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quick study

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A small fraction of light absorbed by leaves is reemitted as fluorescence. Studies of that process at both large and small scales will help scientists better understand global photosynthesis and its connection to climate.

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Chlorophyll molecules—biology's solar collectors—capture and convert solar energy to sustain almost all life on Earth. As with photovoltaic solar cells, the photosynthetic light-harvesting machinery is not perfectly efficient. In the case of photosynthetic systems, one of those inefficiencies—a small amount of fluorescent reemission of absorbed photons—is offering scientists new ways to understand photosynthesis, the power source of the biosphere.

For several decades, biological scientists have used chlorophyll fluorescence to monitor photosynthesis in laboratory studies. Recent advances in satellite spectroscopy now permit scientists to measure fluorescence over large areas. Such studies can help researchers get a handle on the rate of photosynthesis (called GPP or gross primary production by carbon-cycle scientists) over such expansive regions as the US Corn Belt. At the other end of the spatial scale, technical innovations now permit scientists to study the fluorescence properties of single molecules and to directly observe the quantum states of light-harvesting systems.

The one percent

In the first steps of photosynthesis, captured solar energy migrates through chlorophyll molecules (see the article by Graham Fleming and Rienk van Grondelle, PHYSICS TODAY, February 1994, page 48). A fraction Φ_P of that energy reaches dedicated proteins and successfully initiates photochemistry. Some energy (a fraction Φ_F) is lost to fluorescence and some (a fraction Φ_D) to intrinsic inefficiencies and wastage that occur when photochemical centers are damaged by too much light. When illumination is low, more than 80% of the light energy may be used for photochemistry.

When plants receive more light than they need for photochemistry, Φ_P decreases. One might expect that a larger fraction of the energy would then go to fluorescence and wastage. Plants, however, seem to manage the excess via a regulatory process called nonphotochemical quenching. Invoked by a metabolic feedback mechanism, that process diverts a fraction Φ_N of unneeded energy to heat. To conserve energy, the sum of the above fractions, or quantum yields, must be unity: $\Phi_P + \Phi_F + \Phi_D + \Phi_N = 1$.

As shown in figure 1, the processing of excitation energy in a leaf changes in response to light intensity and plant stress. Note that as conditions are varied, the major change is in the partitioning of energy between photosynthesis and nonphotochemical quenching. In all cases, including drought conditions, the fluorescence quantum yield is about 1%. That said, Φ_F is not perfectly constant under all conditions, and its subtle variations diagnose changes in the major pathways of quenching.

Fluorescence writ large and small

Solar-induced fluorescence (SIF) is the fluorescence from terrestrial plants in their natural environment. It is difficult to measure because it is masked by reflected sunlight with the same wavelengths. High-resolution spectrometers, however, can distinguish the two. They can pull off the separation because the spectrum of sunlight reaching Earth's surface includes absorption lines, called Fraunhofer lines, created by atomic absorbers in the plasma of the solar atmosphere. Reflected light preserves those absorption features, but they are absent from new, fluorescence light.

As figure 2a shows, a spectrum showing the ratio of reflected to incident light intensity will be smooth for nonfluorescing targets. But the spectrum for plants will show peaks that correspond to the Fraunhofer lines because the relative

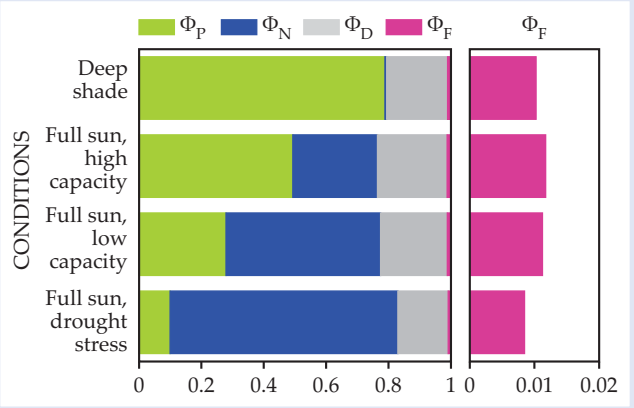

Figure 1. Quantum yields (Φ) for the four pathways used by leaves to process photons depend on whether the leaf is shaded or in full sun, whether the leaf has a high or low photosynthetic capacity, and whether drought stress is present. In the histogram, green denotes photosynthesis; blue, damage control; gray, wastage; and pink, fluorescence. The results shown here were obtained with a laboratory instrument called a pulse amplitude modulated fluorometer. As the right panel shows, the fluorescence quantum yield changes slightly but noticeably with varying conditions. Such variations can be detected by a satellite that makes repeated measurements under similar illumination conditions.

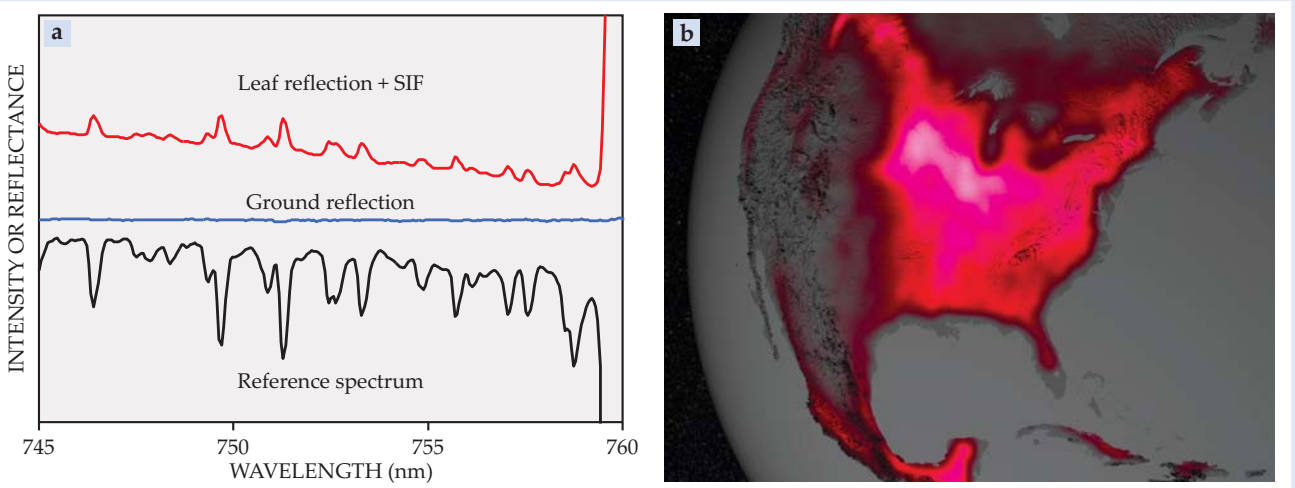

Figure 2. Satellite-derived chlorophyll fluorescence. **(a)** Sunlight arriving at Earth (black spectrum) has absorbance features, called Fraunhofer lines, due to material in the solar atmosphere. The spectrum of light reflected from the ground is very similar to that of the incoming sunlight. Thus a spectrum showing the intensity ratio, or reflectance (blue spectrum, for which the reflecting surface was actually Teflon), is nearly flat. Light measured from a leaf has a reflected and solar-induced fluorescence (SIF) component. Thus the leaf's reflectance (red spectrum) has peaks corresponding to Fraunhofer frequencies. For ease of viewing, the three spectra shown here are offset and the leaf spectrum is expanded by a factor of 10. **(b)** Comparing the relative intensity spectra for leaf and ground allows one to generate maps such as that shown here, obtained during the peak growing season over North America. Bright areas indicate more intense fluorescence. (Courtesy of NASA's Goddard Space Flight Center.) A video showing how the fluorescence changes with the seasons is available at http://www.nasa.gov/content/goddard/seeing-photosynthesis-from-space-nasa-scientists-use-satellites-to-measure-plant-health.

enhancement of the total signal by the added fluorescence light is larger for frequencies corresponding to those absorbance features than it is for other frequencies. Five satellites have achieved SIF measurements. All those measurements, however, have deficiencies because the instruments were designed mainly to do other things. Figure 2b shows an example of data obtained with GOME-2, which passes overhead at midmorning every day and thus observes plants under similar illumination conditions from place to place. The US Corn Belt's high SIF, proportional to the product of Φ_F (see figure 1) and the flux of absorbed photons, results from the region's dense canopy of plants having a high Φ_F.

The rates of photosynthesis and SIF vary greatly, both seasonally and with location on Earth's land masses. Moreover, SIF seems to respond in parallel with GPP. Both are proportional to the respective quantum yields shown in figure 1. Furthermore, plants often respond to seasonal or episodic stress by adjusting the fraction of incident light that is absorbed—for example, by adding or shedding leaves. When light is abundant, plants thereby achieve both long-term (structural) and short-term (physiological) regulation of their light-harvesting systems to match the energy delivered to their photochemical reaction centers with their capacity to use that energy in processes such as carbon dioxide fixation. SIF is sensitive to both types of adjustment, so when observed from space it provides scientists with a useful proxy for photosynthesis.

Meanwhile, work at the scale of a single photosynthetic light-harvesting complex is addressing the sophisticated regulatory mechanisms that lead to the parallel responses of SIF and GPP. By measuring changes in Φ_F in single exemplars of those complexes, one of us (Schlau-Cohen) and coworkers are studying the conformal motions and quantum mechanisms underlying the molecular switch that decides whether the energy of an absorbed photon is dissipated locally in the complex as waste heat or is passed on to other proteins to be used in photosynthesis.

Putting it all together

The information obtained via molecular studies promises to do more than just provide fundamental new insight into the mechanisms regulating photosynthesis. It should also help scientists to build more accurate models for how GPP responds to environmental stress and better understand the extent of plant responses to that stress. Those models currently have a great deal of uncertainty because they can be checked only at a few sites where GPP is directly measured. In contrast, SIF can be measured everywhere by satellite.

Microscopic studies of photosynthetic proteins may lead to a solid understanding of how biochemical mechanisms control SIF. If that goal is met, SIF observations can tell us much about photosynthesis on the planetary scale and, in combination with simulations, can give powerful checks on carbon-cycle and climate models. The success of that program will depend on continued advances in understanding the molecular mechanisms of fluorescence and on the provision of new satellites optimized for fluorescence measurement.

Additional resources

▶ L. Guanter et al., "Global and time-resolved monitoring of crop photosynthesis with chlorophyll fluorescence," *Proc. Natl. Acad. Sci. USA* **111**, E1327 (2014).

▶ A. Porcar-Castell et al., "Linking chlorophyll *a* fluorescence to photosynthesis for remote sensing applications: Mechanisms and challenges," *J. Exp. Bot.* **65**, 4065 (2014).

▶ G. S. Schlau-Cohen et al., "Single-molecule spectroscopy of photosynthetic proteins in solution: Exploration of structure–function relationships," *Chem. Sci.* **5**, 2933 (2014).

▶ C. van der Tol et al., "Models of fluorescence and photosynthesis for interpreting measurements of solar-induced chlorophyll fluorescence," *J. Geophys. Res. Biogeosci.* **119**, 2312 (2014).

▶ NASA Jet Propulsion Laboratory, "How does your garden glow? NASA's OCO-2 seeks answer," http://www.jpl.nasa.gov/news/news.php?feature=4135. ■