REVIEW

Benson-Bassham-Calvin cycle contribution to the organic life on our planet

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> "*Science is more about failure than success.*"
> A.A. Benson

Abstract

The review is devoted to the outstanding contributions to the path of carbon in photosynthesis by Professor Emeritus Andrew A. Benson, on the occasion of his death at the age of 97, on January 16, 2015. Benson is the legendary co-discoverer of the photosynthetic reductive pentose phosphate cycle, known to every student of photosynthesis as the Benson-Bassham-Calvin cycle. This pathway evolved into the dominant assimilation mechanism for atmospheric carbon into metabolites. The fundamental ecological and biochemical optimization and evolutionary stability of this mechanism unfolded elegantly in Benson's hands, as he was the first to recognize the building blocks for the synthesis of essential organic compounds that satisfy the energetic needs and demands of most life forms. Photosynthetic carbon metabolism together with other energy and oxidative reactions and secondary biosynthetic processes are critical for the formation of organic matter; and, thereby, the Benson-Bassham-Calvin cycle ensures maintenance of the biosphere.

Additional key words: autotrophic organisms; eukaryotes; photosynthesis; prokaryotes.

Introduction

As a young scientist in the 1940's, Andrew Benson held the world's supply of radioactive carbon dioxide that had a sufficiently long half-life to apply to plants and follow its path to sugars (Calvin and Benson 1948). The ensuing discovery and description of the cyclic sequence of reactions of photosynthetic fixation and reduction of atmospheric carbon into organic substances before 1960 was one of the greatest achievements of the 20th century. This discovery has led not simply to the knowledge accumulation concerning the regular sequence of biochemical reactions taking place in green parts of the plant, but more importantly, to understanding a key photosynthetic process – the phenomenon, thanks to which organic life developed. Floristic eukaryotes are the main sources of food, protection, and sanitation of all heterotrophic creatures, including human beings.

Striking is the fact that this may be the sole discovery of the first order that does not show the other side of medal, *i.e.*, it has not been used to the detriment of all living things.

Thanks to Andrew Benson, the method, which combines the use of radioactive substrates and chromatographic analysis for labeled products, began a new stage in the study of biochemical pathways occurring in living organisms. The significance of this methodological development for biological sciences and science in general is hard to overestimate.

It should be also noted that efforts to improve the efficiency of photosynthetic carbon metabolism have been on-going in the field of photosynthetic biochemistry. Among the most successful results in this direction are those which may be regarded as the link to regulation of the photosynthetic carbon fixation products (Nonomura and Benson 2014).

Andrew Benson's scientific path has been described in several reviews (Benson 2002a, 2002b, Adrianov *et al*. 2007, Titlyanov and Titlyanova 2007, Lichtenthaler *et al*. 2008, Buchanan and Wong 2013). Here, we focused on the Benson-Bassham-Calvin cycle contribution to the organic life on our planet.

Discoverers of the photosynthetic carbon reduction cycle

The credit for the first recognition of the mechanism of photosynthetic carbon metabolism belongs to a trio of American scientists, Andrew A. Benson, James A. Bassham, and Melvin Calvin (Fig. 1). Their enormous erudition in different fields, dedication, keen minds, inquisitive nature, engineering and design talents, and profound understanding of science allowed the exploration and description of the biochemical reaction sequence that fix and reduce atmospheric carbon into organic matter in the green plant cell. And it all came together in a relatively short period of recent history (Calvin and Benson 1948, Benson and Calvin 1950*a*, 1950*b*, Benson *et al*, 1950, Benson 1952, Bassham *et al*. 1954).

The reductive pentose phosphate cycle, named the Benson-Bassham-Calvin cycle in honor of its discoverers, or in accordance with the primary product of CO_2 fixation, C_3 photosynthesis (Fig. 2), was developed by the authors mainly based on experiments with microalgae. They proved that primary CO_2 photoassimilation occurs in the carboxylation reaction of ribulose-1,5-bisphosphate (RuBP) and the first stable products are two molecules of 3-phosphoglyceric acid (3-PGA), which is then reduced to 3-phosphoglyceric aldehyde and dihydroxyacetone phosphate (DOAP) (Fig. 2). These triose phosphates yield hexose phosphate esters that are then used for the synthesis of sucrose and/or starch. Regeneration of RuBP provided interconversion of phosphoric sugar esters (PES) in the sequence of the transketolase and aldolase reactions that lead ultimately to the formation of ribulose-5-phosphate. Then ribulose-5-phosphate is phosphorylated with the expenditure of ATP.

During the same period of time, analogous research was carried out by scientists in the Soviet Union on species of different higher plant families confirming the existence of this cycle in all photosynthetic eukaryotes (Doman 1952, Nichiporovich 1953, Doman *et al*. 1958). At the present time, it is known that the reductive pentose phosphate cycle is inherent not only to all eukaryotic plants and cyanobacteria, but also in most known chemo-autotrophic bacteria and purple phototrophic bacteria

Fig. 1. Discoverers of photosynthetic carbon reduction cycle (from left to right): James A. Bassham, Andrew A. Benson, and Melvin Calvin. Andrew A. Benson gave this photo as a present to Karl Biel in September 09, 1988.
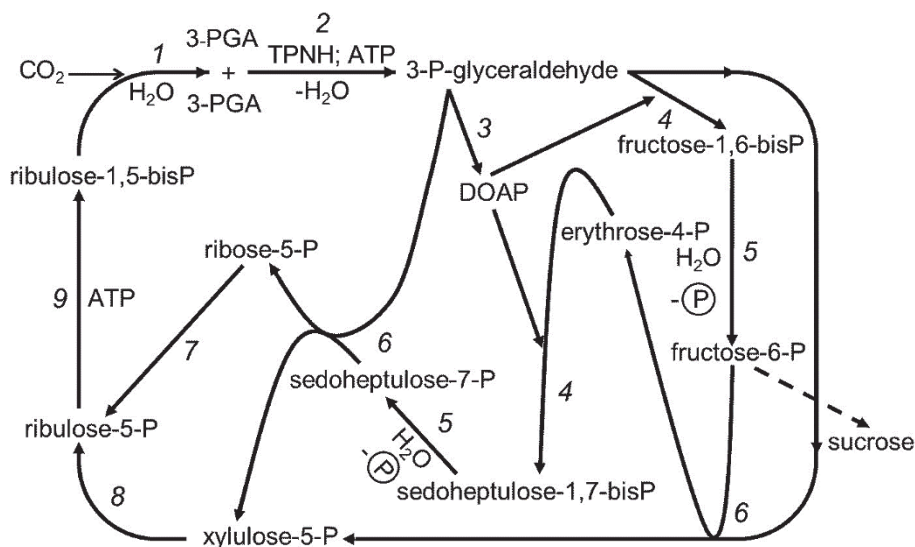

Fig. 2. Photosynthetic carbon reduction cycle. BisP – bisphosphate, P – phosphate, TPNH – reduced triphosphopyridine nucleotide, 1 – carboxydismutase system, 2 – triosephosphate dehydrogenase, 3 – phosphotriose isomerase, 4 – aldolase, 5 – phosphatase, 6 – transketolase, 7 – phosphopentoisomerase, 8 – phosphoketopentose epimerase, 9 – phosphopentokinase.

(Kondratieva 1963, 1996; Bassham and Buchanan 1982).

It was also estimated that during the reduction of CO_2 under illumination, along with PES, plants produce organic and amino acids, such as malate, glycolate, glycerate, alanine, aspartate, glycine, and serine. Intermediates of the glycolate pathway (GOGAT) are physiologically associated with photorespiration and originate from 5-carbon intermediates of the Benson-Bassham-Calvin cycle (Zelitch 1973, 1972; Tolbert 1981, 1997; *etc*.). Formation of alanine and C_4 acids occurrs due to the conversion of 3-PGA, leading out of the reductive pentose phosphate cycle (Tarchevsky 1964, 1982).

Types of photosynthetic carbon metabolism in prokaryotes and eukaryotes

It should be noted that, after discovery of the reductive pentose phosphate cycle, many different ways of photosynthetic carbon fixation and reduction were discovered and described, thanks to Andrew Benson's method, in both prokaryotes and eukaryotes, such as the 3-hydroxy-propionate bicycle (Herter *et al*. 2002, Zarzycki *et al*. 2009); the reducing citrate or Arnon-Buchanan cycle (Evans *et al*. 1966, Buchanan and Sirevåg 1977, Buchanan and Arnon 1990), Crassulacean acid metabolism (CAM) (Osmond and Allaway 1974, Kluge 1976, Osmond 1978, Winter and Troughton 1978), C_4 or cooperative photosynthesis (Hartt *et al*. 1954, Nezgovorova, 1956, 1957, Karpilov 1960, 1969, Kortschak *et al*. 1965, Hatch and Slack 1966); C_3/C_4 photosynthesis (Monson *et al*. 1984), and C_4-CAM photosynthesis (Bil' and Gedemov 1980, Bil' *et al*. 1981, 1983, Shomer-Ilan *et al*. 1981, Nishio and Ting 1987, Guralnick 2002). All of these variations of prokaryotic and eukaryotic phototrophic photosynthesis contribute to the total photosynthetic productivity of aquatic and terrestrial landscapes.

However, none of the currently known pathways for photosynthetic CO_2 fixation neither is as widespread nor carries out such an important role in the creation of organic matter on a global scale, as do the representatives of flora that possess the Benson-Bassham-Calvin cycle.

The specificity of the final photosynthetic products in different eukaryotic species

The anatomical structure of higher plant leaves is usually represented by palisade and spongy parenchymal cells or several layers of palisade cells, and in rare cases, by palisade cells and colorless bundle cells around the vascular bundles (*see e.g*. Biel 1993, Biel *et al*. 2010, 2014; Fomina and Biel 2014). A wide variety of morphology and anatomy is also peculiar to various aquatic photosynthetic species, such as algae and photosymbionts. The variety of the anatomical structure of leaves, for example, in terrestrial C_3 species, often originates from diverse habitats. Even within the same species from different geographic areas, or in the same plant in different seasons, significant differences in the morphology and meso-structure of the photosynthetic apparatus are demonstrated (*see e.g*. Mokronosov 1981, 1983; Biel 1993, Fomina and Biel 2014).

In C_3 plants, several specific variants of primary bio-synthetic assimilates were identified (Mokronosov 1981):

(*1*) species with an absolute predominance of the synthesis of sucrose and starch [up to 90-95% of the CO_2 converted into these compounds in potato (*Solanum tuberosum* L.), sugar beet (*Beta vulgaris* L. subsp. *vulgaris*), and many species of arctic and alpine cryophilic early spring ephemeral flora;

(*2*) species forming a part of the photoassimilates, such as raffinose, stachyose, verbascose, and other galactose-containing oligo- and polysaccharides (this group includes practically all species of the Cucurbitaceae, containing up to 30-40% of the amount of assimilates in oligoses; these compounds are the main transport form of assimilates in Cucurbitaceae);

(*3*) species where, along with the formation of sucrose and starch, phosphohexoses are partially reduced into the sugar alcohols, mannitol and sorbitol. Mannitol, for example, is produced in the leaves of celery (*Apium*), lilac (*Syrínga*), ash (*Fraxinus*), oak (*Quercus*); in thalli of brown algae (Phaeophyceae); and other species. Sorbitol, as a product of photosynthesis and transport form of assimilates, was detected in apple (*Malus*) and other woody Rosaceae;

(*4*) species where a significant portion of the early products of photosynthesis is involved in the shikimate pathway and associated with the synthesis of phenolic compounds [synthesis of phenolic compounds is characteristic for many tree crops, such as tea (*Camellia sinensis*), plants containing tannins]; and

(*5*) species with large pools of serine, glycine, and glycolate (for example, Fabaceae).

The plant world (according to A. T. Mokronosov 1981) demonstrates a significant genotypic diversity in modifications of primary biosynthesis. Nevertheless, they are all variations of either events prior to incorporation of CO_2 in the Benson-Bassham-Calvin cycle or different biosynthetic pathways already occurring in the cytoplasm due to incoming intermediates of this cycle and substantially serve as intermediaries between primary and secondary processes of photosynthetic carbon metabolism.

Targeted regulation of photosynthetic carbon metabolism in plants and algae (Benson and Muscatine 1974, Benson *et al*. 1978, 2009; Blanquet *et al*. 1979, Benson and Nonomura 1992, Nonomura and Benson 1992, 2013; Biel *et al*. 2010, Nonomura *et al*. 2011) was shown in works led

by Andrew Benson, especially, in the lectin cycle (Nonomura and Benson 2014). Lectins possess "lock and key" protein conformations that allow them to bind selectively. Specific substrates bind more tightly than glucose and displace it off of lectin, freeing the energy source for growth. Adaptation of this new technology has broad implications that can lead to crop improvement *via* modulation of the energy flow. This is an elegant scientific advancement of all agriculture.

Origin and development of photosynthetic carbon metabolism and advantages of the Benson-Bassham-Calvin cycle

Analysis of information collected by various scientists enables us to represent the sequence of evolutionary origin and development of photosynthetic carbon metabolism. Its simplest form likely reflects the diversity of autotrophic carbon cycles (Marakushev and Belonogova 2011) in modern anaerobic, chemo- and phototrophic prokaryotes, whereas, higher plants exhibit complex, cooperative interactions of different organelles, cells, and tissues involved in the process of photosynthesis (Biel *et al*. 2014).

In general, the strategy of carbon metabolism adaptation in the evolution of photosynthesis can be summarized as follows:

Anoxygenic photo- and chemotrophs brought to the living kingdom of the Earth the opportunity to replenish the organic compounds consumed through heterotrophic nutrition. Perhaps the selforganization of chemo-autotrophic metabolism in hydrothermal conditions (Marakushev 2008) was the first step of the probiotic evolution, leading to the accumulation of primordial soup. At the same time, improving the structure of pigments and the mechanisms of the photosynthetic electron transport chain enabled to use water as an electron donor. This cardinal step in the evolutionary history of photosynthesis could be performed only with the simultaneous development of aerobic respiration and increasing stability of cellular structures to the adverse effects of oxygen. Oxygenation of the atmosphere and the development of the metabolic pathways for aerobic respiration occurred simultaneously with changes in the composition of volcanic gases in the World Ocean.

The use of oxygen as an electron acceptor by the oxidative electron transport chain allowed ancient oxygenic photosynthetic organisms to intensify greatly recycling of reduced nicotinamide adenine dinucleotide and break down organic compounds to carbon dioxide and water in the central link of the respiratory metabolism, *i.e.*, in the Krebs cycle.

In turn, an increase of the oxygen concentration in the environment and the decrease of its reducing properties intensified the important accumulation of the photosynthetic products. The role of the Benson-Bassham-Calvin cycle in photosynthetic carbon metabolism has significantly increased over eons, but at the same time, the role of the Arnon-Buchanan cycle has been lessened.

In the light of the collective evidence gathered about the Benson-Bassham-Calvin cycle, we are struck by its fundamental ecological and biochemical optimization and evolutionary stability.

In particular, populating the land with floral species caused the urgent need for their adaptation to the deficit of previously inexhaustible substrates in the aqueous medium − water and bicarbonate, and to the extensive solar radiation in unprotected terrestrial habitats having no water column to absorb harmful wavelengths.

In terrestrial environments, especially in higher plants, this caused a great number of structural and functional adaptations throughout the plant body. In photosynthesis, the cooperation between carbon metabolism pathways among different organelles (within the one cell) and differentiated tissues were deployed to optimize the flow of metabolites from light and dark stages of photo-synthesis. Negative impacts of external and internal factors on this process were, thus, prevented.

As a consequence of the developed multifunctional adaptations, the reductive pentose phosphate carbon cycle has not changed its fundamental biochemical nature over millions of years during the evolution. Plants attended to and protected the Benson-Bassham-Calvin cycle, creating the necessary structural and functional improvements, *i.e.*, the development of biochemical and structural add-ins around the cycle. For example, C_4 and CAM plants are not deprived of benefits of the reductive pentose phosphate cycle and its key role in photosynthetic carbon metabolism. The Benson-Bassham-Calvin cycle was, and remains for now, the main depot for the production of basic blocks of organic material.

Today, it is well known that the photosynthetic organisms, which carry out photosynthesis solely using the Benson-Bassham-Calvin cycle, show a wide ecological variety and form most of the basic known flora. We can say figuratively that the reductive pentose phosphate cycle, using energy equivalents of photosynthetic electron transport chain, is the main industry for fixing and reducing atmospheric carbon. The flow of atmospheric carbon dioxide (as well as internal CO_2 released during oxidative processes) to the sites of RuBP carboxylation in the Benson-Bassham-Calvin cycle can be diverse and complex, using special biochemical mechanisms developed in the course of evolution. The primary mechanisms of CO_2 delivery are: (*1*) CO_2 - carbonic anhydrase concentrating mechanism, which is inherent to the majority of algal and a number of terrestrial phototrophs; (*2*) dark fixation of carbon in the β-carboxylation reactions of phospho*enol*pyruvate and its accumulation in the form

of malic acid in cell vacuoles in CAM plants; and, (*3*) C$_4$ pumps of malate and aspartate groups and multiple combinations thereof.

An important task for these biochemical super-structures is an uninterrupted carbon sequestration from atmospheric or aqueous phases and its timely delivery to sites of RuBP carboxylation in the reductive pentose phosphate cycle.

However, these biochemical superstructures also perform some other necessary functions. For example, the

C$_4$ pump in the mesophyll cells of C$_4$ plants are a source of many organic and amino acids (*see e.g.* Biel 1993), and even have the ability to create the primary product of photorespiration – glycolate (*see* ref. in Biel *et al.* 2014, Fomina and Biel 2014) – in addition to its primary task of capture and delivery of CO$_2$ to the cycle. The mesophyll cells of C$_4$ plants can also protect the Benson-Bassham-Calvin cycle; their location around the bundle sheath cells containing the cycle reduces the risk of photodegradation and from being ravaged by reactive oxygen species.

Conclusion

The Benson-Bassham-Calvin cycle evolved as the dominant mechanism for the photoassimilation of atmospheric carbon into metabolites which are then used as the building blocks for the synthesis of essential organic compounds that satisfy the energetic needs and demands of phototrophic cells, heterotrophic tissues of the plant, or in certain cases, its symbiotic partner.

Plants protect the Benson-Bassham-Calvin cycle from inherent stresses of internal and external environments. Protection of the C$_3$ photosynthesis is performed by a huge array of stress-protective agents including various biochemical reactions which neutralize ever-present reactive oxygen species and repair damage. Light

scattering and mechanical protection for the reductive pentose phosphate cycle can be achieved by different types of photosynthetic tissues; and, in the case of endo-symbiotic phototrophs, by hosts. Photosynthetic carbon metabolism and its complex relationships with other energy and oxidative reactions and secondary biosynthetic processes of whole plants form the critical basis for the synthesis of organic matter.

We can only admire that Nature created the floral world to serve as the primary source of organic material for life. What a miracle that it requires only sunlight, carbon, water, and minerals from the Earth.

Addendum

We dedicated this article to Andrew Alm Benson, a distinguished emeritus Professor of Biology at Scripps Institution of Oceanography, University of California, San Diego, and renowned as one of the world's leading plant scientists of the twentieth century, who died peacefully from natural causes on January 16, 2015, at University of California, San Diego's Thornton Hospital (*see e.g.* Vacquier *et al.* 2015).
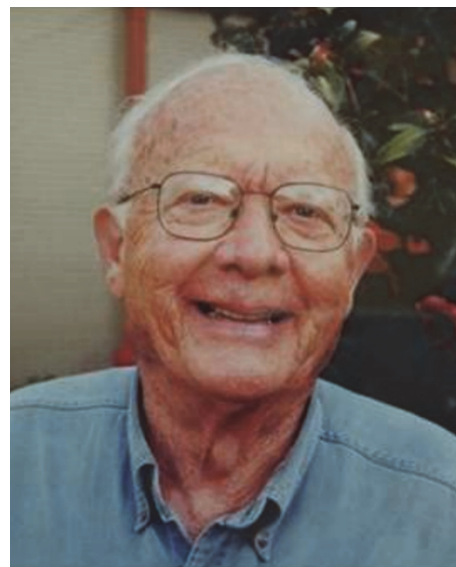
The authors of this paper and a great team of Russian biologists are sincerely grateful to the brilliant scientist, discoverer of the photosynthetic reductive pentose phosphate cycle, Academician of the National Academy of Sciences of the USA, Professor Andrew A. Benson for his outstanding contribution to the development of biological science in general and photosynthesis, in particular.

Fig. 3. Andrew Alm Benson
(*24 September 1917 – †16 January 2015)

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