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HOW DOES PHOTOSYNTHESIS WAKE UP IN THE MORNING?

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YOUNG REVIEWERS



COLEGIO ALTOS DEL CERRO GRANDE AGES: 11-12 In photosynthesis, plants use energy from sunlight to turn carbon from CO₂ in the air into a solid form of carbon that can build the plant's body. Photosynthesis consists of two portions: the reactions that absorb sunlight energy and another set of reactions called the Calvin-Benson-Bassham (CBB) cycle. When the plant "wakes up" in the morning, after a night of darkness, these two processes do not wake up at the same pace, which can damage the plant cells. However, plant cells prevent this problem by regulating these two processes carefully. To understand how photosynthetic organisms switch from night to day, a type of photosynthetic bacteria called cyanobacteria were used to explore how another pathway, called the oxidative pentose phosphate (OPP) pathway, helps with this dark-to-light transition. Our research found that the OPP pathway can help photosynthesis quickly reactivate when light is available and can prevent cell damage from too much light.

WHAT IS PHOTOSYNTHESIS AND HOW DO WE STUDY IT?

Plants do not eat, so how do they get their food? Plants can create their own food using a process called photosynthesis. Photosynthesis uses the energy from sunlight to change carbon dioxide gas from the air into solid carbon that a plant can use as food. The solid carbon is used to build the plant's body, forming structures like lettuce leaves or potato roots that we can eat. To be a source of food, plants must be efficient at growing, which they do by making solid carbon. Understanding the processes that allow plants to grow could help us to improve agricultural production of foods to feed Earth's growing population. But plants are difficult to study. Sometimes they grow too big to be kept in the lab, they grow too slowly for many experiments, and their genes are difficult to change. So how do we study photosynthesis? We can use a type of bacteria called cyanobacteria, which can perform photosynthesis. Cyanobacteria behave like simplistic plants and they can serve as a replacement for plants in laboratory experiments. Cyanobacteria share enough similarities with plants that experimental results using cyanobacteria can also be applied to plants.

Cyanobacteria may be microscopic photosynthesizers, but their small size does not make them insignificant! Cyanobacteria were the first lifeforms to perform the type of photosynthesis that makes oxygen (the kind we see in plants), and they are probably responsible for putting oxygen into Earth's airless atmosphere over 2.4 billion years ago [1]. For our purposes, these tiny, simple microbes make an ideal model organism to use to study photosynthesis in the lab.

HOW PHOTOSYNTHESIS WAKES UP IN THE MORNING

In both cyanobacteria and plants, photosynthesis includes two processes: the light reactions, which use sunlight to make energy, and the **Calvin-Benson-Bassham (CBB) cycle**. The light reactions use cellular machines to absorb light energy from the sun and convert it into chemical energy in the form of high-energy electrons, which are like little packets of energy. These packets of energy are transferred to the CBB cycle to make the carbon molecules that plants or cyanobacteria use to build their bodies. The CBB cycle is dependent on the activity of proteins called **enzymes**, to convert the carbon in the air to solid carbon. These enzymes also need other cellular materials called **intermediates** to make their final products.

Let us imagine a plant, or cyanobacterium, at sunset. Since the light reactions need light to give them energy, they cannot make high-energy electrons without the sun, so those reactions are basically "asleep" when it is dark. The CBB cycle also goes to sleep for the night, as it is dependent on light to wake up some of its enzymes, too

CYANOBACTERIA

Microscopic organisms which create oxygen when they perform photosynthesis, similar to plants, and are used by scientists to study photosynthesis.

CALVIN-BENSON-BASSHAM (CBB) CYCLE

The cycle that allows the formation of solid carbon from carbon dioxide using energy from the light reactions of photosynthesis.

ENZYMES

The protein "workers" of the cell that help chemical reactions take place.

INTERMEDIATES

The compounds used by enzymes to complete reactions. Townsend et al.

(Figure 1A). During the day, these two processes provide energy and carbon to fuel cell growth. While these cycles are inactive at night, photosynthetic cells survive by consuming some of the intermediates formed during the day. This creates an issue, since cellular materials are being used up without being replenished.



Then the sun rises! The machines that perform the light reactions wake up and start producing high-energy electrons. But the CBB cycle is not ready—although its enzymes wake up with the light, they do so much more slowly, and there are very few intermediates left for the enzymes to work with (Figure 1B). With an inactive CBB cycle, the high-energy electrons from the light reactions have nowhere to go, so they build up and are transferred to oxygen molecules. But oxygen does not handle the high-energy electrons well, and it can become a damaging form called **reactive oxygen species (ROS)**, which damages the machinery of the light reactions and, over time, could kill the cell. But photosynthetic organisms have survived this night-to-day transition for millions of generations. Somehow, the CBB cycle wakes up fast enough and gets photosynthesis operating before major damage occurs (Figure 1C). How does this transition happen?

WHAT HELPS PHOTOSYNTHESIS WAKE UP?

Cyanobacteria have many other chemical pathways besides photosynthesis that help them stay alive during the night. For example, cyanobacteria can store some of the carbon they make during the

Figure 1

(A) Photosynthetic processes are not active at night, because no light is available, so cells use up intermediates to stay alive. (B) When cells are exposed to light, the light reactions start but the CBB cycle is slow to wake up and cannot run if no intermediates are left in the cell. Thus, the electrons (e^{-}) from the light reactions cannot go to the CBB cycle, so they end up turning oxygen into harmful reactive oxygen species (ROS). (C) After some time, photosynthesis happens normally again, but it is unknown how this transition happens.

REACTIVE OXYGEN SPECIES

Forms of oxygen which are toxic due to absorbing too much energy in the form of an electron.

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OXIDATIVE PENTOSE PHOSPHATE (OPP) PATHWAY

A pathway that converts sugar molecules to other molecules that can be used in multiple processes, in this case helping photosynthesis.

Figure 2

The OPP pathway supports photosynthesis during dark-to-light transitions. Pieces of the sugar molecules used as fuel for the cells at night are fed into the OPP pathway. When OPP breaks down the sugar, it uses the high-energy electrons from the light reaction machines so that ROS are not formed (yellow arrow). The OPP also "wakes up" some of the CBB cycle enzymes (orange), and it provides important intermediates for the CBB cycle (red).

day, in the form of massive sugar molecules that can be broken into pieces for the cells to use (Figure 2). These pieces are funneled into a series of chemical reactions called the **oxidative pentose phosphate (OPP) pathway**, which breaks down the sugar to make energy for the cells when photosynthesis is inactive. Scientists used to think that photosynthesis happened during the day and the OPP pathway functioned at night, with only one or the other active at a time [2]. Then it was discovered that the OPP pathway is also active during the day, but not to produce energy like it does at night. Instead, in the daytime, the OPP pathway functions to help the organism transition smoothly from night to day, during the time when the CBB cycle is slowly waking up and cannot pick up the electrons from the light reactions.



How does the OPP pathway help? When the pieces of the large sugar molecules are used in the OPP pathway, those processes use up electrons. Therefore, when electrons cannot go to the CBB cycle because it is not awake yet, an active OPP pathway can take up the electrons from the light reactions before they can make ROS. Thus, the OPP pathway helps protect the light reaction machinery by taking away the high-energy electrons before they damage the cell (Figure 2, yellow arrow).

The second challenge of the dark-to-light transition is waking up the CBB enzymes. These enzymes do not wake up as quickly as the light reaction enzymes, but they can be woken up with the chemical

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version of an alarm clock. The OPP pathway produces these alarm-like molecules that help wake up the enzymes of the CBB cycle (Figure 2, orange arrow).

The final obstacle to restarting the CBB cycle is the missing intermediates, many of which were used up throughout the night as the organism tried to survive without the light reactions. The OPP pathway helps replenish some of the missing intermediates by breaking down large sugar molecules (Figure 2, red arrow). However, many of the other intermediates are not replenished by this pathway. How does an organism get more of these necessary intermediates? This question has not been fully answered, although one theory is that an alternative process called the **Entner-Doudoroff (ED) pathway** may replenish these intermediates in cyanobacteria [3]. Disruption of the ED pathway decreases growth of cyanobacteria, suggesting the pathway can replenish the missing intermediates. However, the way plants replenish these intermediates is yet to be discovered, since plants do not have the ED pathway.

In summary, the OPP pathway not only helps photosynthetic organisms survive the night, but it also helps these organisms transition from night to day, by promoting a quick "restart." This role makes the pathway photoprotective, which means it can protect the photosynthetic machinery from the potentially damaging effects of light and keep the cellular processes functioning efficiently.

LASTING SIGNIFICANCE

Previously, the idea that the OPP pathway stabilizes photosynthesis was only theoretical [4]. This new work provided experimental evidence of how the OPP pathway could help cyanobacteria cope with the stress of the dark-to-light transition [2]. The major impact of this work is that the results can be applied to plants, since cyanobacteria and plants share the same CBB reactions. Future research using cyanobacteria to learn how to optimize the interactions between the OPP pathway and the CBB cycle could lead to discoveries that could improve photosynthesis. By translating these discoveries to plants, we might be able to make crops grow better, which would help to feed the world's increasing population.

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ENTNER-DOUDOROFF PATHWAY

A pathway found mostly in bacteria, allowing them to break down sugars using unique reactions.

ORIGINAL SOURCE ARTICLE

Shinde, S., Zhang, X., Singapuri, S., Kalra, I., Liu, X., Morgan-Kiss, R. M., et al. 2020. Glycogen metabolism supports photosynthesis start through the oxidative pentose phosphate pathway in cyanobacteria. *Plant Physiol.* 182:507–17. doi: 10.1104/pp.19.01184

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11 and 12 year old school children who despite being native speakers of Spanish enjoy and also have a good command of English, and above all they like to learn about new things. A highly dynamic, cheerful and unruly children that seek new challenges.

AUTHORS

HOPE TOWNSEND

Hope is a senior undergraduate studying microbiology with minors in geology and bioinformatics at Miami University. Hope grew up hating science until high school, where she learned that science is about being humbled by life's complexities and empowered to take advantage of life's processes to change lives. Ever since then, she has been obsessed with science. She has done research on a few different projects in her undergraduate studies, one as the team leader for an international Genetically Engineered Machine (iGEM) competition focusing on photosynthesis in cyanobacteria. She is excited to further challenge herself as an independent researcher in graduate school.



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Avery Imes is an undergraduate majoring in microbiology at Miami University. Together with her fellow authors, she is participating in an international Genetically Engineered Machine (iGEM) project focused on improvement of photosynthesis by metabolic engineering of the Calvin cycle. She aims to continue her education and research in a Ph.D. program next year. Her interest in photosynthesis extends beyond lab work—Avery has a collection of bonsai trees that could greatly benefit from some more efficient photosynthesis.



XIN WANG

Xin Wang is an assistant professor of microbiology at Miami University. His career has expanded from studying microbial ecology in the ocean to synthetic biology of microbes. His current research investigates improvement of photosynthesis in cyanobacteria, aiming to transfer these discoveries to plant research for crop improvement in the near future. He believes that communicating science is a critical part of research and hopes this article will serve as an avenue for our young generations to understand and love both photosynthesis and science in general. *wangx98@miamioh.edu

