Why starch is essential and dispensable

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More than 70% of human nutrition is based on plants with most of our calories coming from starch, a plant-specific polymer of glucose residues concatenated in α -1,4-position. The polymerisation allows to withdraw the otherwise osmotically active monomers from equilibrium circumventing water influx and burst of the cell. This trick was invented in the early stages of evolution, when cyanobacteria acquired the ability to produce large quantities of sugars by photosynthesis. Through endosymbiosis, this trait was passed onto many algae and the land-plant lineage. In recent plants, starch is transiently formed during the day in active chloroplasts, but mobilised from there during the night into storage organs (often underground), endowed with specialised plastids, the amyloplasts. The storage parenchyma of potatoes or the endosperm of cereals is rich in these converted plastids and have shaped entire civilisations as major sources of life energy. It may seem that such a central phenomenon of biology is well understood to the last details, and, in fact, starch synthesis has been intensively investigated over decades. But, still, many aspects of amyloplasts are not clear or even controversial. Two contributions to the current issue shed light into the secret life of amyloplasts and show essential, but also unexpectedly dispensable functions of amyloplasts:

In their comprehensive review, Goren et al. (2018) address not only the complex enzymology of starch synthesis, but also give insights into the much less known subcellular aspects of a starch grain. The core pathway of synthesis from the UDP-glucose substrate, chain elongation, actual starch synthesis, and the introduction of branches and their removal is described in the latest molecular and enzymological detail, including proteins, whose functions are still not yet assigned. As a special merit, this review assembles the still scarce, but

fascinating cellular details of starch grain initiation, which starts from a region rich in unstructured polyglucans, the hylum, from which microtubules emanate forming channels that end in pores at the granule surface and serve as organisation centre to recruit specific starch synthases and FtsZ proteins, prokaryotic ancestors of tubulin that have been preserved in plants and mediate plastid division. The immense diversity of starch size and morphology seen in different plant taxa (serving as useful trait for cyto-taxonomy) seems to be linked with the activity of these FtsZ proteins that form division rings separating the daughter plastids. These genetically regulated features set the framework for the self-organisation of starch blocklets into the lamellar structure characteristic for most starch grains. The morphological features of starch grains are much less understood than their enzymology and, thus, further surprises are to be expected from the analysis of these essential organelles.

Amyloplasts are not evenly spread over the plant tissue, but often accumulate in cells responsible for energy storage. In young seedlings, they are seen in the central part of the root cap, the columella, as well as in the bundle sheath accompanying the vasculature of young shoots. Starch is a dense compound with a considerable specific weight, and therefore, amyloplasts tend to sediment to the lower part of the cell. Based on this phenomenon, more than a century ago, Haberlandt (1900) and Nemec (1900), independently, and even publishing in the same journal, had proposed that the sedimenting amyloplasts would serve as statoliths able to convey the direction of gravity to a cellular signalling machinery that would initiate adjusting growth movements, so called gravitropism. Although plausible, this starch-statolith theory has been mostly based on correlative evidence, and in his provocative contribution to the New Ideas in Cell Biology, Edelmann (2018) provides experimental evidence that make him conclude that this starch-statolith theory might be a ‘red herring’. His approach is logically stringent and very simple: if the sedimentation of amyloplasts is responsible for the perception of gravity, the removal of those cells, where amyloplasts sediment (for the root, the calyptra; for the shoot, the bundle sheath) should result in a loss of gravity sensitivity. For

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the coleoptiles of maize coleoptiles, removal of the bundle sheath fails to give any impact on gravitropic curvature, which is clearly not expected from a model, where amyloplast sedimentation in the bundle sheath acts as susceptor (*in sensu* Björkman 1988—the amyloplasts would not be sensors by themselves for gravity, not even in the starch-statolith model, they would be rather translating the physical input, gravity, into a stimulus that can be perceived). For the root, the removal of the cap, at first sight, confirmed the prediction of the starch-statolith hypothesis—decapped roots do not bend. However, this may not be caused by the inability to sense gravity, but by the inability to respond to gravity by bending—a prisoner with amputated legs would not be able to run out of the opened door, which does not mean that he is not able to see the light coming through the opened door. In fact, by applying Latrunculin B, a drug that eliminates actin filaments, to decapped roots, a spectacular bending is observed that is just inverted (i.e. the roots behave as if they were shoots). While the reason for this inversion is not clear, this outcome clearly shows that decapped roots are able to sense gravity; the calyptra is only needed for the proper manifestation of the resulting response. While these findings do not reveal the mechanism, how gravity is sensed, it is clear that the sedimentation of amyloplasts is dispensable for the sensing. The sedimentation of amyloplasts has been found to depend on microtubules (Godbolé et al. 2000), which is not surprising, if one takes into account, how starch granules form from a hylum along microtubule channels—microtubules, as tubular lever endowed with high rigidity, might therefore be a candidate for the sensor that can mediate sensing outside of the regions with obvious amyloplast sedimentation (reviewed in Nick 2013). The amyloplasts would then not be a necessary condition for gravity sensing, but just an amplifier of the

microtubular lever at best. This would also be expected from the evolutionary context—a sensor that is crucial for survival (for instance in growing seedlings that have to reach the surface) should be robust enough to function even under conditions of starvation (when the presumed ‘statoliths’ are consumed, because the starch has to be mobilised to survive).

Amyloplasts certainly belong to the plant-cell structures with the largest impact on human civilisation—meanwhile not only for food and feed, but also for applications in bioeconomy. The two contributions to the current issue illustrate that we just have started to get a first glimpse into the cellular functions of these essential (but sometimes dispensable) organelles.

Compliance with ethical standards

Conflict of interest The author declares that there is no conflict of interest.

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