Which Factors Control Starch Granule Initiation?

Bischof, Sylvain

DOI: https://doi.org/10.1105/tpc.20.00502

Posted at the Zurich Open Repository and Archive, University of Zurich
ZORA URL: https://doi.org/10.5167/uzh-197587
Journal Article
Published Version

Originally published at:
Bischof, Sylvain (2020). Which Factors Control Starch Granule Initiation? Plant Cell, 32(8):2449-2450.
DOI: https://doi.org/10.1105/tpc.20.00502
Storage and remobilization of sugar molecules play important roles for the growth and survival of living organisms. Besides a few exceptions, animals store carbohydrates in the form of soluble glycogen while green plants and algae bank glucans as insoluble starch. Starch forms the basis of human nutrition and constitutes a renewable raw material for industry, thus highlighting its importance for humankind.

Starch is a nonstructural polymer composed of linked glucose units forming inert granules within the chloroplast. In leaves, transitory starch is synthesized during the day from photosynthetic assimilates and subsequently degraded to provide energy for growth at night (reviewed by Pfister and Zeeman, 2016). The enzymes controlling starch synthesis and degradation have been extensively studied, and recent attention has also been given to factors controlling starch granule initiation. Notably, plants lacking PROTEIN TARGETING TO STARCH2 (PTST2) or its interaction partner MYOSIN-RESEMBLING CHLOROPLAST PROTEIN (MRC) and MAR BINDING FILAMENT-LIKE PROTEIN1 (MFP1) have reduced numbers of starch granules per chloroplast (Seung et al., 2017, 2018; Vandromme et al., 2019). In this issue of *The Plant Cell*, Abt et al. (2020) characterize the function of STARCH SYNTHASE5 (SS5) in starch metabolism and show that this enzymatically inactive protein plays an important role within the nexus of factors regulating the number of starch granules formed in chloroplasts.

The plant model organism Arabidopsis (*Arabidopsis thaliana*) contains six starch synthases. Five of them elongate glucan chains to make amylopectin and amylose, the two polysaccharide types found in starch. Abt and colleagues (2020) observed that the sixth starch synthase, SS5, was present throughout the plant kingdom but lacked a conserved glycosyltransferase1 (GT1) domain (see figure). Structural modeling indicated that SS5 has a surface carbohydrate binding site conserved with SS4. Consistently, recombinant SS5 was able to bind maize (*Zea mays*) starch but not to actively transfer ADP-glucose onto it. Furthermore, SS5 was not able to produce glucans when expressed in yeast (*Saccharomyces cerevisiae*), confirming that SS5 was not an enzymatically active glucosyltransferase.

Plants lacking SS5 did not display a strong visible phenotype (see figure) and overall starch levels remained similar to those of the wild type, except at the end of the night, when ss5<sup>−/−</sup> had slightly more starch. Scanning electron micrographs of purified starch granules and light micrographs of embedded tissue sections showed that ss5-deficient plants had fewer but larger starch granules (see figure). Together, these data suggested that SS5 was not primarily involved in starch synthesis or degradation but rather in starch granule initiation.

Immunoprecipitation followed by mass spectrometry of tagged SS5 revealed an interaction with SS4 and MRC. Coimmunoprecipitation experiments validated the interaction between SS5 and MRC and showed that the coiled-coil domain of SS5 was required for this interaction. In vivo localization experiments of fluorescent transcriptional fusions revealed that SS5...
was localized in the chloroplast, consistent with the presence of an N-terminal chloroplast transit peptide (see figure). Interestingly, the authors found that SS5 and MRC colocalized in small puncta, suggesting the existence of a possible structural “platform” regulating starch granule homeostasis.

To understand the functional relationship between SS5 and known granule initiation factors, the authors created several double mutants with ss5^{−/−} and quantified the resulting number and size of starch granules per chloroplast. Interestingly, the additional loss of SS5 did not enhance the phenotype of mrc^{−/−}, indicating that SS5 and MRC function in the same pathway. A similar epistatic relationship was observed between SS5 and MFP1. In contrast, the loss of SS4 or PTST2 in addition to SS5 enhanced the phenotype of the single ss5^{−/−} mutant, suggesting that SS5 may act independently from SS4 and PTST2 in starch granule initiation.

In summary, Abt and colleagues (2020) coined SS5 as a new player in the network of factors determining starch granule initiation. Future investigations will tackle the complex relationships between all these factors and also likely shed light on the exact nature of SS5-MRC-containing puncta, whose function remains enigmatic.

Sylvain Bischof
Assistant Features Editor
Department of Plant and Microbial Biology
University of Zürich, Switzerland
sylvain.bischof@uzh.ch
ORCID ID: 0000-0003-2910-5132

REFERENCES
Abt, M., Pfister, B., Sharma, M., Eicke, S., Bürgy, L., Neale, I., Seung, D., and Zeeman, S.C. (2020). STARCH SYNTHASE5, a noncanonical starch synthase-like protein, promotes starch granule initiation in Arabidopsis. Plant Cell 32: 2543–2565.
Pfister, B., and Zeeman, S.C. (2016). Formation of starch in plant cells. Cell. Mol. Life Sci. 73: 2781–2807.
Seung, D., Boudet, J., Monroe, J., Schreier, T.B., David, L.C., Abt, M., Lu, K.J., Zanella, M., and Zeeman, S.C. (2017). Homologs of PROTEIN TARGETING TO STARCH control starch granule initiation in Arabidopsis leaves. Plant Cell 29: 1657–1677.
Seung, D., Schreier, T.B., Bürgy, L., Eicke, S., and Zeeman, S.C. (2018). Two plastidial coiled-coil proteins are essential for normal starch granule initiation in Arabidopsis. Plant Cell 30: 1523–1542.
Vandromme, C., Spriet, C., Dauvillé, D., Courseaux, A., Putaux, J.L., Wychowski, A., Krzewinski, F., Facon, M., D’Hulst, C., and Wattebled, F. (2019). PII1: A protein involved in starch initiation that determines granule number and size in Arabidopsis chloroplast. New Phytol. 221: 356–370.
Which Factors Control Starch Granule Initiation?
Sylvain Bischof

*Plant Cell* 2020;32;2449-2450; originally published online June 30, 2020; DOI 10.1105/tpc.20.00502

This information is current as of January 25, 2021

| References | This article cites 5 articles, 3 of which can be accessed free at: /content/32/8/2449.full.html#ref-list-1 |
|------------|-------------------------------------------------------------------------------------------------|
| Permissions | https://www.copyright.com/ccc/openurl.do?sid=pd_hl1532298X&issn=1532298X&WT.mc_id=pd_hl1532298X |
| eTOCs      | Sign up for eTOCs at: http://www.plantcell.org/cgi/alerts/ctmain |
| CiteTrack Alerts | Sign up for CiteTrack Alerts at: http://www.plantcell.org/cgi/alerts/ctmain |
| Subscription Information | Subscription Information for *The Plant Cell* and *Plant Physiology* is available at: http://www.aspb.org/publications/subscriptions.cfm |

© American Society of Plant Biologists
ADVANCING THE SCIENCE OF PLANT BIOLOGY