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Mini Review

Future Starch Analyses-Necessity for Higher Time and Local Resolution

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Abstract

Starch is chemically a relatively simple particle consisting of two homo-biopolymers, amylopectin and amylose, with only α-1,4 and α-1,6 linked glucosyl units. Starch is a natural storage carbohydrate in plants and algae and is an essential source for nutrition, animal feeding, as well as raw material for the industry. Despite increasing knowledge in the last decades, detailed structural information and understanding of its turn-over are largely lacking. Most data were generated using bulk experiments, what obviously now come to limitations for a deeper insight in starch metabolism. Here we focus on some unavoidable questions arising from existing data, related to starch biosynthesis, degradation, and structure, where these limitations strongly emerge.

Keywords: Starch; Starch structure; Starch metabolism; Starch biosynthesis; Starch breakdown

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Introduction

Starch is the main energy provider in human nutrition as well as a raw material for industrial purposes and is mostly produced from cereal crops and tuber plants as *e.g*. potato. In most cases, higher plants form two types of starch, assimilatory (or transitory) starch and reserve (or storage) starch, which differ in quantity per plant, shape, size, metabolism, and biochemistry, but the internal structure of starch seems evolutionary conserved. Rising global temperature is causing major climatic challenges, particularly in terms of plant adaptation to changing environments. To sustain agricultural production, it becomes increasingly important to develop/identify and characterize plants that are able to adapt under such unfavorable growing conditions to secure crop production. This strongly demands for developing stress resistant varieties with improved starch characteristics for food as well as non-food production, such as in the pharmaceutical-, glue-, paper-, garments, textile-, bioplastic- and wood- industry. Therefore, a better knowledge of starch metabolism is needed.

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So far, several parameters of starch are not understood, as *e.g.* structural composition, the synthesis and degradation, regulation of the granule number, and the overall granule morphology. It is not surprising that the number of proteins involved directly or indirectly in starch metabolism is, and will further, increase. The analytics of starch in the moment is often limited by the use of average data. Today our knowledge of starch reflected *e.g*. entire tissues or organs. However, first indications reveal, that starch metabolism is altered at divers leaf ages, development stages, or in different tissues [1-3]. Thus, characterization of single tissues, cells, plastids, or starch granules are essentially missing, what is of high interest to understand starch turn-over in more detail and requires the development of new starch analytical techniques.

Clear limitations are related to the formation of starch granules. Here enzymatic/proteinic as well as mechanistic data are widely lacking. Several mutants were described with altered amount of starch granules per chloroplast in the model plant Arabidopsis. However, we are far away from understanding the process of formation and also do not know all proteins involved. The initiation of starch granules is highly complex, and several pathways are interconnected and allow alternative possibilities [1,4-7]. Even the number of starch granules is not totally fixed. Questions as, is the alteration related to different properties of the plastids, such as metabolism and development, or are that statistically fluctuations arise. Similarly, it is not understood why different sizes and morphologies of starch granules within one tissue, one cell, or even one plastid occur.

Different pathways exist in plants for starch degradation, especially when comparing the degradation of transitory and storage starch. Also related to that, many questions are unanswered. How the different starch particles get degraded simultaneously? Is there an integration network that allows the detection of single granule degradation? Is there a coordination of the degradation in various plastids within one cell? Also here single cell, single plastid, and single granule analyses are important. As example, for various plants transitory starch degradation is connected with a phosphorylation/dephosphorylation cycle on the starch granule surface [8,9]. Thus, we do not understand, what defines the exact phosphorylation position within an amylopectin molecule (Figure 1D), how deep in the surface of starch granules phosphorylation/dephosphorylation occurs, are these events even distributed over the surface and/or within an amylopectin molecule, exit differences for starches from various plant species? These questions are also interesting for industrial applications of starch, as phosphorylation of starch is the only known natural covalent modification. This together with the inner starch structure is important for the physical properties of starches, which influences parameters as swelling power, starch solubility, gelatinization, retrogradation, syneresis, and rheological behavior.

Discussion

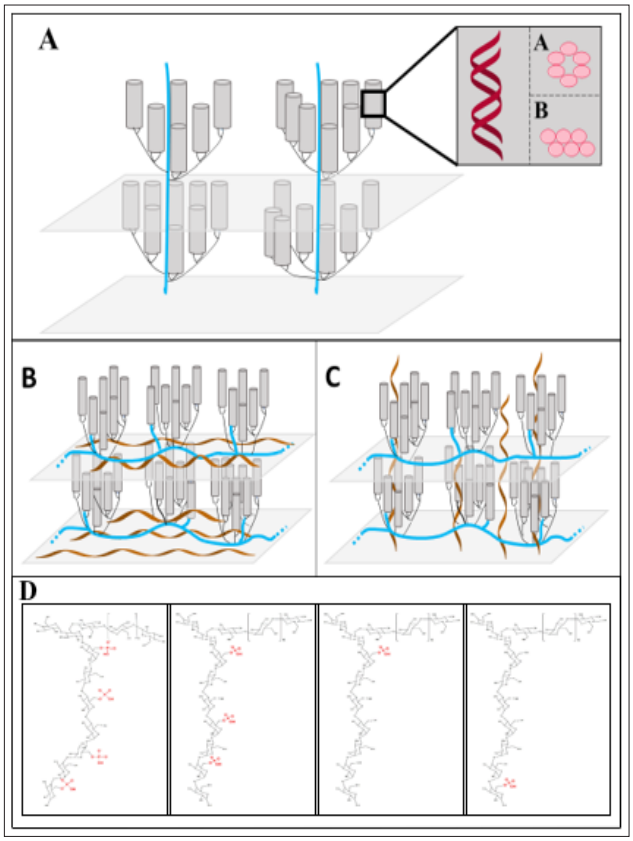

Figure 1: Open starch characteristics: the structure of amylopectin, the alternative phosphorylation positions within amylopectin, and the possible position of amylose. Alternative lamellae of crystalline and amorphous material (9nm repeat distance) formed by amylopectin molecules. Double helices (depicted as cylinders) are generated by short side chains of amylopectin that have vicinal intramolecular positions. These double helices can be organized as A-type and B-type allomorph (enlargement in illustration **A**). The orientation of the long chains of amylopectin molecules is the difference of the cluster model (**A**) in comparison to the building block backbone concept (**B**). In the later the long chains are oriented perpendicularly to the double helices and essentially parallel to the surface of the entire starch particle, whereas in the cluster model (**A**) they are oriented parallel to the double helices. The possible location of amylose (brown helices) is depicted in **B**. However, in principle also a mixture of both locations is possible. (**D**) The positions of phosphorylation within the amylopectin are depicted for C6- Phosphorylation. An even distribution of the phosphorylation, a random distribution of the phosphorylation positions, a phosphorylation only in close vicinity to the branching points, or phosphorylation close to the non-reducing end of a side chain is shown. However, also backbone chain phosphorylation is possible, but not illustrated.

However, widely accepted structural models of both glucans forming starch, amylopectin and amylose are still lacking. Currently, two main models of amylopectin, the cluster model and the building block backbone concept exist, that describe the amylopectin structure (Figures 1A-1C). They differ in the position of the long chains. In the cluster model, the long chains have essentially the same orientation as the double helices and penetrate two or more layers of double helices. Whereas in the building block backbone concept, long chains are perpendicularly oriented to the double helices and form the backbone within each amorphous lamella [10-12]. However, also the precise location of amylose is obscure (Figures 1B & 1C). These models rely on average data and so our current knowledge is strongly limited. A higher time resolution of the analyses could show, whether starch granules during synthesis reveal altered inner structure compared with established granules. Moreover, this structural information would help to understand the initiation of starch granules and the enzymes/proteins that are involved. The inner starch structure seems to be evolutionary conserved. However, how this results in totally different starch granule morphologies is unknown. *In planta* flat, discoid, and spherical starch granules were reported. Also tiny granules that are smaller than 1µm and starches with more than 100µm can be detected. However, there are indications that the size and morphology are not only genetically determined, but also influenced by metabolic alterations of the plant [1,5,13]. Manipulation of starch granule morphology and size are important parameters for increasing starch yield and changing starch properties.

Conclusion

Overall, our knowledge related to structural, biosynthetic, and degradation aspects of starch metabolism has increased massively in the last decades, but we still lack basic understanding. Analyses will benefit from abandon average data and consider higher time resolution. Enlarging our insights will allow preparing starch-crops better adapted for the ongoing climatic changes.

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