

# Photorespiration: The Futile Cycle?

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Photorespiration, or C<sub>2</sub> photosynthesis, is generally considered a futile cycle that potentially decreases photosynthetic carbon fixation by more than 25%. Nonetheless, many essential processes, such as nitrogen assimilation, C<sub>1</sub> metabolism, and sulfur assimilation, depend on photorespiration. Most studies of photosynthetic and photorespiratory reactions are conducted with magnesium as the sole metal cofactor despite many of the enzymes involved in these reactions readily associating with manganese. Indeed, when manganese is present, the energy efficiency of these reactions may improve.

Keywords: photorespiration ; oxygenation ; photosynthesis ; metal cofactor ; atmospheric CO<sub>2</sub> ; climate change ; crop yield ; metabolic interactions ; kinetics

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## 1. Introduction

Photorespiration involves the oxygenation of ribulose-1,5-bisphosphate (RuBP) to form 3-phosphoglycerate (3PGA) and 2-phosphoglycolate (2PG) and the subsequent carbon oxidation pathways that release CO<sub>2</sub> under light conditions <sup>[1][2][3][4][5]</sup>. Because it produces 2PG, a compound “toxic” to many enzymes in photosynthetic metabolism, and oxidizes organic carbon without seemingly generating ATP, photorespiration is generally considered a wasteful process. The following sections examine how the photorespiratory pathway converts 2PG into glycolate, the only carbon source for the photosynthetic carbon oxidation cycle <sup>[6]</sup>, a cycle that together with nitrogen assimilation, C<sub>1</sub> metabolism, and sulfur assimilation generates essential amino acids and intermediate compounds <sup>[7]</sup>. Moreover, the three enzymes involved in the initial photorespiratory steps within chloroplasts—Rubisco, malic enzyme, and phosphoglycolate phosphatase—have metal binding sites that accommodate either Mg<sup>2+</sup> or Mn<sup>2+</sup>, and balance between the binding of these enzymes to Mg<sup>2+</sup> or Mn<sup>2+</sup> may shift the relative rates and energy efficiencies of photosynthesis and photorespiration <sup>[8]</sup>.

## 2. Photosynthesis vs. Photorespiration

### 2.1. Rubisco

Atmospheric CO<sub>2</sub> concentration has increased more than 20% during the past 35 years <sup>[9]</sup>. The major sink for this CO<sub>2</sub> is the approximately 258 billion tons per year that photosynthetic organisms convert into organic carbon compounds through carbon fixation via the Calvin–Benson pathway <sup>[10]</sup>. This pathway begins with Rubisco (Ribulose 1,5-bisphosphate carboxylase–oxygenase), the most abundant protein on the planet <sup>[11]</sup>.

Rubisco comes in three forms <sup>[12]</sup>:

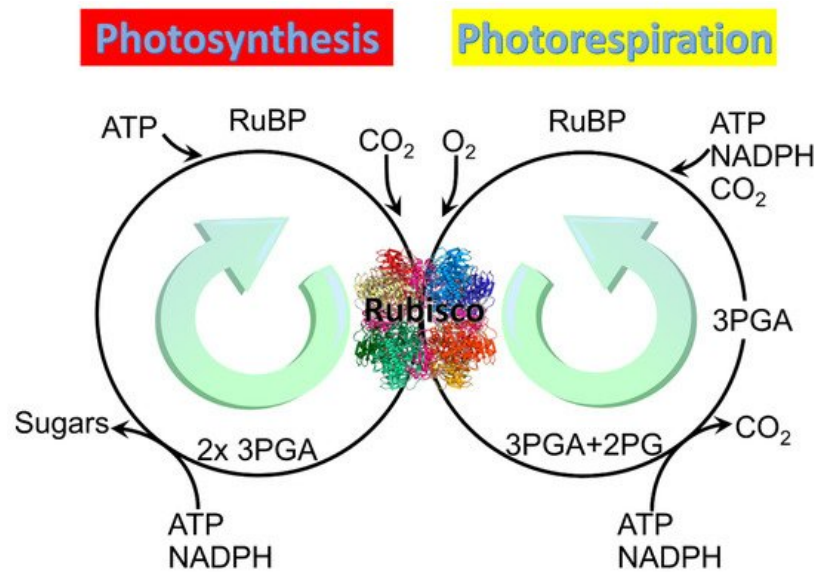
Form I, which is found in cyanobacteria, proteobacteria, chlorophyte algae, heterokont algae, and haptophyte algae, and higher plants, is the most common <sup>[13][14]</sup>. It is a hexadecamer containing eight identical large subunits (~55,000 M<sub>r</sub>), each with a metal-binding site, and eight small subunits (~15,000 M<sub>r</sub>). The large subunits are coded by a single plastomic gene, whereas the small subunits are coded by a nuclear multigene family that consists of 2 to 22 members, depending on the species <sup>[15]</sup>. Complex cellular machinery is required to assemble this form of Rubisco and to maintain its activity <sup>[16]</sup>. Form I Rubisco, until recently, had resisted all efforts to generate a functional holoenzyme *in vitro* or upon recombinant expression in *E. coli* <sup>[17]</sup>.

Form II Rubisco, found in proteobacteria, archaea, and dinoflagellate algae, contains one or more isodimers with subunits that share about 30% identity to the large subunit of Form I Rubisco <sup>[8]</sup>.

Form III Rubisco, found in archaea, has one or five isodimers composed of subunits homologous to the large subunit of Form I Rubisco <sup>[8]</sup>.

Form II and Form III Rubisco show greater similarity in their primary sequence to one another than either do to the large subunit of Form I Rubisco <sup>[8]</sup>.

All three forms of Rubisco catalyze not only the reaction in which the carboxylation of the five-carbon sugar RuBP generates two molecules of the three-carbon organic acid 3-phosphoglycerate (3PGA), but also an alternative reaction in which oxidation of RuBP generates one molecule of 3PGA and one of 2PG (Figure 1) [8]. The carboxylation pathway of photosynthesis expends 3 ATP and 2 NADPH per RuBP regenerated and produces a carbon in hexose [18], whereas the oxygenation pathway of photorespiration reportedly expends 3.5 ATP and 2 NADPH per RuBP regenerated but produces no additional organic carbon [19][20].



**Figure 1.** Two main reactions of Rubisco: Photosynthesis and photorespiration. Rubisco structure picture credit: Laguna design / science photo library.

Rubisco must be activated before it can carboxylate or oxygenate RuBP. Activation of the three forms of Rubisco involves binding of  $\text{Mn}^{2+}$  or  $\text{Mg}^{2+}$  [21][22]. Binding of  $\text{Mg}^{2+}$  requires carbamylation of Rubisco by the addition of  $\text{CO}_2$ . One histidine at the active site of Rubisco rotates into an alternate conformation, resulting in a transient binding site where  $\text{Mg}^{2+}$  is partially neutralized by the conversion of two water molecules to hydroxide ions and coordinated indirectly by three histidine residues through the water molecules. Subsequently, the hydroxide ions cause a lysine residue at the active site to become deprotonated and rotate 120 degrees into the *trans* conformer, which brings its nitrogen into close proximity to the carbon of  $\text{CO}_2$ , allowing for the formation of a covalent bond that produces a carbamyl group. This carbamyl group causes the  $\text{Mg}^{2+}$  ion to transfer to a second binding site, after which the histidine that first rotated returns to its original conformation [23]. It is unclear whether binding  $\text{Mn}^{2+}$  follows a similar mechanism and whether it requires an activator  $\text{CO}_2$  to be bound first [21][22]; hence, understanding the mechanism of  $\text{Mn}^{2+}$  binding to Rubisco is important to future research on Rubisco kinetics. During in vitro studies, Rubisco is often activated at pH 8.0 in the presence of  $\text{CO}_2$  and either  $\text{Mg}^{2+}$  or  $\text{Mn}^{2+}$ .

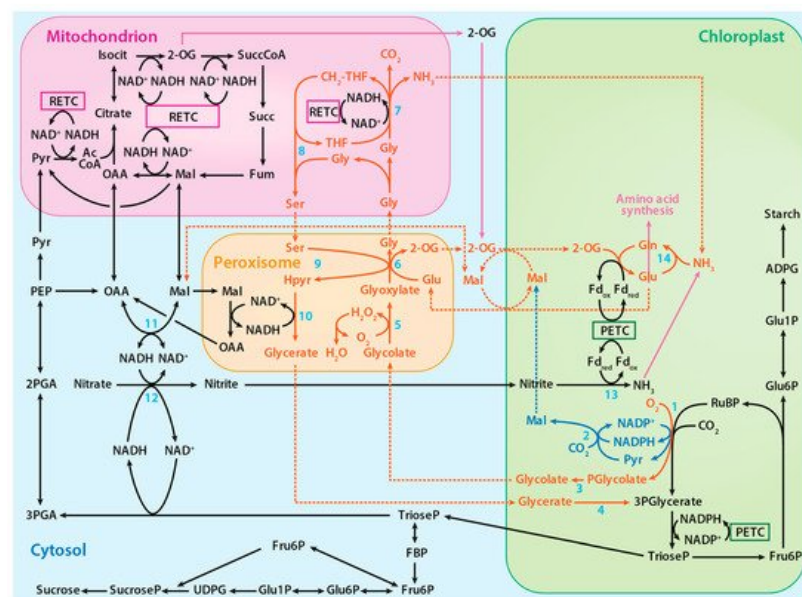
Rubisco can also bind to other metals. When bound to  $\text{Fe}^{2+}$ ,  $\text{Ni}^{2+}$ ,  $\text{Cu}^{2+}$ ,  $\text{Ca}^{2+}$ , or  $\text{Co}^{2+}$ , Rubisco may exhibit some carboxylase and oxygenase activity [24]. For example, one study found that Rubisco from *R. rubrum*, when bound to  $\text{Co}^{2+}$ , was incapable of carboxylation but still capable of oxygenation [24]. Another study found that Rubisco from spinach performed both carboxylation and oxygenation when bound to  $\text{Ni}^{2+}$  or  $\text{Co}^{2+}$  [25]. When bound to some other metal ions, including  $\text{Cd}^{2+}$ ,  $\text{Cr}^{2+}$ , and  $\text{Ga}^{2+}$ , Rubisco cannot catalyze either carboxylation or oxygenation [24]. Although it is known that the metal ion plays a role in stabilizing the activator carbamate and determining the active site's structure, its effect upon the reactions catalyzed by Rubisco is still not completely understood. One hypothesis is that  $\text{Mg}^{2+}$ , because of its electron-withdrawing properties, polarizes the C2 carbonyl of RuBP, which favors the removal of the C3 proton and thereby contributes to enolization [21].

NADPH complexes strongly with Rubisco and acts as an effector molecule to maintain the Rubisco catalytic pocket in an open conformation that more rapidly facilitates  $\text{CO}_2\text{-Mg}^{2+}$  activation when  $\text{CO}_2$  and  $\text{Mg}^{2+}$  are present in suboptimal concentrations [26][27][28][29]. The crystal structure of Rubisco with both  $\text{Mg}^{2+}$  and NADPH as ligands indicates that NADPH binds to the catalytic site of Rubisco through metal-coordinated water molecules [26]. The activated enzyme catalyzes either carboxylation or oxygenation of the enediol form of the five-carbon sugar ribulose-1,5-bisphosphate (RuBP) [14][21][22][30][31].

## 2.2. Balance between Carboxylation and Oxygenation and Metal Cofactors

Several factors alter the balance between Rubisco carboxylation and oxygenation and, thereby, alter the relative rates of photosynthesis and photorespiration. These include the concentrations of  $\text{CO}_2$  and  $\text{O}_2$  at the active site of Rubisco, the specificity of the enzyme for each gas, and whether the enzyme is associated with  $\text{Mg}^{2+}$  or  $\text{Mn}^{2+}$  [32]. These divalent cations share the same binding site in Rubisco [14][22][33], and in tobacco, Rubisco associates with both metals and rapidly exchanges one metal for the other [32]. Nonetheless, nearly all recent studies on the photosynthetic and photorespiratory pathways have been conducted in the presence of  $\text{Mg}^{2+}$  and absence of  $\text{Mn}^{2+}$  [8]. Rubisco binding of  $\text{Mg}^{2+}$  accelerates carboxylation, whereas binding of  $\text{Mn}^{2+}$  slows carboxylation [25][34][35][36][37][38]. Chloroplastic  $\text{Mg}^{2+}$  and  $\text{Mn}^{2+}$  activities seem to be regulated at the cellular level because in isolated tobacco chloroplasts, activities of the metals were directly proportional to their concentrations in the medium [32]. The thermodynamics of binding  $\text{Mg}^{2+}$  to Rubisco were similar for enzymes isolated from a Form I and a Form II species [32]. By contrast, the thermodynamics of binding differed greatly between the two Rubisco forms when the enzymes were associated with  $\text{Mn}^{2+}$  [32].

$\text{Mg}^{2+}$  and  $\text{Mn}^{2+}$  have nearly identical ionic radii but highly disparate electron configurations:  $\text{Mg}^{2+}$  ( $1s^2 2s^2 2p^6$  or [Ne]) has a very stable outer shell [8], whereas  $\text{Mn}^{2+}$  has five unpaired d electrons ( $1s^2 2s^2 2p^6 3s^2 3p^6 3d^5$  or [Ar] $3d^5$ ) that are susceptible to many redox reactions. An aerated solution of activated  $\text{Mn}^{2+}$ -Rubisco exhibits a long-lived chemiluminescence when RuBP is added [39][40]. This chemiluminescence was attributed to a spin-flip within the  $\text{Mn}^{2+}$  3d manifold, leading to an excited quartet ( $S = 3/2$ )  $d^5$  electronic configuration that decays over the course of 1 to 5 min back to the sextet ( $S = 5/2$ ) ground state electronic configuration [39]. Excited states are intrinsically better oxidants and reductants (larger reduction/oxidation potentials) than their corresponding ground states [41][42][43]; thus, the observed chemiluminescence opens the possibility that the RuBP- $\text{O}_2$ - $\text{Mn}^{2+}$ -Rubisco excited state may be quenched via electron transfer. Consequently, the liberated reducing equivalent could participate in the reduction of  $\text{NADP}^+$  to NADPH (Figure 2, blue pathway). In this way, oxidation of RuBP via  $\text{O}_2$  may proceed in a spin-allowed manner, while the  $\text{Mn}^{2+}$  remains “innocent” in the generation of the oxygenated RuBP precursor.  $\text{Mn}^{2+}$ -centered redox may still proceed, with oxidation of excited  $\text{Mn}^{2+}$  to  $\text{Mn}^{3+}$  occurring in a manner independent of, but parallel to, substrate oxidation.



**Figure 2.** The proposed photorespiratory pathway within the context of photosynthetic carbon and nitrogen metabolism. The solid red lines represent reactions of the photorespiratory pathway, the solid blue lines represent reactions of the proposed alternative photorespiratory pathway, the solid purple lines represent reactions of amino acid synthesis, and the dotted lines represent associated transport processes. Numbered reactions are catalyzed by the following enzymes: 1. Rubisco, 2. Malic enzyme, 3. Phosphoglycolate phosphatase, 4. Glycerate kinase, 5. Glycolate oxidase, 6. Glutamate:glyoxylate aminotransferase, 7. Glycine decarboxylase complex, 8. Serine hydroxymethyltransferase-1, 9. Serine:glyoxylate aminotransferase, 10. Hydroxypyruvate reductase-1, 11. Malate dehydrogenase, 12. Nitrate reductase, 13. Nitrite reductase, and 14. Glutamine synthetase. PETC designates photosynthetic electron transport chain and RETC, respiratory electron transport chain. Adapted from ref. [8]. Copyright 2018 Springer Nature Ltd.

In wheat leaves, the ratio of  $\text{Mn}^{2+}$  to  $\text{Mg}^{2+}$  contents increased as the  $\text{CO}_2$  levels increased and when the nitrogen source was nitrate rather than ammonium [32]. Nitrate assimilation into amino acids in shoots is heavily dependent on photorespiration, whereas ammonium assimilation is much less so. This indicates that plants shifted to Rubisco

Mn<sup>2+</sup> binding in order to compensate for the slower photorespiration rates and slower amino acid production that would otherwise occur under elevated CO<sub>2</sub> and nitrate nutrition.

### 2.3. The Photorespiratory Pathway

The 3-phosphoglycerate produced during photorespiration, like that produced during photosynthesis, is converted to triose phosphate and used to regenerate RuBP. On the other hand, 2-phosphoglycolate is converted to glycolate by phosphoglycolate phosphatase. In the peroxisome and mitochondrion, a series of reactions converts glycolate to glycinate, which is ultimately returned to the chloroplast to regenerate RuBP (Figure 2) [8]. In addition to Rubisco, several other chloroplast enzymes in the photorespiratory pathway, including malic enzyme and phosphoglycolate phosphatase, bind either Mg<sup>2+</sup> or Mn<sup>2+</sup> [8]. The plastid isoform of malic enzyme in *Arabidopsis* and tobacco catalyzes the reverse pyruvate synthesis reaction (pyruvate + CO<sub>2</sub> + NADPH → malate + NADP) [44][45]. Phosphoglycolate phosphatase, which is responsible for the hydrolysis of 2-phosphoglycolate to glycolate, binds to and is activated by either metal [46]. Hypothesized is an alternative photorespiratory pathway that increases photorespiration energy efficiency by generating malate (RuBP + O<sub>2</sub> + CO<sub>2</sub> + H<sub>2</sub>O → glycolate + malate + 2Pi) when Mn<sup>2+</sup> binds to these enzymes (Figure 2) [8].

## 3. Conclusions

Is photorespiration simply a futile cycle? The answer is “no”. Multiple lines of evidence show its crucial role in many plant processes. Despite heroic efforts to suppress photorespiration, disrupting any photorespiratory reaction usually proves detrimental to plants [47][48]. The reassimilation of CO<sub>2</sub> from photorespiration [49] and the important role played by photorespiration in the acclimation of plants to conditions, such as salinity [50] and elevated CO<sub>2</sub> [51], are topics that are beyond the scope of this review but nevertheless provide important evidence showing that photorespiration is not a wasteful process. There are many promising directions for further studies on photorespiration; for example, examining Mn<sup>2+</sup> interactions with Rubisco, further exploring the reassimilation of photorespired CO<sub>2</sub>, and exploring how the biochemical processes related to photorespiration contribute to its role in adaptation to various conditions will probably reveal that plant carbon fixation and respiration is more energy efficient than what has been previously assumed.

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