Journal of Plant Physiology xxx (2014) xxx–xxx

Contents lists available at ScienceDirect

Journal of Plant Physiology

journal homepage: www.elsevier.com/locate/jplph

Review

The biodiversity of carbon assimilation

Peter G. Kroth*

Department of Biology, University of Konstanz, Universitaetsstr. 10, 78457 Konstanz, Germany

ARTICLE INFO

Article history:
Received 9 May 2014
Received in revised form 20 July 2014
Accepted 21 July 2014
Available online xxx

Keywords:
Algae
Carbon concentrating mechanism
Evolution
Pyrenoid
Rubisco

ABSTRACT

As all plastids that have been investigated so far can be traced back to endosymbiotic uptake of cyanobacteria by heterotrophic host cells, they accordingly show a high similarity regarding photosynthesis, which includes both the photosystems and the biochemical reactions around the CO_2 fixation via the Calvin–Bassham cycle. Major differences between the different algal and plant groups may include the presence or absence of carbon concentrating mechanisms, pyrenoids, Rubisco activases, carbonic anhydrases as well as differences in the regulation of the Calvin–Bassham cycle. This review describes the diversity of primary carbon fixation steps in algae and plants and the respective regulatory mechanisms.

Contents

Introduction

All organismic life on earth is based on carbon molecules. Accordingly the enzymatic fixation of atmospheric or dissolved CO_2 into larger organic molecules was the evolutionary invention that allowed the production of biomass required for life. The first product of CO_2 fixation usually is 3-PGA which is converted into different types of carbohydrates which subsequently can be transformed into other substances that are essential for the cell, like lipids or amino acids. The carbohydrates themselves can be used either as low-osmotic polymeric storage products (Oren, 2007), as components of cell walls, or simply being secreted. Although archeae and eubacteria developed a number of different ways to fix CO_2 biochemically, it is the reductive pentose phosphate pathway in plants and algae, employing Rubisco as the key enzyme, which is mostly used for primary production (Berg, 2011). As Rubisco is a very ancient enzyme, one could expect that during the long evolutionary periods, there was sufficient time for evolution to optimize this enzyme regarding turnover rate and substrate specificity. However, research in the recent decades revealed a rather poor performance of this enzyme type, including a low turnover rate, a low affinity for CO_2 (Spreitzer, 1999), together with a tendency to react with oxygen (Ogren and Bowes, 1971) during an oxygenase reaction, resulting in subsequent energy-consuming photorespiration reactions (Ogren, 2003; Sage, 2013; Sage and Stata, 2015). Thus algae and plants had to develop strategies to overcome the limitations of Rubisco's enzymatic properties. One possible way to achieve this goal, is to increase the cellular enzymatic activity. Accordingly most organisms generate large amounts of Rubisco protein per cell to increase the total enzymatic activity (Ellis, 1979). Furthermore there are Rubisco types with varying catalytic and regulatory properties in different organismal groups (Tabita et al., 2008). Another

* Tel.: +49 07531 884816; fax: +49 07531 884047.
E-mail address: Peter.Kroth@uni-konstanz.de

http://dx.doi.org/10.1016/j.jplph.2014.07.021
0176-1617/

obstacle especially for aquatic prokaryotic and eukaryotic organisms is that they may have to cope with potentially CO_2 limited conditions. The availability of dissolved inorganic carbon (DIC: CO_2 plus bicarbonate (HCO_3^-)) may depend for instance on the water depth or the water composition. While CO_2 can easily diffuse in air, CO_2 dissolved in water has a limited diffusibility. In seawater DIC mostly appears as bicarbonate (HCO_3^-), while in fresh water these ratios can be more variable (Zhang et al., 2014). As CO_2, and not bicarbonate, is the substrate of Rubisco, facilitated enzymatic conversion of HCO_3^- into CO_2 by carbonic anhydrases (CAs) is one way to increase CO_2 fixation by Rubisco, while the additional utilization of other carboxylating enzymes with either a higher affinity for CO_2 or specificity for bicarbonate represents another option. A detailed study on this option is given by Maberly et al. (2015). Processes involving carbonic anhydrases and a pre-fixation of CO_2 have been termed carbon concentrating mechanisms (CCMs) and they can already be found in the prokaryotic cyanobacteria (see Giordano et al., 2005; Meyer and Griffiths, 2013; Reinfelder, 2011). This review presents a general overview of the diversity of key elements of carbon fixation in plants and algae: the carboxylating enzymes (Rubisco), and the presence or absence of CO_2 concentrating mechanisms and pyrenoids in the different groups of oxygenic photoautotrophic organisms.

CO_2 fixation as a key process for the establishment of life on earth

There are numerous theories on how life on earth has evolved (Cavalier-Smith, 2001; Miller, 1953). The most recent theory proposes that the first cells originated from hot hydrothermal vents in the oceans in porous mineral material consisting of metal sulfides serving as redox catalysts (Martin and Russell, 2003; Russell et al., 2010). Important issues for the successful establishment of the earliest cells the creation of reactions chambers separated by biological membranes as well as the production of biomass allowing an increase of biological material by growth and division of cells (Lane et al., 2013). As reduced carbon is the most essential backbone of biological systems, the development of the first enzymes that allow the fixation of the – at that time (about up to 2–2.5 Ga ago, Raven et al., 2012) – highly abundant carbon dioxide must have been a major breakthrough. Two types of organisms capable of autotrophic CO_2-fixation are known, chemoautotrophic and photoautotrophic organisms (Erb, 2011). The first group uses chemical energy directly, while the second group utilizes the energy of sunlight in order to fix CO_2. Up to now a number of biochemical CO_2 fixing processes have been described that all perform different reactions. If the theory holds true that cells originated in hydrothermal vents as described above (Martin and Russell, 2003), then it is likely that the first carboxylases might have been related to those that perform the bacterial Wood–Ljungdahl (or reductive acetyl-CoA) pathway (Huber and Wächtershäuser, 1997; Wood, 1991). The respective enzymes of this pathway (carbon monoxide dehydrogenase/acetyl-CoA synthase) use H_2 to reduce carbon dioxide to carbon monoxide which in a second step is fixed to a methyl group forming acetyl-CoA (Ragsdale, 2008). This reaction is the only one of the known carboxylating reactions with a positive net ATP balance (Ragsdale, 2008). Other, probably later developed, pathways to fix CO_2 are the reductive citric acid cycle (Arnon–Buchanan cycle; Evans et al., 1966), the 3-hydroxypropionate bicycle (Zarzycki and Brecht, 2009), the hydroxypropionate/hydroxybutyrate cycle (Berg et al., 2007), the dicarboxylate/hydroxybutyrate cycle (Huber et al., 2008), and finally the Calvin–Bassham –Benson cycle (Bassham and Calvin, 1957), which is the essential pathway for photoautotrophic reactions. In addition to these metabolic enzymes, a number of other enzymes have been described that include assimilatory carboxylases (that merely have the function to introduce functional groups), anaplerotic carboxylases (like for instance within the TCA-cycle), biosynthetic carboxylases (generating building blocks for instance in fatty acid synthesis) and redox balancing carboxylases (in some bacteria) (see Erb, 2011). Although nature apparently developed the principle of creating biomass via carboxylases several times independently (Schada von Borzyskowski et al., 2013), the process of CO_2 fixation via the Calvin cycle using the enzyme ribulose-bisphosphate carboxylase (Rubisco) apparently had the strongest impact on the development of life on this planet especially when combined with oxygenic electron transport, like we do find it in cyanobacteria as well as in plastids of eukaryotic algae and land plants.

Evolution of eukaryotic photoautotrophs

Fossil records of bacterial biofilms indicate that unicellular organisms related to modern cyanobacteria might have been among the first organisms that coupled light driven biomass formation and CO_2 fixation with the cleavage of water resulting in a release of oxygen (Rasmussen et al., 2008). After the establishment of oxygenic photosynthesis the oxygen content of the oceans and the atmosphere did not increase instantly. Indeed it took another 1.5 billion years until the released oxygen was not instantly captured by reductive substances in the oceans and a net release of oxygen was possible (Blank and Sanchez-Baracaldo, 2010). Although CO_2 concentrations during that time of the early earth development, when cyanobacteria were the dominant oxygenic photoautotrophs, were still rather high (Raven et al., 2011), the modern cyanobacteria possess sophisticated CO_2 concentrating mechanisms that allow trapping of CO_2 within the cells and thus enhanced Rubisco efficiency (see below). There is a large biodiversity of cyanobacteria (Schirrmeister et al., 2013), but considering their restrictions as prokaryotes with regard to an asexual lifestyle and the absence of higher organized life forms, endosymbiotic processes involving cyanobacteria probably were the key events during evolution that allowed the development of higher organisms (Keeling, 2013). Photosynthesis as we know it from land plants thus obviously is an invention of the cyanobacteria (Archibald, 2009) and apparently has never been developed de novo in eukaryotes (at least that we know of from extant organisms). Instead, eukaryotic cells took up cyanobacteria via an endosymbiotic process (Fig. 1) and converted them into organelles (Bhattacharya et al., 2007; Cavalier-Smith, 2013). It is more or less consensus today, that all studied plastids in algae and plants (with one exception, *Paulinella chromatophora* (Nowack et al., 2008)) can be derived from a primary endosymbiosis in which a eukaryotic host cell took up a cyanobacterium and converted it into an organelle (Delwiche and Palmer, 1997). Additionally, secondary and tertiary endosymbioses occurred in which eukaryotic algae, either ancestors of green algae or red algae, or even diatoms, haptophytes, or cryptophytes had been taken up by eukaryotic host cells (see Fig. 1 and also Keeling, 2013 for a current view on these processes). Accordingly plastids have been transmitted again and again during the endosymbiotic processes, thus it is not too surprising to see that all the plastids in general show very similar photosystems and photosynthetic reactions. Smaller differences here are mostly due to adaptations to environmental conditions or to genetic or biochemical modifications. Regarding for instances the regulation of Rubisco and the subsequent redox regulation of the reactions of the Calvin–Bassham cycle, there may be substantial differences in different algal groups (see Wilhelm et al., 2006; Michelet et al., 2013; Mekhalfi et al., 2014).

Rubisco as the key player of photosynthesis

In total, about 10^{17} g (100 Gt) of CO_2 are supposed to be converted into biomaterials and organic compounds per year (Field et al., 1998). All oxygenic photosynthetic organisms utilize Rubisco enzyme for CO_2 fixation instead of the other five autotrophic

Please cite this article in press as: Kroth PG. The biodiversity of carbon assimilation. J Plant Physiol (2014), http://dx.doi.org/10.1016/j.jplph.2014.07.021