that the absorbance of light can be readily measured, the gas-phase DNA ions are dilute. Instead, Daly *et al.* use the mass spectrometer to measure the action of the polarized light on the DNA molecule. Facile release of a photoelectron upon irradiation gives a signal caused by the formation of the charge-reduced anion. The laser light pulses are polarized, so the efficiency of photoelectron removal depends on the helix handedness. By monitoring the intensity of the distinctive charge-reduced species as a function of the polarization, they are able to determine the chirality of the molecule. This type of experiment can isolate any given molecular complex because each analyte is unequivocally defined by its mass-to-charge ratio.

Prior work by this group revealed coexisting structures formed by oligonucleotides in the presence of cations or organic molecules (*4*); this work was aimed at understanding the balance of forces that guide folding and self-assembly. Stoichiometry and quantitative measurements of nucleic acid complexes were readily made by combining mass and ion-mobility spectrometries, but this approach could not determine chirality or details of secondary structure. Mass-resolved electronic CD ion spectroscopy complements other structural mass spectrometry methods because it can provide secondary structure information in addition to molecular identity.

Daly *et al.* also studied complexes of DNA with ammonium and potassium counterions and obtained a tantalizing glimpse of the effects of individual molecule solvation. The wavelength dependence of the action of polarized light followed the same trend as data obtained in solution, albeit with differences in magnitude, indicating that structures are preserved and that these gas-phase results are relevant to molecules in solution. They extended their measurement on human telomeric DNA sequences to determine enantiomeric ratios of mixtures of G-quadruplex topologies. Intriguingly, the difference in electron-detachment efficiency for the left-handed molecule and the right-handed molecule under a given circularly polarized light is equivalent to the slight enantiomeric excess in the products—up to 1% at some wavelengths—thereby demonstrating the high sensitivity as well as the potential of this new method. ■

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PHOTOSYNTHESIS

The simplicity of robust light harvesting

A universal design principle underlies photosynthetic antenna systems

By **Christopher D. P. Duffy**

Photosynthetic 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 are 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 photoinhibition (*7*). Although effective repair mechanisms exist, they are slow and metabolically costly. Therefore, a suite of reg-

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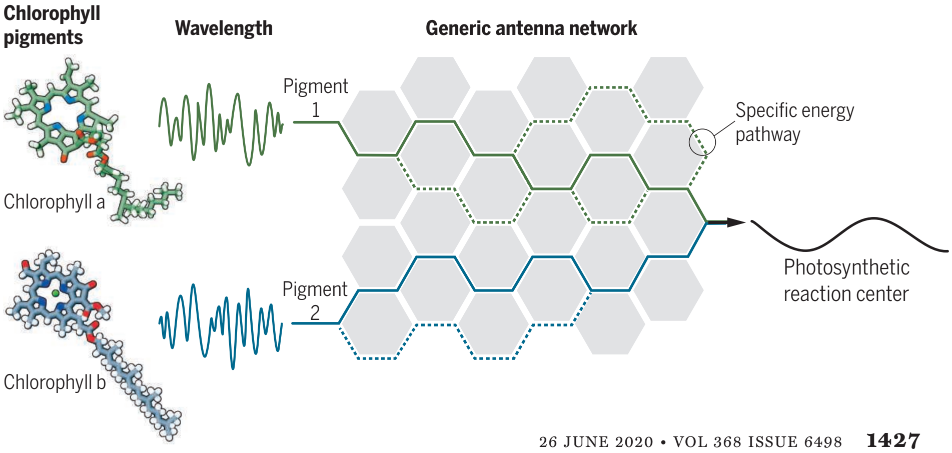
Photosynthetic antenna that handles the noise

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.



GRAPHIC: N. CARY/SCIENCE

ulatory 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 LHCII 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

"…the evolutionary driving force behind the development of photosynthetic antennae is not maximization of efficiency but the cancellation of noise."

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 LHCII 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 photoinduced 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. Moreover, the finding indicates that to build such a system, one must start from the simple requirements of two similar absorbing species that are tuned to the steepest region (not the strongest) of the spectrum of available light. Fine structural details are important, but they come as refinements to this simple underlying principle. ■

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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

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