BACTERIAL GLYCOGEN AND PLANT STARCH BIOSYNTHESIS

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Introduction

The biosynthesis of α-1,4-polyglucans is an important process by which living organisms accumulate energy reserves to be used when carbon nutrients are no longer available from the environment. The main advantage of using polysaccharides as storage reserves is that because of their high molecular weights and other physical properties they have little effect on the internal osmotic pressure in the cell. The metabolic routes leading to polyglucan synthesis were elucidated after the discovery of nucleoside-diphosphate-sugars by L F Leloir and coworkers in the 1950s.[1] This finding led to the conclusion that biosynthesis and degradation of glycogen occur by different pathways.

Glycogen synthesis in mammalian cells is relatively well understood, including the specificity of glycogen synthase for UDP-glucose as well as its regulation through hormonally induced post-translational protein modification.[2] Textbooks of biochemistry usually describe these metabolic schemes in detail. The biosynthesis of polysaccharides in bacteria and plants is, in contrast usually described in less detail. These organisms accumulate glycogen (bacteria) or starch (plants) by metabolic pathways which are different in a number of respects from those occurring in animals. Despite the difference in the final product (glycogen or starch), in bacteria and in plants ADP-glucose is the glucosyl donor for the elongation of the α-1,4-glucosidic chain. Moreover, in both organisms, the main regulatory step of the metabolism takes place at the level of ADP-glucose synthesis. It is the aim of this contribution to describe the biosynthesis and regulation of glycogen in bacteria and of starch in plants, and to compare the characteristics of these metabolic routes in the different organisms. This area of biochemistry provides ample opportunity for teachers to emphasise to their students the unity of life.

Occurrence and functions of bacterial glycogen

Glycogen is a major intracellular reserve polymer in bacteria, being reported in over 40 different species, including Gram negative, Gram positive, archaebacteria and photosynthetic bacteria.[3,4] Glycogen is a branched polyglucose with about 90% of its glucose residues in α1,4-glucosidic linkages and the rest in α1,6 linkages,[3] the percentage of α-1,6-linkages varies depending on the species as well as on the stage of the polyglucan synthesis.[5] A number of bacterial species (*Rhodopseudomonas capsulata*, *Streptococcus mitis* and the archaebacterial strain *Sulfolobus solfataricus*) optimally synthesize glycogen during exponential growth.[3] However, for many bacterial species the rate of glycogen accumulation increases during stationary phase. Usually, glycogen levels are higher when there is a carbon excess in the media and/or when growth is limited by a lack of a required nutrient (ammonia, amino acids, sulfur or phosphate).[3,4] Nitrogen deficits lead to the largest accumulation of glycogen. Depending on the nutritional conditions as well as the growth phase of the organism, glycogen storages can reach up to 50% of the dry weight of the cell.[3,4]

Mutants of different bacterial species (including an *Escherichia coli* deletion mutant) having defective structural genes for the glycogen biosynthetic enzymes and which are unable to synthesize glycogen, grow as well as their wild type parent strains.[4] Thus, glycogen is not required for bacterial growth. However, a more prolonged survival rate is observed in the cells accumulating the polysaccharide compared with the glycogen-less mutants. Two lines of evidence suggest a main role for glycogen as an energy- and carbon-storage compound.[3,4] Firstly, glycogen appears to prevent RNA and protein degradation when bacterial cells are under starvation conditions indicating that glycogen provides carbon and energy for cell survival under stress. Secondly, in spore-forming bacteria, the glucan accumulates prior to the onset of sporulation and is then rapidly degraded with concomitant spore formation.

Bacterial glycogen synthesis

Synthesis of glucosyl linkages occurs through the transfer of the glucosyl unit from a nucleoside-diphosphate-sugar to an appropriate acceptor.[1] In mammalian tissues and in eukaryotic microorganisms, glycogen synthesis is mediated by transferring a glucosidic residue from UDP-glucose to the non-reducing end of the α-1,4-poly-glucan.[1,2] The same mechanism is true for glycogen synthesis in bacteria, except that prokaryotes utilize ADP-glucose instead of the UDP-derivative as the glucosyl donor.[2] Thus, the reactions sequence by which glycogen is synthesized in bacteria was established as follows:

$$\text{ATP} + \alpha\text{-glucose-1-P} \rightleftharpoons \text{ADP-glucose} + \text{PPi} \quad (1)$$

$$\text{ADP-glucose} + (\alpha\text{-1,4-glucan})_n \rightarrow (\alpha\text{-1,4-glucan})_{n+1} + \text{ADP} \quad (2)$$

$$\text{linear 1,4-}\alpha\text{-glucan} \rightarrow \text{branched 1,6-}\alpha\text{-1,4-}\alpha\text{-glucan} \quad (3)$$

Experimental evidence strongly supports the above pathway as the main route for glycogen synthesis in most (if not all) bacteria.[4] It has been shown that extracts of several prokaryotic species contain both an ADP-glucose pyrophosphorylase [ATP:α-D-glucose-1-P adenylyltransferase; EC 2.7.7.27] as well as ADP-glucose specific glycogen synthase [ADP-glucose:1,4-α-D-glucan 4-α-D-glucosyltransferase; EC 2.4.1.21], the enzymes catalyzing reactions 1 and 2, respectively. Glucan branching enzyme [1,4-α-D-glucan:1,4-α-D-glucan 6-α-D-1,4-α-D-glucano)transferase; EC 2.4.1.18] activity (equation 3) has also been characterized in many bacterial extracts, including various photosynthetic prokaryotes. Studies carried out with bacterial mutants, either with deficit or overproduction of glycogen, have demonstrated that the levels of the polyglucan in these organisms correlate with their levels of glycogen synthase or ADP-glucose pyrophosphorylase activity.[3,4] Interestingly, UDP-glucose pyrophosphorylase deficient mutants of *Escherichia coli* are able to accumulate normal amounts of glycogen, reinforcing the idea that UDP-glucose is not the precursor for the polysaccharide synthesis in bacteria.[4]

Consideration of the main carbon utilization pathway occurring in different bacteria aids a better understanding of glycogen biosynthesis. This not only clarifies the source of the carbon and the energy, both of which are necessary for glycogen production, but also reveals that a consistent pattern is usually observed between the main carbon metabolism in the organism and the regulation of the glycogen biosynthetic route.[5] We can adopt a broad classification criterion and divide bacteria in three groups: (*i*) bacteria using glucose assimilation as their major carbon metabolism; (*ii*) bacteria performing anoxygenic photosynthesis; and (*iii*) cyanobacteria. The first group comprises the Enterobacteriaceae and related heterotrophic organisms, which can obtain energy from glucose degradation, either via the Embden-Meyerhof or Entner-Doudoroff pathways.[6] In the second group are photosynthetic prokaryotes that cannot metabolize glucose (eg *Rhodospirillum rubrum*) but can grow either heterotrophically in the light or dark on various tricarboxylic acids, or autotrophically on CO_2 and H_2 (essentially in the absence of O_2). The third group includes bacteria that carry out an oxygen evolving photosynthetic process like that in chloroplasts of higher plants.[7] The origin of the carbon for glycogen synthesis in cyanobacteria is atmospheric CO_2 photosynthetically assimilated.

Structure and functions of starch

Starch is present in most green plants in practically every type of tissues: leaves, fruits, pollen grains, roots, shoots, and stems.[8,9] Sucrose and starch are the two main end products of carbon fixation during photosynthesis in higher plants.[10] Starch is the major intracellular reserve polysaccharide in photosynthetic organisms and constitutes a principal food of many animals including man.[11] In leaves, starch is formed during the light period and is degraded in the dark. The polyglucan accumulated during development of storage or seed tissues is actively catabolized at the time of germination to serve as a source of carbon and energy.[12] The biosynthetic and degradative processes of leaf starch are therefore more dynamic than that in reserve tissues.

Starch has long been recognized by its iodine staining properties as well as by the characteristic microscopic appearance of the granule.[9,11,13] It is composed of two major polysaccharides, amylose and amylopectin,[11,13] which are distributed radially in starch granules in such a way that their single reducing end-groups orient towards the centre,

with synthesis occurring at the opposed outer non-reducing extreme.[11] Amylose is an essentially linear α-1,4-glucan whereas amylopectin consists of α-1,4-glucan chains joined by numerous α-1,6-branch points typically occurring every 5 or 6 glucose residues.[11,13] In most starches, the amylose fraction has occasional secondary chains attached by α-1,6-linkages.[11] Both amylose and amylopectin contain a few phosphate groups mainly at C-6 of glucose residues.[11] Amylopectin branching is fairly asymmetric and its unit chains fall into two groups with chain lengths of more than 49, and between 12 and 42 glucosyl units.[9] Two models of the amylopectin structure have been proposed, both consisting of an arrangement of the branching of the unit chains in cluster formation.[9,11]

Starch biosynthesis

Reactions leading from glucose-1-P to starch in green algae and higher plants are very similar to those described for bacterial glycogen formation. ADP-glucose pyrophosphorylase (see eqn 1) produces the nucleoside-diphosphate-sugar used by starch synthase, an enzyme that catalyzes the reaction shown by eqn 2, and is highly specific for ADP-glucose.[8,9] Soluble starch synthases present in leaves are virtually unable to utilize UDP-glucose as a substrate, whereas the starch-bound form of the enzyme can use UDP-glucose although the affinity for this compound is 15–30 fold lower than for ADP-glucose.[8,9] The pathway is completed by the action of plant branching enzyme (see eqn 3). The substrate specificity of starch synthase together with other genetic evidence,[14,15] strongly suggests that starch is predominantly (if not solely) synthesized through the ADP-glucose pathway.

Three isoenzymes of starch synthase (two soluble and a starch-bound form), and three forms of the branching enzyme have been characterized in different plant species.[9,12] The isoenzymes may differ in specificity for elongation for different sizes and for the distance at which the branch point is inserted.[9] It is believed that the existence of isoenzymes causes the above described asymmetric structure of amylopectin.[9,12]

In plant cells starch metabolism is compartmentalized in specialized organelles called plastids. Chloroplasts and amyloplasts in photosynthetic and non-photosynthetic tissues, respectively, are the plastids that metabolize starch.[9] Chloroplasts primarily provide carbohydrates for biosynthetic processes (including starch production) since they contain all the components to perform photosynthesis.[10,16,17] In contrast, amyloplasts and other non-photosynthetic plastids must import both carbon and energy for synthetic pathways.[16] Figure 1 is a scheme for the flux of carbohydrates occurring in cells of higher plants, emphasizing how they are related to starch.

In leaf cells of higher plants photosynthetic carbon assimilation or the reductive pentose-phosphate pathway (RPPP) is carried out in the chloroplast stroma (Fig 1A). This reductive cycle utilizes ATP and NADPH, produced from the light energy in the thylakoid membranes, to fix CO_2 to form carbohydrates, with 3-P-glycerate and triose phosphates as the initial products.[10,16,17] Fructose-6-P is an intermediate of the RPPP from which the route to starch (a final product of the process) synthesis may be initiated.[16] Thus, starch formation occurs entirely inside the chloroplast which not only supplies the carbon but also for the ATP necessary for the process.[17]

As also shown in Fig 1A sucrose, the other major end product of photosynthesis, is synthesized in the cytosol.[10] This implies that carbon assimilated photosynthetically undergoes a partitioning between different cellular compartments.[10,16,17] Those processes involved in the transfer of photosynthates across the chloroplast envelope play a key role in the regulation of photosynthesis.[16] The Pi/triose-phosphates/3-P-glycerate translocator (usually named the 'Pi-translocator') is the most important system in the chloroplast envelope responsible for the partitioning of photosynthate.[17,18] In the light, this translocator exports triose-phosphates from the chloroplast thereby supplying carbon for cytosolic sucrose synthesis. The pathway from triose-phosphates to sucrose also forms Pi which may be utilized as the mandatory counter exchanger anion of the Pi-translocator.[16–18] This Pi and that derived from starch formation is utilized to regenerate ATP through photophosphorylation inside the chloroplast (Fig 1A). Pi recycling is important to maintain high rates of photosynthesis.[17]

Sucrose is the main form by which carbohydrates are transported to other tissues of the plant.[16] Fig 1B shows that non-photosynthetic cells degrade sucrose in the cytosol producing intermediates that can be imported into the amyloplast for starch synthesis.[16] Although most of the experimental data strongly support the idea that in these organelles

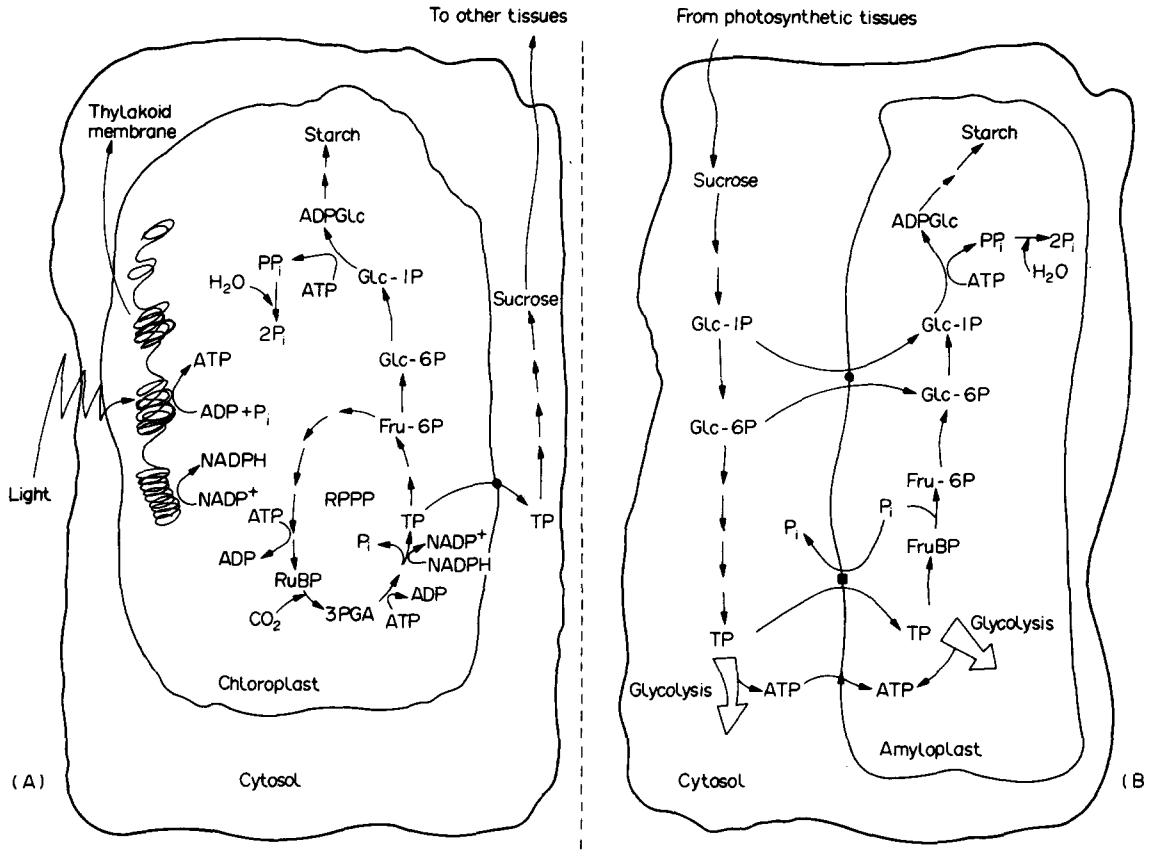

Figure 1 *Carbon metabolism and starch synthesis in photosynthetic (A) and non-photosynthetic (B) cells of higher plants. Abbreviations: TP, triose-phosphates (glyceraldehyde-3-P and dihydroxyacetone-P); RuBP, ribulose 1,5-bisP; 3PGA, 3P-glycerate; FruBP, fructose 1,6-bisP; Fru-6P, fructose 6-P; Glc-1P, glucose 1-P; Glc-6P, glucose 6-P; ADPGlc, ADPglucose. Translocators of plastid envelopes are symbolized as follows: ●, Pi-translocator; ■, glucose-P translocator; ▲, adenylate translocator*

the polyglucan is built up through the ADP-glucose pathway,[8–10,16] less is known about the principal transport occurring across the amyloplast envelope. Two main possibilities exist and they are shown in Fig 1B. One involves the import of glucose-P through a specific translocator, and the second comprises the activity of a Pi-translocator similar to that present in chloroplasts.[16,18] In the second case, triose-phosphate from sucrose degradation is imported in a counter-exchange with Pi. Another point that is currently unclear is the origin of ATP for amyloplastic starch synthesis. It is likely that ATP is produced by glycolysis, which may occur in the cytosol as well as inside the plastid. For the first option it is necessary that ATP passes through the envelope, which is mediated by an adenylate translocator.[16]

Regulation of glycogen and starch biosynthesis

ADP-glucose pyrophosphorylase is the regulatory enzyme on the pathway of bacterial glycogen as well as of plant starch biosynthesis.[2–5,8–10,12,14–16] This is strongly supported by numerous experiments, including characterization of bacteria and plants mutants in which overproduction or low accumulation of the reserve polysaccharide correlate with the allosteric properties of the enzyme.[2,4,5,14,15] The regulation of ADP-glucose synthesis in bacteria and plants is in agreement with the generalization that a biosynthetic pathway is effectively regulated at its first unique step.

Many studies have shown that ADP-glucose pyrophosphorylase is allosterically regulated by metabolites, the specificity of the regulator depending on the organism. From the relationship between enzyme regulation and the major carbon metabolism contributing for glycogen or starch formation in different organisms, the following common sense

statement may be made: the extent of synthesis of polysaccharide is higher when cellular carbon and energy are in excess.[2,4,5]

Table 1 summarizes the regulatory and structural properties of ADP-glucose pyrophosphorylases from bacteria, green algae and higher plants. As can be seen, the enzyme from bacteria actively degrading glucose (Embden-Meyerhof glycolytic route or Entner-Doudoroff pathway) is activated and/or inhibited by intermediates of the degradative route. Thus, the well-studied enzymes from Enterobacteriaceae (*Escherichia coli* and *Salmonella typhimurium*) have been characterized as homotetramers that are allosterically activated by fructose-1,6-bisP and inhibited by AMP (Table 1).[4,5] Fructose-1,6-bisP increases the apparent affinity for substrates and also partially reverses the inhibition caused by AMP in these pyrophosphorylases. The regulatory properties, together with the fact that ATP is a substrate of the enzyme indicate that the energy charge of the cell is important for the control of glycogen synthesis in these organisms. Relatively high concentrations of the glycolytic intermediate fructose-1,6-bisP is a signal of carbon excess accompanied by high levels of cellular energy (high ATP and low AMP values). The enzymes from *Serratia marcescens*, *Enterobacter hafniae* and *Clostridium pasteurianum*, although very sensitive to AMP inhibition, are exceptions because they do not seem to be activated to any great extent by any physiological compound.[5]

In contrast, the organisms that utilize the Entner-Doudoroff pathway have ADP-glucose pyrophosphorylases activated by fructose-6-P and pyruvate (Table 1).[4,5] These organisms do not contain phosphofructokinase. Thus, fructose-1,6-bisP may not be an important metabolite in hexose assimilation. Some anoxygenic photosynthetic bacteria, such as *Chromatium vinosum*, *Rhodobacter capsulata* and *Rhodomicrobium vanniellii*, can also only metabolize hexose via the Entner-Doudoroff pathway and thus their ADP-glucose pyrophosphorylases are activated by fructose-6-P as well as by pyruvate (Table 1).[3–5]

Table 1 shows that some anoxygenic photosynthetic bacteria contain ADP-glucose pyrophosphorylase activated only by pyruvate.[3–5] These organisms, *Rhodospirillum rubrum*, *Rhodospirillum tenue* and *Rhodocyclus purpureus*, are capable of growth under heterotrophic conditions in the dark or in the light and autotrophic conditions in the light. Generally they grow very well on pyruvate and tricarboxylic acid cycle intermediates as carbon sources and photosynthetic electron donors, but they are unable to grow with hexose as the carbon source.[8]

Of interest are the anaerobic photosynthetic bacteria. These show great flexibility in their carbon assimilation pathways: thus *Rhodobacter gelatinosa*, *Rhodobacter globiformis* and *Rhodobacter sphaeroides* can metabolize hexoses either via the Entner-Doudoroff or the glycolytic pathways.[2–5] Their ADP-glucose pyrophosphorylases are not only activated by pyruvate and fructose-6-P but also by fructose-1,6-bisP and inhibited by Pi and AMP (Table 1).[3,5]

ADP-glucose pyrophosphorylases from organisms that perform an oxygenic photosynthesis and utilize the RPPP to fix CO_2 have 3-P-glycerate and Pi as the most important activator and inhibitor, respectively.[8,9,14,15,19,20] Indeed, Table 1 shows that all the enzymes so far characterized from cyanobacteria, green algae and photosynthetic tissues of higher plants exhibit these regulatory properties. This appears to be the same as for the pyrophosphorylases from non-photosynthetic cells of plants[9,14,15,21–23] (Table 1). The carbon source for starch synthesis in non-photosynthetic tissues of plants may be considered as indirectly derived from the RPPP, since sucrose used for such purpose is transported from the leaf where it is synthesized *de novo* (Fig 1).

Interestingly, 3-P-glycerate is the first product in CO_2 fixation via RPPP (Fig 1) and its accumulation is a metabolic signal of a very active photosynthetic process. On the other hand, Pi is a product of the RPPP as well as of the starch formation through the hydrolysis of PPi catalyzed by pyrophosphatase. Under light conditions Pi is maintained at low levels because it is utilized as a substrate to regenerate ATP by photophosphorylation.[17] High Pi concentrations indicate a low photosynthesis rate and consequently low cellular energy and carbon availability. Once again, this picture agrees with high energy charge and carbon excess driving towards reserve polysaccharide synthesis.

In eukaryotic cells of higher plants, regulation of ADP-glucose pyrophosphorylase by 3-P-glycerate and Pi is quite important for photosynthetic partitioning between plastids and

Table 1 Carbon metabolism and regulatory and structural properties of ADP-glucose pyrophosphorylase in different organisms

Organism	Main carbon pathway	Major reserve polyglucan	ADP-glucose pyrophosphorylase		
			Allosteric regulators		Quaternary structure
			Activator	Inhibitor	
Prokaryotes					
Enterobacteria					
Escherichia coli *Salmonella typhimurium* *Enterobacter aerogenes*	Embden-Meyerhof glycolytic pathway	Glycogen	Fructose-1,6-bisP	AMP	Homotetramer (α_4)
Aeromonas formicans *Micrococcus luteus* *Mycobacterium smegmatis*		Glycogen	Fructose-1,6-bisP Fructose-6-P	AMP ADP	
Serratia mercescens *Enterobacter hafniae* *Clostridium pasteurianum*		Glycogen	None	AMP	
Agrobacterium tumefaciens *Arthrobacter viscosus* *Chromatium vinosum* *Rhodobacter capsulata* *Rhodomicrobium vannielii*	Entner-Doudoroff pathway	Glycogen	Pyruvate Fructose-6-P	AMP ADP	
Rhodobacter gelatinosa *Rhodobacter globiformis* *Rhodobacter sphaeroides*	Glycolysis and Entner-Doudoroff pathways	Glycogen	Pyruvate Fructose-6-P Fructose-1,6-bisP	AMP Pi	
Rhodospirillum rubrum *Rhodospirillum tenue* *Rhodocyclus purpureus*	TCA cycle Reductive carboxylic acids cycle	Glycogen	Pyruvate	None	
Cyanobacteria *Synechococcus* 6301 *Synechocysits* 6803 *Anabaena* 7120	Oxygen evolving photosynthesis RPPP	Glycogen	3-P-glycerate	Pi	Homotetramer (α_4)
Eukaryotes					
Green algae					
Chlorella fusca *Chlorella vulgaris* *Chlamydomonas reinhardtii*	RPPP	Starch	3-P-glycerate	Pi	
Higher Plants					
Photosynthetic tissues (leaves of spinach, *Arabidopsis*, wheat, maize, rice)	RPPP	Starch	3-P-glycerate	Pi	Heterotetramer ($\alpha_2\beta_2$)
Non-photosynthetic tissues (Potato tubers, maize endosperm)	Degradation of sucrose imported from photosynthetic tissues	Starch	3-P-glycerate	Pi	Heterotetramer ($\alpha_2\beta_2$)

cytosol.[10,16,17] As described above, carbon fixed photosynthetically in the chloroplast stroma is patitioned to the formation of the two major products starch and sucrose (Fig 1).[10,16] The partitioning occurs through the Pi-translocator which mediates the strict counter exchange of triose-phosphates and Pi across the plastid envelope.[17,18] In this way, the balance of 3-P-glycerate and Pi in cytosol and chloroplast stroma determine the rates of sucrose and starch formation. It has been established that ADP-glucose pyrophosphorylase is accurately regulated by the 3-P-glycerate:Pi ratio.[8–10,14,15,24] *In vivo* studies have demonstrated that the regulation is of physiological significance because the higher is the 3-P-glycerate:Pi ratio at the chloroplast the higher is the rate of starch biosynthesis, and *vice versa*.[8,9]

Structure of ADP-glucose pyrophosphorylases

All of the work done on ADP-glucose pyrophosphorylase from different sources shows that the higher plant enzyme differs from the bacterial protein not only in allosteric regulatory properties but also in structure (Table 1). The enzymes from *E coli* and *S typhimurium* are encoded by a single gene locus that gives rise to a homotetramer with molecular mass about 200 kDa.[3] The enzyme from photosynthetic and non-photosynthetic tissues of higher plants is more complex in structure, being heterotetrameric ($\alpha_2\beta_2$) with two subunits (α and β) differing in molecular mass, antigenicity and amino acid sequence.[4,14,15,22,23,25,26] Overall biochemical and genetic evidence indicates that the higher plant ADP-glucose pyrophosphorylase is encoded by two distinct genes.[26]

A comparison of *E coli* and rice seed small subunit pyrophosphorylase sequences shows about 29% identity at the amino acid level between bacterial and plant proteins, suggesting a common origin for these two genes.[15] Conserved sequences in the primary structure are found at the substrate and activator sites, the main difference being that the activator site is at the *N*-terminus in bacteria and at the *C*-terminus in plant enzyme.[15] Comparison of the structure of the enzyme from different higher plants reveals a high structural homology between small subunits.[21,22,26] About 86% identity is observed when primary sequences of rice endosperm and spinach leaf small subunits are compared[27] for example. In contrast, the larger subunit of plant ADP-glucose pyrophosphorylase was found to be more divergent and shows less sequence identity.[21,27]

Of particular interest are the properties of ADP-glucose pyrophosphorylase from cyanobacteria. As shown in Table 1, these organisms are the only prokaryotes performing a chloroplast-like oxygen evolving photosynthesis, fixing carbon by RPPP, the whole process exhibiting a strong resemblance to that occurring in higher plants.[7] Different evidence supports the cyanobacterial origin of the chloroplast.[7] Despite these similarities with plants, cyanobacteria synthesize a glycogen-like polysaccharide as the major reserve carbohydrate[28] in a similar manner to that observed in bacteria. Recent studies have shown that ADP-glucose pyrophosphorylase from cyanobacteria possesses properties intermediate between the bacterial and plant enzymes.[20] Thus, cyanobacterial pyrophosphorylase is regulated by 3-P-glycerate and Pi[19,20] and is immunologically more related to the spinach leaf than to the *E coli* protein.[20] However, the enzyme from cyanobacteria is homotetrameric in structure[20] as observed for bacterial enzyme. From this, it is quite possible that during evolution there was gene duplication in the plant photosynthetic systems of the pyrophosphorylase gene and then divergence of the genes to produce two different peptides. Both subunits are required for optimal activity of the native plant ADP-glucose pyrophosphorylase. The reason for this gene duplication as well as in which intermediate period during evolution it took place are unknown at the present time.

Concluding remarks

Synthesis of glycogen in bacteria and of starch in plants exhibit important differences with glycogen formation in animals, mainly with respect to enzyme specificity and regulation. In the former organisms α-1,4-polyglucans are synthesized predominantly through the ADP-glucose pathway.

ADP-glucose pyrophosphorylase is the regulatory enzyme in the biosynthetic routes leading to glycogen and starch biosynthesis in bacteria and plants, respectively. The enzyme is subject to allosteric regulation, with the regulatory metabolite(s) being different in the different organisms. So far, regulation is rationally associated with activation of the enzyme at high cellular carbon and energy levels.

Comparative studies of ADP-glucose pyrophosphorylases from different sources have established relationships between structure and function as well as changes undergone by this protein during evolution. Current information on the matter needs further experimental work to improve our understanding of the processes leading to starch and glycogen biosynthesis from a biochemical and evolutionary point of view.

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