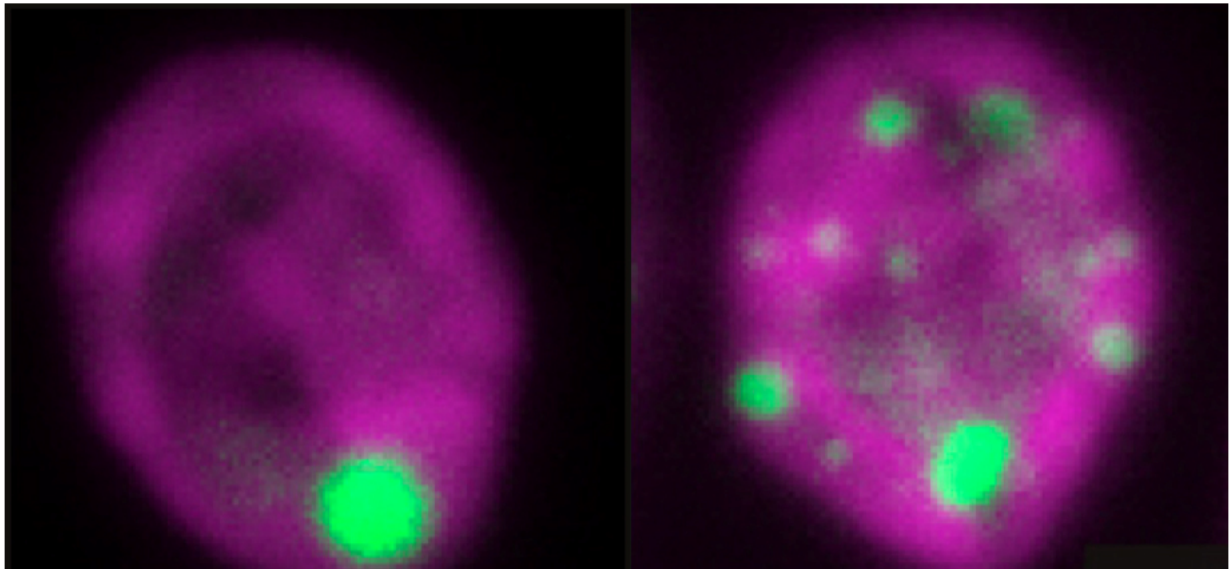


Researchers explore how a carbon-fixing organelle forms via phase separation

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The left panel shows a type of single-celled algae known as *Chlamydomonas reinhardtii* with its chloroplast (purple) containing only a single pyrenoid (green). The SAGA1 mutant shown on the right displays several extra pyrenoids. Credit: Alan Itakura

Plants, algae and other photosynthetic organisms remove carbon dioxide from the air, incorporating it into starches in a process known as carbon fixation. In green algae, which contribute up to a third of global carbon fixation, this activity is greatly enhanced by an organelle called the pyrenoid. A new paper by Princeton researcher Martin Jonikas, assistant

professor of molecular biology, and colleagues, which appeared online in the journal *Proceedings of the National Academy of Sciences* on August 27, 2019, investigates a gene important for regulating pyrenoid shape and number, and enhances our understanding of this essential component of the global carbon cycle.

In algae, as in plants, the task of [carbon fixation](#) is carried out by an enzyme known as Rubisco within the chloroplast, the cellular compartment where photosynthesis takes place. In plants, Rubisco occurs throughout the chloroplast, but in algae, Rubisco molecules cluster together to form a distinct structure, the pyrenoid.

This structure assembles via a process known as phase separation in a manner similar to how oil forms clusters when placed in water. The pyrenoid is surrounded by a [starch](#)-based sheath. In most species, the pyrenoid also contains tubules that extend into it from the thylakoid, where light-dependent reactions of photosynthesis occur. Thylakoid tubules convey concentrated [carbon](#) dioxide to Rubisco, greatly improving the enzyme's efficiency—something that is very important for algae since they live in aquatic environments where carbon dioxide can be hard to access.

Prior studies by Jonikas' group have shown that the pyrenoid is not a permanent feature of the cell, but instead dissolves during cell division then re-forms as small clusters of phase-separated proteins that coalesce into a larger mass. Algal chloroplasts normally have only one pyrenoid because, like oil poured onto water, phase-separated protein clusters aggregate together to minimize their exposed surface area.

While conducting a screen for genes affecting pyrenoid function in the green alga *Chlamydomonas reinhardtii*, [graduate student](#) and the study's first author Alan Itakura and postdoctoral researcher Leif Pallesen, both in the Jonikas group, uncovered a gene called SAGA1 (Starch Granules

Abnormal-1), the loss of which causes [cells](#) to grow poorly. When the researchers, including the study's co-first author, Kher Xing (Cindy) Chan in Howard Griffiths' group at the University of Cambridge, examined the [mutant cells](#), they noticed that SAGA1 mutants possess multiple pyrenoids—up to 10 per cell. This was surprising since normal cells almost always contain just one pyrenoid. Intrigued, the team decided to investigate further.

Because the SAGA1 protein is predicted to contain a starch-binding domain, the researchers first explored whether loss of the SAGA1 gene affects the architecture of the starch plates that make up the pyrenoid sheath. Indeed, the pyrenoids in SAGA1-deficient cells have fewer and abnormally elongated starch plates in their sheaths. The authors also found evidence that the SAGA1 protein binds to Rubisco. Together, these data suggest that SAGA1 helps direct the proper formation of the pyrenoid's starch sheath, and the attachment of Rubisco to it.

But why would loss of SAGA1 affect pyrenoid number? The study results suggest that the increased [surface area](#) of the defective starch sheaths lead to the formation of multiple pyrenoids. Normally, the starch plates are sized appropriately to create a single pyrenoid, but the elongated starch plates in SAGA1 mutants pinch off portions of the matrix, resulting in extra pyrenoids.

Although this model explains why more pyrenoids might appear in SAGA1 mutants, it doesn't explain why excess pyrenoids hamper cell growth. The authors found that Rubisco levels are unchanged in SAGA1 mutants, suggesting that the same amount of protein is distributed across multiple pyrenoids. However, the researchers noticed that most of these extra pyrenoids lack a thylakoid tubule network. Pyrenoids without a thylakoid network would be starved of [carbon dioxide](#), suggesting the Rubisco they contain is idled and not contributing to growth.

The work provides a useful new model to explain how a peripheral component, the starch sheath, helps cells regulate their number of pyrenoids. The authors suggest that such a mechanism may also apply to the biogenesis of other phase-separated organelles such as stress granules.

More information: Alan K. Itakura et al, A Rubisco-binding protein is required for normal pyrenoid number and starch sheath morphology in *Chlamydomonas reinhardtii*, *Proceedings of the National Academy of Sciences* (2019). [DOI: 10.1073/pnas.1904587116](https://doi.org/10.1073/pnas.1904587116)

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