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Editorial

Starch Biosynthesis in Crop Plants

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Abstract: Starch is a water-insoluble polyglucan synthesized inside the plastids of plant tissues to provide a store of carbohydrate. Starch harvested from plant storage organs has probably represented the major source of calories for the human diet since before the dawn of civilization. Following the advent of agriculture and the building of complex societies, humans have maintained their dependence on high-yielding domesticated starch-forming crops such as cereals to meet food demands, livestock production, and many non-food applications. The top three crops in terms of acreage are cereals, grown primarily for the harvestable storage starch in the endosperm, although many starchy tuberous crops also provide an important source of calories for various communities around the world. Despite conservation in the core structure of the starch granule, starches from different botanical sources show a high degree of variability, which is exploited in many food and non-food applications. Understanding the factors underpinning starch production and its final structure are of critical importance in guiding future crop improvement endeavours. This special issue contains reviews on these topics and is intended to be a useful resource for researchers involved in improvement of starch-storing crops.

Keywords: archaeology; building block backbone model; cereals; cluster model; dental calculus; endosperm; field trial; glucan water dikinase; Poaceae (grasses); starch

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1. Introduction

Starch produced in plant tissues represents an important component of the human diet, providing the bulk of caloric intake. Archaeological evidence points to the importance of starch in the human diet well before evidence of human civilization and crop domestication [1]. Modern humans use huge volumes of storage starches from domesticated crops for direct food consumption, animal fodder, and a wide range of industrial purposes. Consequently, there are currently unprecedented pressures on global food and fuel supplies, due to an increasing world population (estimated to be 9.6 billion by 2050) and, at the same time, loss of agricultural land to urban growth, as well as climate change. In particular, enhanced affluence in many emerging world economies exacerbates these problems as meat consumption and automobile ownership increase, placing extra demands on crop yields to meet requests for livestock production and bio-fuels for fossil fuel replacements. Human civilization is reliant on a surprisingly narrow range of crops to supply its basic caloric requirements and of these, cereals provide the bulk of the calories in human and livestock diets. In addition, cereal starches are an important raw material for many non-food uses. Despite major advances in crop production brought about by the green revolution [2], based on current population growth, food production must increase 50% by 2030 and double by 2050 in order to meet projected demands [3,4]. The demand for higher-yielding starch-based crops is therefore greater than ever. In addition, over-consumption of carbohydrate-rich foods in some parts of the world are leading to health epidemics such as obesity and type-two diabetes [5]. The high proportion of starch products consumed in the diet mean that this important source of calories can have a major impact on human and animal health, in particular, starch quality characteristics such as relative rates of digestibility influence blood sugar levels and lower gut (colon) health [6]. A fundamental understanding of the process of starch biosynthesis in relation to the final structure of the starch granule and the relationship of its biochemical pathway to other metabolic pathways in plants is therefore a critical prerequisite for rational approaches to cereal crop improvement. Starch content in source leaves is recognized as an important factor governing overall plant health and productivity, as well as influencing the quality of vegetation used for grazing by livestock [7,8]. Given the importance of starch as a raw material, improvements in starch yield in major crops, such as maize (*Zea mays* L.), rice (*Oryza sativa* L.), and wheat (*Triticum aestivum* L.) will contribute greatly to food security.

In recent years, advances have been made in understanding the structural organization of the starch granule and the mechanism of starch biosynthesis in plants, in particular, storage starch synthesis in cereal endosperms. Such basic science has guided several biotechnological approaches to the improvements of starch yield and quality in both cereal and tuberous crops. Plant breeding has also resulted in yield gains of crops in the field, based on knowledge of the starch biosynthetic pathway and of source-sink relationships during plant development. It is important to realize that plant performance enhancements observed in controlled environments do not necessarily translate under field conditions. Ancestral plant genomes also hold promise for the improvement of new cereal varieties. It will be important to bridge the gap in our knowledge between the biochemical pathways involved in starch metabolism and how these biochemical processes result in the higher order structures found in all starch granules.

2. Special Issue Overview

Following the invitation of the Editorin-chief Peter Langridge, four articles have been published in a special issue of *Agronomy* entitled "Starch Biosynthesis in Crop Plants". The special issue contains three review articles dealing with (1) archaeological studies of starch use in human populations, (2) starch structure, (3) starch biosynthesis in grasses (Poaceae), and a field study on wheat plants showing reduced expression of the starch phosphorylating enzyme glucan, water dikinase (GWD) using RNA interference (RNAi).

The review by Copeland and Hardy [9] provides fascinating context to the study of starch biosynthesis and its use by humans and our hominid ancestors. Starch granules surviving intact within dental calculus from prehistoric human remains and from ancient cooking pots in more recent times provide compelling evidence for the use of starchy foods throughout human history and are testament to the resilience of starch granules as a form of long-term carbohydrate storage. The authors urge caution in the use of available evidence in making claims about the contribution of starchy foods in the diet throughout human evolution and the botanical origins of the various recovered samples of archeological starch. Nevertheless, evidence of increased copy number of the human salivary α-amylase gene (*AMY1*) during human development [10], to the degree that *AMY1* represents as much as 50% of total salivary protein [11], indicates the importance of starch in the human diet. The review makes an intriguing case for the important role of dietary starch in human evolution, arguing that the rapid increase in human brain size from the Middle Pleistocene was biologically affordable when rich sources of glucose were available in the form of starchy foods. In particular, the use of fire around 400,000 years ago made the caloric content of plant starches more readily accessible, and it was at this time that the *AMY1* gene copy number was increasing [12].

Our current understanding of starch granule structure is the subject of the review by Bertoft in this special issue [13]. Despite wide variation in granule size and morphology amongst different plant species, the basic levels of structural organization of the granule are remarkably conserved from the level of Ångströms to micrometers. The review covers aspects of the structural organization and characteristics of the two glucose polymers found in starch, amylose and amylopectin, and the variation in their molecular structures according to different plant species. The major component of starch is amylopectin and this architecturally complex polymer essentially defines the structural and physicochemical properties of the granule. Following detailed discussion of higher-order, molecular organization of the granule, including the distinctions between the different crystalline allomorphs, blocklet organization, and growth rings, the review deals with the two major models describing organization of the structural units in amylopectin. A widely accepted model is the cluster model, originally proposed by Nikuni in 1969, and independently by French in 1972 [14]. The cluster model is a development of the trichitic model suggested by Meyer in 1895. In this review Bertoft argues that a second model, termed the building block backbone model, fits more closely to recent data analysis of α-dextrins isolated from amylopectin [15]. Despite much progress in elucidating the complex architecture of the starch granule, aspects of its three-dimensional structure are still not clear. This comprehensive review of starch structure has important implications to our perception of the biological processes involved in starch biosynthesis and granule assembly.

The third review in this special issue deals with starch biosynthesis in grasses (Poaceae) [16]. Cereals (domesticated grasses grown for the starch reserves in their endosperms) represent six out of the top seven crops grown worldwide [17]. Since cereal yields essentially underpin world food and feed supply, it is critical we understand the biological factors contributing to the major yield component of these important crops. In addition to cereal-derived starch, forage grasses are a central component of the diets of many domesticated animals around the world. Starch biosynthesis in vegetative tissues of the Poaceae is an important determinant of forage quality and overall biomass. Many of the details of the starch pathway discussed in this review are also applicable to other important dicotyledonous crops, e.g., underground tubers. Prior to dealing specifically with the biochemical pathway of starch synthesis, the review outlines cellular development of the endosperm tissue, as well as aspects of cytosolic metabolism involved in delivering carbon to the amyloplast for starch biosynthesis. This is particularly pertinent given the fact that cereal endosperms appear to be unique amongst plant tissues in expressing an extra-plastidial isoform of ADP-glucose (ADP-Glc) pyrophosphorylase (AGPase), responsible for the delivery of the bulk of the carbon used for storage starch biosynthesis. In addition to AGPase, all of the other classes of starch biosynthetic enzymes are dealt with and the review highlights new developments in our understanding of amylose biosynthesis and the starch granule initiation process.

The final paper in this special issue is a field study by Whan et al. comparing the growth of wheat plants with reduced expression of GWD in controlled, glasshouse conditions versus the field [18]. GWD is involved in starch granule mobilization through the covalent introduction of phosphate residues to glucose moieties in amylopectin. Previous studies showed that wheat plants with RNAi-mediated suppression of GWD in the endosperm showed increased early vigour, increased biomass and yield [19]. These studies were conducted in a single-pot glasshouse trial and the present study evaluated the performance of the GWD-suppressed plants under field conditions in three locations. The field study highlighted consistencies between field and glasshouse-grown plants with respect to enhanced flag leaf area and rachis nodes but importantly, also showed that there were differences (reductions) in tiller number and therefore overall grain yield at different sites. This is an important study, highlighting variance that may be expected when transferring results from glasshouse to field.

3. Conclusions

Starch has played a central role in human nutrition and development since before humans became crop cultivators. Currently, starch production by the major crops (cereals) underpins our food supply and it is imperative to understand the structure and biosynthesis of this complex biopolymer if we are to direct improvements in yield and food quality in a rational manner. I hope this special issue is a useful resource for students as well as researchers and agronomists working in the field of starch biology.

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Abbreviations

The following abbreviations are used in this manuscript:

ADP-Glc	ADP-glucose
AGPase	ADP-glucose pyrophosphorylase
AMY1	salivary α-amylase
GWD	glucan, water dikinase
RNAi	Interference RNA

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