



Bacteria “Read” Light To Gain a Competitive Advantage

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ABSTRACT Photosynthesis, the process of converting solar energy into stored chemical bonds, represents the primary mechanism by which biological organisms utilize photons. Light can also be used to activate a number of photosensory compounds and proteins designed to carry out tasks, such as DNA repair, gene regulation, and synchronization with the diurnal cycle. Given that sunlight is incident upon many environments, it is not farfetched to think that life may have evolved other as-yet-undetected mechanisms to profit from solar irradiation. In this issue, Maresca and coworkers detail their observations of light-enhanced growth of several non-photosynthetic actinobacteria, as well as describe the potential photosensitizer responsible for this phenotype and discuss the regulatory networks involved (J. A. Maresca, J. L. Keffer, P. P. Hempel, S. W. Polson, et al., *J Bacteriol* 201:e00740-18, 2019, <https://doi.org/10.1128/JB.00740-18>). This study opens the door to many intriguing questions about the use of light as information in nonphotosynthetic biological systems.

KEYWORDS *Actinobacteria*, cryptochrome, *Cyanobacteria*, energy efficiency, light, photosynthesis

Light is responsible for life as we know it. The advent of photosynthesis allowed an organism to extract energy from photons and store it in chemical bonds, ultimately coupling this energy to its metabolism in order to survive and grow. Oxygenic photosynthesis subsequently changed the atmospheric landscape of Earth, leading to a flush of life and biomass, without which life would look dramatically different (1). Over millions of years, decaying biomass, and animals that consumed said biomass, were transformed into fossil fuels, and its exploitation has allowed advancements in agriculture, transportation, and technology. Humankind has greatly benefited from the products of ancient solar energy, not only for conveniences we take for granted, such as cars, airplanes, and plastics, but also for the ability to generate fertilizers, artificial light, and heat that have allowed humans to proliferate and societies to rise. Light also impacts the Earth through temperature gradients which contribute to the diversity of environments that life can survive in, and thus, the variety of life itself.

The conversion of photon energy by photosynthesis is one of the longest-studied phenomena, and yet, there remain significant knowledge gaps in our understanding of the mechanisms and diversity involved in this process. Cyanobacteria, the early ancestors of algae and green plants, perfected two types of light-dependent enzymes, termed “reaction centers,” that carry out the conversion of solar energy into chemical bond energy. The photosystem II (PSII) reaction center is responsible for the generation of oxygen gas derived from water and photons, while the photosystem I (PSI) reaction center catalyzes the light-driven transfer of electrons, generated by the water-splitting reaction, to oxidized ferredoxin. A large proportion of the electrons donated to ferredoxin by PSI are used to produce the more stable biological reductant, NADPH (2), which is indispensable in living cells. The reactions catalyzed by both PSII and PSI are thermodynamically unfavorable but are driven to completion at the expense of the energy contained in visible photons. Nonphototrophic organisms must use other

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driving forces, such as nutrients like sugars, for the production of reduced ferredoxin, NADPH, and ATP in order to fuel their metabolism.

Because the generation of these reducing equivalents in a phototroph is principally tied to the flux of photons, the cellular energy availability fluctuates as a function of light. The dynamic mechanisms for how phototrophs respond to fluctuating light conditions in order to maintain balance in the intracellular ATP and NADPH levels involve a multitude of pathways (3–5) and are, in general, not well understood. In an analogous fashion, nonphototrophs must also react to changing organic carbon and nutrient availability. When there is an oversupply, alternative pathways have to manage the processing and/or storage of these excess nutrients in order to maintain energy balance. For microbial communities consisting of both phototrophs and nonphototrophs, the phototrophs provide the community with a rich source of nutrients excreted into the extracellular milieu (6, 7). Concentrations of these organic nutrients are highest during the day when photosynthesis is active and therefore fluctuate depending on photon flux. Nonphototrophs often assimilate nutrients by expressing proteins that bind the particular nutrient or element they require, either as a response to nutrient limitation or by chemically sensing a desired compound (8). Since nutrient availability is predictable with time of day in these types of communities, if an organism were able to use sunlight as a sensor for initiating the assimilation, usage, and storage machinery before nutrients are excreted, it could in theory gain a growth advantage over the other organisms in the community. Exploiting light in this way would require control of light sensing, just as phototrophs require acute control over their responses to the light-dark transitions in order to adjust electron flux to maintain an optimal energy balance. This fine control is enabled by sensing and absorption of a variety of wavelengths of light. Photosynthetic organisms employ a plethora of pigments (9), such as chlorophylls, carotenoids, flavins, pterins, cyanins, bilins, and others, to efficiently capture the visible regions of the electromagnetic spectrum. This pigment set also contributes to survival and fitness by allowing some organisms to capture light that is unused by others in its local environment (10). This is a widely utilized practice in natural environments where communities of organisms must compete for finite resources or when nutrient cycling allows for symbiosis, for example, in aquatic zones, dense microbial mats, or in the canopy (11).

Biology is a master of creating ingenious solutions from a small set of materials, such as these pigments and proteins, and is one of the most prolific recyclers of all time. As microbes, including *Cyanobacteria*, evolved and the complexity of life increased, certain apparatus were shared among different organisms through lateral gene transfer (LGT) (12). The pigments so critical for photosynthesis may have other uses in nonphototrophs, and these LGT events have facilitated their evolution to enable both types of bacteria to exploit new environments and metabolic mechanisms. As one might imagine, the ability to measure day length is an integral function for a phototroph (13); however, it is just as important to nonphototrophs, as it aids in growth and development by synchronizing activity via circadian rhythms. Over a hundred years ago, it was observed that blue light stimulates plants to grow toward light, but the pigment responsible remained obscure or “cryptic” for a long time and so was termed a “cryptochrome” (14). Cryptochromes are now known to be widespread among all of biology and are responsible for the circadian rhythm, a 24-h cycle composed of biochemical, physiological, and behavioral processes. Blue light has also been found to regulate a number of metabolic processes in both prokaryotes (regulation of energy metabolism, motility, and virulence) and eukaryotes (chromosome segregation, gene expression, and cellular metabolism) (15). Photolyases represent another type of enzyme that is activated by light and has DNA-repairing activity. Cryptochromes and photolyases comprise a superfamily of flavoproteins that respond to UV-A (320 to 400 nm) and blue light, although cryptochromes appear to have largely lost the DNA repair activity. Nonphototrophs have taken advantage of these enzymes to enhance their fitness in both constant and changing environments (16).

The question now arises whether there are other mechanisms by which nonpho-

totrophs may capitalize on the light-sensing cryptochrome and photolyase enzymes, aside from the circadian rhythm and DNA repair roles. A new study by Maresca et al. (17) details a novel light-enhanced growth response of a group of freshwater nonphototrophic actinobacteria to certain wavelengths of light, specifically near-UV light (375 nm) and, to a lesser extent, blue light (425 nm). These wavelengths suggest that a cryptochrome or photolyase is the likely photoreceptor responsible for the physiological changes experienced in this group of *Actinobacteria*. While some actinobacteria do contain other photoactive proteins, including rhodopsin-type photosystems, the enhanced-growth phenotype is present even when these photosystems are not functional due to an absence of the retinal cofactor. Since this cofactor is required for light absorption, the rhodopsin cannot function as a light sensor or proton pump without it. Furthermore, retinal absorbs green light, which is not consistent with the wavelengths that were observed to promote enhanced growth, further supporting the idea that the observed phenotype is due to the activity of a member from the flavoprotein superfamily. When the genomes of three actinobacterial strains displaying this phenotype were sequenced and compared, it was found that two proteins in the cryptochrome/photolyase superfamily were shared among all strains, and in fact, these were the only proteins with homology to light-sensing domains. Interestingly, these fall into three separate clades, and other species that encode homologs to all three proteins include other actinobacteria and some phototrophs, such as cyanobacteria.

If these actinobacteria contain light-harvesting pigments and rudimentary reaction centers (i.e., nonfunctional rhodopsin) but are not themselves able to do photosynthesis, what is the mechanism for their light-enhanced growth? The authors hypothesized that light was being used as a signal to upregulate certain functions related to heterotrophic growth. Indeed, they found that transcriptional changes in carbohydrate transport and metabolism were upregulated in the light, also coinciding with an increase in transcription of the gene encoding the putative CryB-type cryptochrome. Because actinobacteria are highly abundant in sunlit aquatic surface environments, it seems likely that upregulation of sugar transport and metabolism is a mechanism to consume the excreted nutrients of primary producers, which are also plentiful in these locations. By coordinating the expression of their scavenging machinery with the onset of light, they may be gaining a competitive advantage over other microbes and organisms in the environment that depend on the detection of chemical substrates for transcriptional regulation.

The bacterial world is cutthroat, and any increase in energy efficiency can have profound effects on fitness and survival. Actinobacteria appear to have found a way to synchronize their metabolism with that of their phototrophic neighbors, so that they are primed for maximum organic carbon uptake by the moment it is released. The novelty here is that they do this by using light as an information source to initiate a regulatory cascade. This mechanism may have a significant impact on the amount and variety of genes needing to be retained, an important consideration for microbes with small genomes and one that undoubtedly affects the amount of energy expended in protein synthesis. Further investigation will be required to understand the signaling pathway(s) involved in the translation of light information into a physical response, but doing so may reveal just how widespread this scheme is. Members of the cryptochrome/photolyase superfamily have found their way into the genomes of most living organisms; it is possible that they have found unique functions giving rise to as-yet-unknown means of utilizing solar energy, either as information or power. This work begins to scratch the surface to reveal potentially novel mechanisms and incites our imaginations for developing new ways that biology and humankind can interact with light.

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