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Abbreviations

RuBP: Ribulose-1, 5-Bisphosphate; GS/GOGAT: Glutamate Synthase/Glutamine Synthetase; PGA: Phosphoglyceric Acid; ROS: Reactive Oxygen Species

Mini Review

Photorespiration: a Multipurpose Process

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Introduction

Photorespiration results from Ribulose-1, 5-Bisphosphate (RuBP) oxygenation catalyzed by RuBP carboxylase/oxygenase (rubisco). This oxygenase function, like carboxylation, only occurs in the presence of light and is therefore called photorespiration; its first product is a 3C compound, phosphoglyceric acid, which goes into the Benson-Calvin cycle, and a 2C compound, phosphoglycolic acid. In principle, phosphoglycolic acid has no function in cell metabolism. The two functions of rubisco act competitively, and the photorespiratory rate varies from 15 to 45% of gross photosynthesis [1]. The rate of photorespiratory CO_2 release, which is 3 to 8 times the respiration rate, is increased by light, temperature, and O_2 content. Therefore, in conditions of high light and high temperatures, the photorespiration of C_3 plants is increased, and the photosynthetic rate and biomass production are decreased [2]. Phosphoglycolic acid, produced in photorespiration, is dephosphorylated to glycolic acid, exported from the chloroplast to the peroxisome, and oxidized to glyoxylic acid. Glyoxylic acid is then aminated, generating glycine, a glutathione precursor for the ascorbate/glutathione antioxidant system [3]. The formation of glycine is coupled to the Glutamate Synthase/Glutamine Synthetase (GS/GOGAT) system in the chloroplast, and the glutamic acid formed is exported to the peroxisome, where transamination takes place, giving up the amino group ($-NH_2$) to form glycine. The second amino group for the second glycine comes from the deamination of serine to hydroxypyruvate in the peroxisome itself [1]. The glycine formed is transported to the mitochondria, where two glycines (2C each) are transformed into a serine (3C), releasing photorespiratory CO_2 and the amino group to form a glycine. The serine formed returns to the peroxisome, where it is deaminated to hydroxypyruvic acid, releasing the second amino group to form the second glycine, resulting in a balance in the flow of N if the cycle is continued. However, in this organelle, hydroxypyruvic acid is reduced to glyceric acid, and this migrates to the chloroplast, where it is phosphorylated to phosphogliceric acid (PGA) to enter the Benson-Calvin cycle, consuming at least one ATP. Therefore, of every four carbons (two glycines) that enter photorespiration, three are recovered in phosphoglyceric acid, and one is lost in CO_2. In this pathway, in addition to the consumption of ATP for the formation of phosphoglyceric acid, there is the consumption of NADPH in the reduction of hydroxypyruvic acid to glyceric acid in the peroxisome [3]. This consumption of ATP and NADPH in the photorespiratory pathway will be necessary under photoinhibition conditions when an excess of light is associated with environmental stresses reducing CO_2 assimilation and NADPH consumption [3].

Functions of the Glycolate/Glycerate Photorespiratory Pathway

The evolution of the rubisco enzyme initially took place in an atmosphere rich in CO_2 and poor in O_2 when the first plants appeared on Earth [4]. With the proliferation of life on the planet, the atmosphere became richer in O_2 produced by the photosynthesis of these first plants, and the oxygenase action inherent in the rubisco enzyme began to take hold. The appearance of mutant plants with the glycolate-glycerate cycle of photorespiration, where part of the C is recovered, made them more efficient than those without it. During plant evolution, only those with the photorespiration cycle survived [1,4]. The P-glycolic acid generated by the oxygenase function of rubisco has no specific role in plant metabolism. It would be a carbon loss if there were no glycolate-glycerate cycle. In this photorespiration cycle, 3/4 of the C is recovered, with one PGA (3C) generated and one CO_2 released [1]. Photorespiration can synthesize all amino acids from the transamination of glycine and serine produced during photorespiration. The flow of nitrogen in photorespiration is ten times greater than the flow in primary N assimilation, according to Lorimer and Andrews (1981) [4]. The photorespiratory nitrogen cycle accounts for most of the incorporation of NH_3 into leaves in most C_3 plants in the presence of light [5]. Another vital role of photorespiration is for NH_3 incorporation in leaves [3], especially in the tropics with a definite dry and rainy season that causes a rapid flush of nitrogen at the beginning of rains, called the "Birsch" effect [6]. During this fast flush of nitrogen in dry/wet soils, photorespiration can be essential in leaf NH_3 reassimilation of NH_4^+ assimilated at the root and transported to shoot as organic compounds. The GS/GOGAT system associated with photorespiration in the leaf can be a pathway for specific amino acid synthesis (glycine and serine), important as organic nitrogen accumulation for recycling after soil nitrogen depletion [5-7]. The nitrogen flux in photorespiration can be ten times superior to that in its assimilation system [3, 5]. In addition, when photorespiration is inhibited, this effect also strongly inhibits nitrate assimilation. Thus, nitrate assimilation depends on photorespiration [7].

Photorespiration is a process that uses light energy and can, therefore, serve to prevent photoinhibition, especially in C3 plants [2,5]. Photoinhibition is due to the exposure of the leaf to high light intensities, above 600 to 800 µmoles. $m^{-2}.s^{-1}$, associated with environmental stresses that reduce photosynthesis, as water stress causing stomatal closure, salinity also causing stomatal closure in plus of salt toxicity, high or low temperatures, slowing down Calvin cycle reactions or nitrogen deficiency, reducing rubisco activity [8]. In these conditions, where there is a little photosynthetic reduction of CO_2, and the excess energy generated by the high luminosity, associated with oxidation due to the high O_2/CO_2 ratio, would lead to the production of Reactive Oxygen Species (ROS), as H_2O_2, which causes irreversible damage to the integrity of the thylakoid membranes and reaction centers, especially photosystem II [8]. Photorespiration under these conditions can be used to dissipate excess ATP and NADPH; to generate internal CO_2, maintaining rubisco activity; and to consume strong oxidants such as ROS, through the action of antioxidant systems, as the cycles of violoxanthin/zeaxanthin, the ascorbate/glutathione, and others mechanisms of dissipation of photosystems energy [8]. Consequently, it can be reduced to improve net A, as in C_4 plants, but not eliminated because it is a necessary process with protective effects, especially for tropical marginal agro environments [3,8]. However, photorespiration has been viewed as a wasteful process because of the consumption of ATP and $NADPH_2$, and it is considered an unfavorable consequence of plants having evolved when the atmosphere contained much higher levels of carbon dioxide than it does today [9,10]. The benefit of engineering strategies to reduce photorespiration rate is to increase soybean yield [9, 10]. Nevertheless, the Darwin theory of "Natural selection" is still

valid [11], and "individuals having any advantage, however slight, over others, would have the best chance of surviving. On the other hand, any variation in the least degree injurious will be rigidly destroyed. This preservation of favorable individual differences and variations, and the destruction of those which are injurious, I have called Natural Selection or the Survival of the Fittest [11]". Thus, if photorespiration were harmful to plant growth, it would disappear during evolution [11], which was not the case. Therefore, photorespiration has multipurpose functions. To recover ¾ of C produced by the oxygenase action of rubisco and producing CO_2 when stomata are closed, for example, to maintain rubisco activity under this condition for the recovery. To reduce photoinhibition effects, consuming the excess of ATP and $NADPH_2$ produced and not consumed by photosynthesis. To produce glutathione from the photorespiratory glycine and maintain the antioxidant system ascorbate/glutathione, which is crucial to avoid photo inhibition. To assimilate N and synthesize amino acids, especially in tropical regions, with an increase in N in soils at the beginning of the rainy season, among other functions.

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