Minireview

Carbon dioxide assimilation in oxygenic and anoxygenic photosynthesis*

Bob B. Buchanan
Department of Plant Biology, University of California, Berkeley, CA 94720, USA

Received 1 September 1991; accepted in revised form 12 March 1992

Key words: thioredoxin, Co₂ assimilation, oxygenic photosynthesis, anoxygenic photosynthesis

Abstract

This article represents a summary of our contemporary understanding of carbon dioxide assimilation in photosynthesis, including both the oxygen-evolving (oxygenic) type characteristic of cyanobacteria, algae and higher plants, and the non-oxygen-evolving (anoxygenic) type characteristic of other bacteria. Mechanisms functional in the regulation of the reductive pentose phosphate cycle of oxygenic photosynthesis are emphasized, as is the reductive carboxylic acid cycle—the photosynthetic carbon pathway functional in anoxygenic green sulfur bacteria. Thioredoxins, an ubiquitous group of low molecular weight proteins with catalytically active thiols, are also described in some detail, notably their role in regulating the reductive pentose phosphate cycle of oxygenic photosynthesis and their potential use as markers to trace the evolutionary development of photosynthesis.

Abbreviations: NADP-GAPDH—NADP-glyceraldehyde 3-phosphate dehydrogenase; FBPase—fructose 1,6-bisphosphatase; FTR—ferredoxin-thioredoxin reductase; Rubisco—ribulose 1,5-bisphosphate carboxylase/oxygenase; SBPase—sedoheptulose 1,7-bisphosphatase; PRK—phosphoribulokinase; NADP-MDH—NADP—malate dehydrogenase; CF1—ATPase—chloroplast coupling factor; G6PDH—glucose 6-phosphate dehydrogenase

Introduction

Life on our planet obtains its substance and energy through the process of photosynthesis, a grand device by which photosynthetic organisms use the electromagnetic energy of sunlight to synthesize carbohydrates (CH₂O) and other cellular constituents from carbon dioxide and water.

\[ \text{CO}_2 + 2\text{H}_2\text{O} \xrightarrow{\text{light}} (\text{CH}_2\text{O}) + \text{O}_2 + \text{H}_2\text{O} \]

Photosynthesis may be broadly divided into two phases: a light phase, in which the electromagnetic energy of sunlight is trapped and converted into ATP and NADPH, and a synthetic phase, in which the ATP and NADPH generated by the light phase are used, in part, for biosynthetic carbon reduction. As described below, light also functions in the regulation of the synthetic or carbon reduction phase of photosynthesis and in related biochemical processes of chloroplasts (Buchanan 1980, 1991).

In most plants, the major products of photosynthesis are starch (formed in chloroplasts), and sucrose (formed in the cytosol) (Cséke and Buchanan 1986). Both of these products are formed from photosynthetically generated dihydroxyacetone phosphate (DHAP) via pathways that in some respects are similar to the gluconeogenic pathway of animal cells. In the first case, DHAP is converted to hexose phos-
phates, which, in turn, are converted to starch within the chloroplast. In sucrose synthesis, DHAP (or a derivative) is transported to the cytosol and is there converted to sucrose.

All oxygenic (oxygen evolving) organisms from the simplest prokaryotic cyanobacteria to the most complicated land plants have a common pathway for the reduction of CO₂ to sugar phosphates. This pathway is known as the reductive pentose phosphate (RPP), Calvin–Benson or C₃ cycle.

Although the RPP cycle is the fundamental carboxylating mechanism, a number of plants have evolved adaptations in which CO₂ is first fixed by a supplementary pathway and then released in the cells in which the RPP cycle operates. One of these supplementary pathways, the C₄ pathway, involves special leaf anatomy and a division of biochemical labor between cell types. Plants endowed with this pathway, through greater efficiency, are able to flourish under conditions of high light intensity and elevated temperatures. A second supplementary pathway was found in species of the Crassulaceae and is called Crassulacean acid metabolism (CAM). These plants are often found in dry areas and fix CO₂ at night into C₄ acids. During the day, the leaves can close their stomata to conserve water while CO₂ released from the C₄ acids is converted to sugar phosphates by the RPP cycle using absorbed light energy.

CO₂ fixation is also found in bacteria, both photosynthetic and non-photosynthetic. The purple sulfur and purple non-sulfur bacteria employ the RPP cycle, as do plants (Bassham and Buchanan 1982, Tabita 1988). The photosynthetic green sulfur bacteria, however, use ferredoxin-linked carboxylases in a pathway known as the reductive carboxylic acid cycle (Buchanan and Arnon 1990). The ferredoxin-linked carboxylases also function in CO₂ assimilation in diverse types of fermentative and methanogenic bacteria. Finally, in photosynthetic green non-sulfur bacteria, the path of carbon assimilation is unknown.

In this article, we first describe the path of carbon in oxygenic photosynthesis (the reductive pentose phosphate cycle, reductive carboxylic acid cycle, and the unknown pathway).

Oxygenic photosynthesis

The crux of the pathway is the carboxylation of ribulose 1,5-bisphosphate to produce two molecules of 3-phosphoglycerate (Fig. 1). Sequentially, the next steps (the reductive phase of the cycle) are those in which ATP and NADPH, produced by the light reactions, are consumed in the reduction of 3-phosphoglycerate to glyceraldehyde 3-phosphate. To complete the cycle (the regeneration phase), intermediates formed from a portion of the glyceraldehyde 3-phosphate are utilized via a series of isomerizations, condensations and rearrangements that result in the conversion of glyceraldehyde 3-phosphate to pentose phosphate, eventually ribulose 5-phosphate. Phosphorylation of ribulose 5-phosphate by ATP regenerates ribulose-1,5-bisphosphate, thus completing the cycle. The portion of glyceraldehyde 3-phosphate not used to sustain the cycle constitutes net product and serves as a source of carbon for synthesis of chloroplast starch and for transport to the cytosol. The enzymes which catalyze steps in the cycle, identified in Table 1,