluctuations in light intensity (9).

As well, light harvesting is not finely tuned in a molecular sense. Instead, the picture is one of robustness in the face of external conditions (10) and even genetic manipulation. An extreme example is found in the model plant Arabidopsis thaliana, from which LHClI is eliminated through genetic manipulation. In response, an ersatz antenna is formed from assemblies of the remaining minor light-harvesting proteins (11). Although these mutant plants may not thrive like their wild-type counterparts, they are certainly photosynthetically competent. If there is some universal organizational principle behind light harvesting, it does not appear to lie in the molecular detail.

Arp et al. have taken a new approach to investigating the question of universal organization. By applying network theory, they have determined the most basic organizational requirements necessary for a light-harvesting system to function optimally. The authors used a very generalized model of the antenna as a network of interconnected sites that can represent individual pigment states within delocalized multipigment states across the antenna. Energy enters this network from one or more input channels that reflect light absorption through different types of pigments. Two input channels were chosen as a minimal model (see the figure), which is reasonably representative of several real antenna systems, such as chlorophyll a and b in LHClII or bacteriochlorophyll c and e in the antenna of green sulfur bacteria (12). Absorbed energy can take many different paths through the antenna. However, all paths terminate at a single output channel representing photon-induced charge separation. Such a system is subject to a high degree of input noise. External noise comes from rapid fluctuations in the incident radiation, whereas internal noise originates from the structural dynamics of the antenna. This results in a noisy output that fluctuates between underpowered, optimal, and overpowered states. The underpowered state is metabolically insufficient, whereas the overpowered state risks photoinhibition. The question then is whether the inputs are arranged in such a way that the output spends most of its time at the optimal state, thereby minimizing output noise.

The input channels represent different groups of light-absorbing pigments. As such, they are each defined by the wavelength and rate at which they absorb. If their intrinsic rates (determined by chemical properties and stoichiometry) are assumed to be identical, then the overall rate of absorption is determined solely by the intensity of available light at that wavelength. Consider, for example, two limiting regimes. If the two channels are identical (i.e., a single channel), then antenna homogeneity minimizes internal noise. However, having a single absorbing species makes the system very sensitive to external noise. Conversely, if the two channels differ strongly in both wavelength and absorption rate, then internal noise dominates. Optimum output is generated in an intermediate regime where the two inputs have similar wavelengths but different absorption rates. This is achieved by locating the pair in a region of the spectrum of available light that has the steepest gradient. With only this consideration in mind, Arp et al. predicted, with a high degree of accuracy, the absorption profile of green plants, purple bacteria, and green sulfur bacteria.

The finding of Arp et al. is important because it suggests that the evolutionary driving force behind the development of photosynthetic antennae is not maximization of efficiency but the cancellation of noise. "...the evolutionary driving force behind the development of photosynthetic antennae is not maximization of efficiency but the cancellation of noise."

NEUROBIOLOGY

Guide cells help navigate axon regeneration

Rebuilding the flatworm visual system after injury requires guidepost-like muscle cells

By Rachel Roberts-Galbraith

During embryonic development, neurons project nascent axons that navigate through space to find their targets. Axonal-growth paths forged by these pioneer axons depend on chemical and physical cues from cells that can include guidepost cells, which directly interact with nascent axons and induce them to grow, stop, or turn (1). A series of guidepost cells can serve as "stepping stones" to organize the complex growth of an axon in space (2, 3). Although guidepost cells direct axon formation during embryonic development in diverse model organisms, their existence often is transient. Thus, it was unclear whether guidepost-like cells promote axon regeneration and whether regenerative guidepost cells are constitutive or induced by injury. On page 1447 of this issue, Scimone et al. (4) pinpoint regenerative guidepost-like cells in the visual system of freshwater flatworms called planarians.

Planarians are well known for their ability to regenerate diverse cell types in predictable patterns even in the face of severe injuries or amputations (5). One of the most recognizable features of the planarian body is a pair of crossed eyespots, which consist of pigment cells that form optic cups and photoreceptor neurons that nestle their photosensitive elements within the pigmented cups (6). From the eyespots, planarian photoreceptor neurons project axons through space to connect to the cephalic ganglia (a bilobed, horseshoe-shaped brain). The eyespots are positioned dorsally and the brain ventrally in the planarian head. Thus, photoreceptor axons must project ventrally and also turn to make either contralateral or ipsilateral
The simplicity of robust light harvesting
Christopher D. P. Duffy

Science 368 (6498), 1427-1428.
DOI: 10.1126/science.abc8063