Photorespiration

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Photorespiration is the light-dependent release of CO₂ from photosynthetic organisms and is caused by O₂ substituting for CO₂ in the first step of photosynthetic CO₂ fixation.

Introduction

The enzyme that is responsible for fixing CO₂ in photosynthesis, Rubisco (ribulose-1,5-bisphosphate carboxylase/oxygenase; EC 4.1.1.39, can also fix O₂ (Bowes et al., 1971). Rubisco favours CO₂ over O₂ by a factor of up to 100, but the concentration of O₂ in the atmosphere is much higher than that of CO₂. As a result, about one molecule of O₂ is fixed by Rubisco for every three molecules of CO₂. When O₂ is substituted for CO₂, the toxic product phosphoglycolate results. Plants metabolize phosphoglycolate, but this requires energy and causes the loss of some reduced carbon as CO₂. Thus, photorespiration inhibits photosynthesis by three mechanisms. First, photorespiration interferes with CO₂ fixation at Rubisco; second, it uses energy that could otherwise be used for photosynthetic carbon reduction; and third, it causes the release of CO₂ from previously fixed carbon (Sharkey, 1988). Photorespiration substantially reduces the efficiency of photosynthesis in most plants, especially crop plants, with a few exceptions such as Zea mays, which overcomes photorespiration by chemically preconcentrating CO₂.

Photorespiratory Pathway and Control

When Rubisco fixes CO₂, two molecules of phosphoglycolate are produced; when O₂ is used, one phosphoglycolate and one phosphoglycolate are produced (Figure 1). Photorespiration involves conversion of the phosphorylated phosphoglycolate to the amino acid glycine. This is followed by the conversion of two glycine molecules (two carbons each) to the amino acid serine (three carbons) plus one molecule of CO₂ and one of ammonia. Finally, the serine is converted to glycerate and then phosphoglycerate. There is a net loss of one CO₂ and one ammonia for each two oxygenation events. The released ammonia must be refixed and the ammonia cycling that results from photorespiration accounts for ten times more ammonia fixation than does protein synthesis.

Because photorespiration detoxifies phosphoglycolate produced by Rubisco, limiting photorespiration by reducing the capacity for phosphoglycolate metabolism harms plants. Mutant plants have been generated that lack the ability to carry out steps in glycolate metabolism. These plants could be selected because they grew poorly or not at all in normal air but could be rescued by growth in high-CO₂ atmospheres, which suppress the oxygenation reaction (Somerville, 1986). Seven different classes of mutants were recovered, indicating that there are at least seven proteins that are required for photorespiration that are not essential for plant growth and reproduction in the absence of photorespiration.

Because photorespiration is needed to detoxify phosphoglycolate, all hope for reducing photorespiration lies in improving the specificity of Rubisco for CO₂ over O₂. Rubiscos with higher specificity have evolved and the Rubiscos found in most C₃ crop plants today have the highest specificity of any organism on Earth. However, this specificity has come at the cost of high catalytic efficiency. There exist Rubiscos that are much faster than C₃ Rubiscos, but they have lower specificities for CO₂ over O₂. Given the changes in global CO₂ concentration, some investigators believe there is more to gain by moving a higher-efficiency Rubisco into C₃ plants and accepting the losses caused by photorespiration in exchange for the higher capacity of the Rubisco.

Compartmentation of Photorespiration

The reactions of photorespiration occur in three different compartments in higher plants: the chloroplast, the peroxisome and the mitochondrion (Figure 1). The reactions begin in the chloroplast with the oxygenation of ribulose bisphosphate. The phosphoglycolate produced is dephosphorylated inside the chloroplast and the glycolate then moves to the peroxisome. Peroxisomes have substantial amounts of catalase to break down hydrogen peroxide (H₂O₂). The oxidation of glycolate to glyoxylate produces H₂O₂ and reactions that generate H₂O₂ normally occur in peroxisomes. The glyoxylate is transaminated to glycine, which moves to the mitochondrion.

Inside the mitochondrion glycine meets one of two fates. One half of the glycine molecules are taken apart to yield CO₂, ammonia and a one-carbon fragment on tetrahydrofolate. This last compound donates the carbon from the first glycine to a second glycine molecule to make serine. The serine leaves the mitochondrion and goes back to the peroxisome. Here it gives up its amino group, which is used
in the transamination of glycolate to glycine, resulting in hydroxypyruvate.

Hydroxypyruvate is reduced to glycerate, which moves to the chloroplast. Glycerate in the chloroplast is phosphorylated to phosphoglycerate. This phosphoglycerate re-enters the carbon metabolism of photosynthesis. For each two ribulose bisphosphate molecules oxygenated, three phosphoglycerate molecules plus one CO₂ molecule result (Figure 2).

The transamination from serine to glycolate to make hydroxypyruvate and glycine accounts for half of the needed ammonia. The other half comes from refixation of the ammonia released during glycine decarboxylation in the mitochondrion (Figure 3). The glutamine synthetase/glutamate synthase (GS/GOGAT) pathway refixes the ammonia, consuming both ATP and reducing power. This adds to the energetic cost of photorespiration.
Photorespiration and Global O₂ and CO₂ Concentrations

Rubisco is believed to have evolved when the CO₂ concentration was very high and O₂ was nearly absent from the atmosphere. The ability of Rubisco to use O₂ instead of CO₂ was, therefore, not important during early Rubisco evolution. During the 2 billion years after the evolution of Rubisco, the CO₂ level in the atmosphere fell almost 90%, but free O₂ was still almost nonexistent. However, about 1.5 billion years ago, O₂ gas started to accumulate in the atmosphere. At 500 million years before present, the O₂ concentration had increased to approximately the levels we have today but CO₂ was still high. Because the interaction between O₂ and CO₂ is competitive, photorespiration was still not a significant factor in photosynthetic organisms.

It is estimated that between 450 to 500 million years ago land plants appeared on Earth followed by a rapid decline in CO₂ in the atmosphere. The relatively low CO₂ and high O₂ concentrations would have caused significant rates of photorespiration for the first time about 450 million years ago. Between 30 and 50 million years ago, the CO₂ level fell to very low levels and photorespiration was probably a significant impediment to plant growth. About this time, the ability to chemically concentrate CO₂ by making a four-carbon carboxylic acid evolved. This C₄ pathway evolved in a number of different plant families independently as a result of the strong evolutionary pressure exerted by photorespiration (Ehleringer et al., 1991). Plants that do not use this pathway are called C₃ plants and must cope with photorespiration.

Turning to more recent times, the global CO₂ concentration has increased by about 20% during this century. Because of this increase, photorespiration has decreased by 20% worldwide. As the CO₂ concentration continues to increase in the future, photorespiration will continue to fall. This should lead to increased crop yields. The increases in plant growth caused by decreased photorespiration are predicted to exceed any negative effect of increased temperature (Long, 1991). However, increased CO₂ in the atmosphere could lead to more violent weather, which could more than offset the productivity gains due to reduced photorespiration.

In today’s atmosphere, the energetic cost of the CO₂ pump of C₄ plants is roughly equal to the energetic cost of photorespiration suffered by C₃ plants. However, these costs are affected by other environmental conditions in addition to the CO₂ concentration in the atmosphere. Most important is temperature. The rate of oxygenation and thus photorespiration is stimulated by high temperature because the specificity of Rubisco for CO₂ over O₂ is worse at high temperature. In today’s atmosphere, at 35°C, the cost of photorespiration exceeds the cost of the C₄ pump but at 25°C the cost of photorespiration is less than that of the C₄ pump. This is why C₄ plants are more common in the tropics than in temperate regions. At about 30°C, the cost of photorespiration is about the same as the cost of the C₄ pump.

As the CO₂ concentration in the atmosphere increases, the temperature at which these two costs are equal will increase until, at 700 ppm CO₂, this crossover point is estimated to be 42°C. In other words, when the CO₂ concentration doubles, C₄ plants will be favoured only in extreme environments. This is not to say that C₄ plants will
become less efficient, rather that C₃ plants will become more efficient as the rising CO₂ in the atmosphere suppresses photorespiration. Thus changes in photorespiration rates could affect competition between C₃ and C₄ plants and alter species composition and diversity in many ecosystems.

Functional Significance of Photorespiration

Photorespiration is clearly deleterious to plants. Often, the stimulation of photosynthesis that occurs in high CO₂ results only from the suppression of photorespiration by CO₂. Does photorespiration provide some evolutionary advantage over a hypothetical plant lacking photorespiration? Or is photorespiration only a metabolic mistake: evolutionary baggage reflecting the fact that the global CO₂ concentration was high and O₂ concentration was low when Rubisco evolved (Andrews and Lorimer, 1978)? While not a unanimous opinion, the general consensus is that photorespiration is primarily an evolutionary relic. Rubisco routinely makes a number of metabolic mistakes, including production of pyruvate (Andrews and Kane, 1991) and xylulose bisphosphate (Edmondson et al., 1990). Photorespiration and production of other oxidized products of ribulose bisphosphate (Kane et al., 1998) are further examples.

However, there are two ways that plants benefit from photorespiration. The first is in the production of the amino acids glycine and serine. These amino acids can be found in the phloem transporting carbon from photosynthesizing leaves (Madore and Grodzinski, 1984). While this is not the only method the plant has for synthesis of these compounds, the plant can none the less use these amino acids for protein synthesis. This also provides the plant with another method of end-product synthesis. Under some conditions, especially at low temperature, the processes of starch synthesis and sucrose synthesis may not go fast enough to process all of the carbon fixed in photosynthesis. Then, glycine and serine can be additional end products that allow photosynthesis to go faster than synthesis of starch plus sucrose. When this happens, adding O₂ will stimulate CO₂ uptake as opposed to the normal situation where adding O₂ inhibits CO₂ uptake because of the costs associated with photorespiration (Harley and Sharkey, 1991).

A second way that photorespiration can be useful to the plant is as an alternative electron sink when CO₂ is not available. The light-dependent reactions of photosynthesis produce reduced compounds used in photosynthetic reactions. Management of reducing power developed as a result of absorbing sunlight is an important concern for plants. When the energy in sunlight is not managed properly, leaves are damaged. Leaves exposed to excess light can take hours to days to regain all of their capacity for photosynthesis, a phenomenon called photoinhibition. The primary management method appears to involve the xanthophyll zeaxanthin, but photorespiration can also help manage excess light, especially during drought. When plants have too little water, the stomata on the leaves close, restricting water loss but at the same time restricting CO₂ entry. The CO₂ concentration inside the leaf quickly falls to the compensation point, where photosynthesis goes just fast enough to fix the CO₂ released in photorespiration. As the falling CO₂ concentration inhibits photosynthesis, photorespiration increases. Because photorespiration requires about the same amount of energy as photosynthesis (per ribulose bisphosphate consumed), the energy consumed by photosynthesis plus photorespiration remains roughly constant as the stomata close and photorespiration replaces photosynthesis (Stuhlfauth et al., 1990).

These two functions of photorespiration can be demonstrated. However, it is unlikely that these two functions provided an evolutionary constraint leading to photorespiration, because the basic mechanism of oxygenation of ribulose bisphosphate evolved at a time when there was no free O₂. It is possible that these two functions are now important to the plant and provide evolutionary pressure to maintain photorespiration despite its costs to the plant. However, in both cases, there already exist mechanisms that can perform the required function better than photorespiration. In the first case, the capacity for starch and sucrose synthesis far exceeds the capacity for glycine and serine synthesis. In the second case, the mechanism of dissipating excess light that involves zeaxanthin can dissipate much more energy than can photorespiration in most leaves. Thus, while these two functions of photorespiration may be useful to the plant, the overall effect of photorespiration is deleterious: plants would be better off without photorespiration.

If photorespiration is primarily a metabolic mistake, perhaps it can be eliminated through genetic engineering. So far it has been possible to make the specificity of Rubisco worse through genetic methods. While disappointing in themselves, these results show that it is possible to manipulate the processes that lead to photorespiration. Perhaps some day it will be possible to engineer a plant that lacks photorespiration. In the meantime, increasing global CO₂ concentrations will suppress photorespiration.

References


Further Reading


