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The Prospects of Rubisco Improvement

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Abstract

Due to its key role in photosynthesis and apparent inefficiency, Ribulose-1, 5-bisphosphate carboxylase/oxygenase (Rubisco) was a target to numerous attempts to ameliorate its kinetic properties and thereby to enhance the photosynthetic rate. Nevertheless, an improved enzyme was not found. The lack of success results from optimal adaptation of Rubisco to the gaseous environment, wherein it resides and the reciprocal relation between its catalytic turnover and affinity for CO_2. Consequently, any improvement in one of these parameters is accompanied with a decrease in the other. Even if an improved Rubisco is found, its influence on the photosynthetic performance will be minor as additional factors limit the photosynthetic rate and since regulatory mechanisms coordinate the carboxylation capacity with the plant need for photo assimilates.

Keywords: Carbon dioxide (CO_2); Catalysis; Enzyme; Kinetic properties; Mutant; Oxygen (O_2); Photorespiration; Photosynthesis; Rubisco (ribulose-1, 5-bisphosphate carboxylase/oxygenase)

Abbreviations: Kcat: Catalytic Turnover; PGA: 3-Phosphoglycerate; RuBP: Ribulose-1, 5-Bisphosphate; Rubisco: Ribulose-1, 5-Bisphosphate Carboxylase/Oxygenase; Sc/o: Specificity Factor

Introduction

Rubisco inefficiency

Every year about 10^{11} tons atmospheric CO_2 are fixed in the biosphere by Ribulose-1, 5-bisphosphate carboxylase/oxygenase (Rubisco, EC 4.1.1.39), the most abundant enzyme in nature, which is found in all photoautotrophic and most chemoautotrophic organisms. The enzyme catalyzes the carboxylation and oxygenation of ribulose-1, 5-bisphosphate (RuBP), the primary reactions of photosynthesis and photorespiration, respectively. Two molecules of 3-phosphoglycerate (PGA) are produced in this carboxylation reaction, whereas the oxygenation yields one molecule of PGA and one molecule of 2-phosphoglycolate. PGA is reduced in the Calvin cycle to triose-phosphates that are used either for biosynthesis of carbohydrates or for regeneration of the primary CO_2-acceptor, RuBP. Phosphoglycolate is recycled via the photorespiratory pathway back to the Calvin cycle intermediates with a loss of one molecule of CO_2 and one of NH_3 during condensation of two glycine molecules into serine.

Despite its central role in photosynthesis, Rubisco catalysis is considered slow and inefficient as the catalytic turnover (Kcat) is low (120-720 carboxylations/catalytic site/min), and the affinity for substrate CO_2 is also low (Km(CO_2) = 10-300 μM) compared to the CO_2 concentration in air-equilibrated water (~10 μM). Moreover, competition between the carboxylation and oxygenation decreases the apparent affinity for CO_2 in the presence of O_2. In addition, photorespiratory CO_2 evolution further decreases the net rate of photosynthesis. However, not only O_2 inhibits RuBP carboxylation; Rubisco itself produces undesired side-reaction inhibitors of its catalysis and activation [1,2].

Consequently, and to maintain sufficient carboxylation rates, photosynthesizing cells allocate large proportion of their nitrogen resources and accumulate high concentrations of the enzyme (Rubisco constitutes approximately half of the soluble leaf proteins, [3]). Considering these constraints on the Rubisco action, the free energy differences in Calvin cycle reactions and assessment of the effect of differential expression of Rubisco using antisense technology on the rate of photosynthesis, RuBP carboxylation has been considered the main limiting step of carbon fixation under saturating irradiance and limiting CO_2 concentrations [4-8].

Although the mechanism underlying Rubisco catalysis is common for enzymes from various phylogenetic origins, their kinetic properties differ considerably [9]. Rubisco evolved under the CO_2-rich and O_2-poor ancient atmosphere of earth. Under those conditions there was no evolutionary pressure for an enzyme with a high specificity factor[1] and affinity to CO_2 and, indeed, in chemoautotrophic bacteria Rubisco affinity for CO_2 and its specificity factor are generally low [10]. As the CO_2 concentration decreased and that of O_2 increased in the atmosphere along with

the emerging photoautotrophs, the bacterial Rubisco became extremely inefficient. This inefficiency of the bacterial Rubisco can be exemplified by the high CO_2 requirement of mutants of the cyanobacterium *Synechocystis* PCC6803 and the higher plant *Nicotiana tobaccum*, in which the genuine enzyme was replaced with that of the purple bacterium *Rhodospirillum rubrum* [11-13].

The lack of fitness of the primordial Rubisco to the altering atmosphere triggered two evolutionary trends that raised its activity in the contemporary ambient atmosphere: 1) the development of CO_2 concentrating mechanisms, CCM, (e.g. active inorganic-carbon (Ci) uptake in aquatic photosynthetic organisms and C4 or Crassulacean acid metabolism (CAM) in terrestrial plants) that elevate the CO_2 concentration in the vicinity of the carboxylation site and, consequently, increase the carboxylation to oxygenation rate ratio [2,14]) an increase in the enzyme affinity for CO_2 that is accompanied by an increase in its specificity but with an apparently unavoidable decrease in the Kcat of the enzyme [9,15].

The attempts to ameliorate the kinetic properties of rubisco

Due to its relative inefficiency, and considering its importance, Rubisco attracts the attention of biochemists and genetic engineers who try to improve its kinetic properties by genetic manipulations with the aim to increase its efficiency and, thereby, alleviate the limitations of photosynthesis and eventually to increase the yield of plants. The main effort is dedicated to obtaining Rubisco variants with better specificity and lower Km (CO_2) [16,17].

However, despite intensive efforts devoted over the last five decades for this mission, only little success was achieved. Indeed, technical problems make the isolation of Rubisco mutants difficult: Rubisco from plants and cyanobacteria is a hexadecamer built of eight small and eight large subunits. In eukaryotes, the small subunit is encoded in the nucleus, whereas the large subunit is encoded in the chloroplast. The multiplicity of the chloroplasts and the scarcity of transformation vectors for the chloroplast genome complicate the directed mutagenesis of Rubisco large subunit in eukaryotes. As a result of these obstacles, only a few of transformation systems that allow directed mutagenesis of Rubisco in the genuine organism have been developed: one in the cyanobacterium *Synechocystis* PCC 6803, wherein the genes encoding both subunits of Rubisco are found in a single operon [18], and another in the unicellular green alga *Chlamydomonas reinhardtii* that has a single chloroplast [19]; only a few reports appear on transformation of Rubisco in higher plants [13].

The alternative approach, mutagenesis of heterologous Rubisco expressed in a host such as Escherichia coli, has a limited use as only prokaryotic Rubisco from a few species such as the cyanobacterium Synechococcus and the purple bacterium *R. rubrum* was expressed so far in *E. coli* presumably due to difficulties in enzyme assembly. Moreover, the effect of the mutated Rubisco on photosynthetic rate cannot be evaluated in non-photosynthetic hosts. Alternatively, improved Rubisco variants could be screened from mutant populations by applying selection conditions that allow preferentially or exclusively the growth of the required phenotype [18,20,21]. In spite of the fact that several hundred Rubisco mutants were examined, mutants with a phenotype "better" than the wild type were not found (see ref 16 for a review). This inability to obtain more efficient mutants raises doubts as to whether conceptual rather than technical reasons prevent the isolation of such a phenotype.

The constraints of generation a better rubisco

The hidden assumption in the attempt to improve Rubisco is that the enzyme is not fully adapted to the ambient atmosphere and, hence, its replacement with a more efficient catalyst would improve the rate of photosynthesis [22]. Is this a valid assumption? Is it plausible that Rubisco, the catalyst that plays such a key role in carbon assimilation, is found in every phototroph and the function of which has critical implications on the photoautotrophic growth, is not subject to an effective Darwinian selection that makes it optimally adapted to the gaseous (CO_2 and O_2) environment wherein it is found?

To evaluate the prospect for raising the rate of photosynthesis by improving Rubisco performance, we have to examine whether more efficient enzyme could be found and whether introducing such an enzyme will indeed improve photosynthesis. Since Rubisco does not bind covalently its gaseous substrates (CO_2 and O_2), elevation of its affinity to CO_2 or its specificity requires tighter binding of the carboxylase transition state intermediate or increase in the binding ratio of the carboxylase to oxygenase transition state intermediates (2-carboxy- or 2-peroxy-3-ketoarabinitol 1, 5-bisphosphate, respectively) to the enzyme. However, tighter binding of the transition state intermediates may slow subsequent catalytic steps and, consequently, reduces the Kcat [9,23]. Indeed, a comparison of the kinetic parameters of Rubisco from diverse phylogenetic origin, as well as from various Rubisco mutants, revealed that an inverse relationship exists between the Kcat and Sc/o and a direct relationship exists between the Kcat and Km (CO_2), i.e., as long as the Km (CO_2) decreases Sc/o increases, but Kcat decreases [9,15,24].

Hence, an improvement in Km (CO_2) or Sc/o results in a decline in the Kcat of the enzyme and eventually the effect on the rate of carboxylation is less pronounced. Practically, this constraint prevents the generation of the 'ideal Rubisco', i.e., an enzyme with high Kcat and Sc/o and low Km (CO_2). Furthermore, it is the net CO_2 fixation rate (the difference between CO_2 fixation and photorespiratory and respiratory CO_2 evolution) rather

The specificity factor (Sc/o) is a combination of the maximal rates (Vcmax, Vomax) and Michaelis-Menten constants (Kc, Ko) of the carboxylation and oxygenation. Multiplication of the specificity factor and the CO2 to O2 concentration ratio denotes the carboxylation to oxygenation rate ratio (38).

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than the carboxylase to oxygenase rate ratio that determines the photosynthetic productivity. Considering that the net CO_2 fixation rate and Sc/o are not altered in the same way as the kinetic properties of the enzyme changes, improvement in Rubisco specificity or affinity to CO_2 does not ultimately raise the rate of photosynthesis and, in some combinations of the kinetic properties, the rate of photosynthesis may even decrease [25].

Savir et al. [15], who examined the effect of the interplay between the kinetic parameters of Rubisco on the net CO_2 fixation rate, found that the kinetic properties of the enzyme are almost optimal with regard to the gaseous environment wherein the enzyme resides. Accordingly, the chance for further improvement of Rubisco by genetic means is limited. A climatic record from Antarctic ice revealed that for 400,000 years, until the industrial revolution, the CO_2 concentration in the atmosphere was between 180 to 280ppm [26]. However, since then the CO_2 concentration has increased to 380 ppm due to anthropogenic activity. Rubisco in C_3 plants is most likely adapted to the pre-industrialization CO_2 concentration. Hence, if a change in the kinetic parameters of the enzyme is needed, it is presumably an adaptation toward the emerging CO_2 concentration, namely an increase in Kcat and Kc and a decrease in Sc/o.

From the photosynthetic efficiency viewpoint, RuBP oxygenation is a wasteful process that produces inhibitory useless products (e.g., phosphoglycolate). In this context the photorespiratory pathway that recycles phosphoglycolate serves as a mean to minimize carbon loss with a cost of excess NADPH and ATP required for re-assimilation of photorespiratory CO_2. However, a waste of energy is not always disadvantageous: Under high illumination, especially when the CO_2 supply is limited, dissipation of excess photochemical energy in the photorespiratory pathway, which otherwise may lead to production of reactive oxygen species, destruction of reaction center 2 and eventually demolition of the photosynthetic apparatus, protects from these photoinhibitory and photooxidative damages [27-29]. Therefore, a decrease in RuBP oxygenation and, consequently, in photorespiration could be detrimental under high irradiance and conditions that stimulate stomatal closure (e.g., during drought or salt stress) and consequently limit the CO_2 supply to the carboxylation site.

The CCM that elevates the CO_2 concentration at the carboxylation site of Rubisco is induced in cyanobacteria and green algae by high oxygenase to carboxylase rate ratio presumably by products of RuBP carboxylation and oxygenation or their derivatives [30]. Consequently, the rate of carboxylation is homeostatically maintained in a wide range of environmental CO_2 and O_2 concentrations. An increase in Rubisco specificity will induce less the CCM, the CO_2 concentration at the carboxylation site will decrease and consequently the photosynthetic rate will not increase. Thus, an increase in Rubisco specificity is not ultimately an advantageous in these organisms.

Beside the Sc/o and Km (CO_2), the Km (RuBP) could also be a target for improvement. The concentration of RuBP in photosynthesizing tissues is low and limits Rubisco activity under conditions conducive to high carboxylation rates (i.e., under light and CO_2 saturation; 5). Over-expression of enzymes involved in regeneration of RuBP, e.g., fructose bisphosphatase/sedoheptulose bisphosphatase in tobacco plants [31] and aldolase and triose-phosphate isomerase in the cyanobacterium *Anabaena* PCC 7120 [32], which presumably raised the RuBP concentration, led to enhancement in the rate of photosynthesis. Raising the affinity of Rubisco to RuBP, which elevates the catalytic turn-over at low RuBP concentrations, is an alternative approach to reduce the RuBP limitation at saturating irradiance and CO_2 concentrations.

The effect of Km (RuBP) on the rate of photosynthesis was hardly evaluated due to the scarcity of Rubisco mutants with altered Km (RuBP) in photosynthetic organisms. However, we have reported on Rubisco mutants in the cyanobacterium Synechocystis PCC 6803 with altered affinity for RuBP [33]. A comparison of the photosynthetic performance between mutants with elevated and reduced Km (RuBP) that have a similar (low) Kcat revealed that the rate of photosynthesis at saturating irradiance and Ci concentrations was not altered in the mutant with the reduced Km (RuBP), whereas in the mutant with the elevated Km (RuBP) the rate of photosynthesis at saturating irradiance and Ci concentrations decreased. However, correlation between Km (RuBP) and Kcat in eleven Rubisco mutants revealed that both increase and decrease in Km (RuBP) over that of the wild type of enzyme were accompanied with a decrease in the enzyme Kcat [33]. If these relationships are inclusive, any improvement of Rubisco affinity to RuBP will be compensated by a decrease in the Kcat of the enzyme.

Would an ameliorated rubisco enhance the photosynthetic rate?

The effect of a mutation in an enzyme that participates in a metabolic pathway on the metabolite flux through the pathway depends on the extent of limitation the enzyme imposes over the flux [34]. The limitation imposed by Rubisco on the rate of photosynthesis was examined by comparing the mass action ratio of the carboxylation reaction with its equilibrium constant [4,6]and by metabolic control analysis [7]. Determination of the mass action ratio revealed that Rubisco is the main rate limiting step of carbon fixation in plants and algae under limiting CO_2 concentrations and saturating irradiance, whereas under saturating irradiance and CO_2 concentrations Rubisco and, consequently, photosynthetic rates are RuBP-limited [5].

More perplexing findings were obtained from a control analysis of Calvin cycle enzymes on the rate of photosynthesis. In this procedure, the effect of modulation of a given enzyme activity or concentration on the rate of the pathway is quantified. This analysis, using antisense technology as tool for altering the

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level of the enzymes in plants, revealed that several Calvin cycles enzymes beside Rubisco (e.g., sedoheptulose-bisphosphatase, aldolase and transketolase) co-limit the rate of photosynthesis, and that the extent of the limitation exerted by Rubisco on the rate of photosynthesis depends on the environmental growth conditions. In cyanobacteria, using Rubisco mutants, we have recently found that the limitation imposed by Rubisco on the rate of photosynthesis is low [32].

However, not only Calvin cycle enzymes limit the rate of photosynthesis, but also entry of Ci from the environment to the carboxylation site by diffusion of CO_2 through the stomata in plants or mediated by Ci-transporters in cyanobacteria and green algae significantly limit the rate of photosynthesis. Hence, the simplistic view of photosynthesis limited by a single bottleneck overestimates the limitation imposed by carboxylation reaction and neglects those of other reactions and processes. Accordingly, the contribution of Rubisco improvement, if this is achievable, would be more modest than that envisaged.

Over-expression of Rubisco, or plant growth at elevated CO_2 concentrations, could be used as tools for simulating the effect of introducing improved Rubisco on plant photosynthesis and growth. Elevation of the CO_2 concentration in the atmosphere increases readily and substantially the rate of photosynthesis of terrestrial plants. However, during long-term exposure, the CO_2-stimulated enhancement of photosynthesis and growth rates is lower. Drake et al. [35] who summarized sixty long-term growth experiments found in average only a 10% increase in the biomass of plants grown in a CO_2-enriched atmosphere, which resulted from an increase in the carbohydrate content and a limited sink capacity that stimulated feed-back inhibition of photosynthesis, increase in stomatal resistance to gas diffusion and a decrease in Rubisco content and, consequently, the increase in the carboxylation capacity was low.

Likewise, it was shown that over-accumulation of Rubisco in transgenic rice over-expressing the small subunit of Rubisco did not increase the rate of photosynthesis or plant biomass accumulation [36]. In this case, the lack of enhancement in photosynthetic rate was attributed to a decrease in the activation level of Rubisco in leaves over-expressing the enzyme. Recently, Ishikawa et al. [37] constructed transgenic rice, which expressed a Rubisco small subunit from sorghum. As a result, the Kcat and Km (CO_2) of the enzyme increased, whereas its specificity factor (Sc/o) slightly decreased. However, also in this transgenic plant the rate of photosynthesis was not improved [37,38].

Apparently maneuvers dedicated to raise the rate of carboxylation beyond a rate dictated by the constraints of the plant induce feed-back processes (e.g., modulation of Rubisco content, activation, and substrate accessibility) that eventually coordinate the carboxylation with the rates of the other photosynthetic reactions. Accordingly, substitution of the genuine Rubisco in a plant with a 'genetically improved enzyme', even if the latter will be CO_2-saturated at the ambient atmosphere, would only moderately increase the biomass under optimal growth conditions. The benefit of introducing such an enzyme, if it is found, to a plant would be in elevation of the efficiency of photosynthesis, water usage and nitrogen utilization.

Conclusions

The feasibility of improving the kinetic properties of Rubisco is low as the enzyme is adapted to the atmosphere wherein it resides and due to the reciprocity between the kinetic parameters that prevents independent change in one of them. As a result of this linkage between the kinetic parameters, any improvement in one of these parameters will be accompanied with a decrease in the other. Even if a successful Rubisco-variant is found, its influence on the photosynthetic performance will be minor as additional factors besides Rubisco limit the rate of photosynthesis and due to regulatory mechanisms, that coordinate the carboxylation capacity with the plant need for photo assimilates.

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