

Plant metabolism

*Is photorespiration an effective mechanism for protecting against photoinhibition?*

CO<sub>2</sub> and O<sub>2</sub> are competitive substrates for the enzyme Rubisco (Ribulose biphosphate carboxylase/oxygenase). Photorespiration is the process where by the enzyme Rubisco fixes molecular oxygen as apposed to carbon, which ultimately leads to the evolution of CO<sub>2</sub> from plants. The process occurs concurrently with photosynthesis in green leaves of C<sub>3</sub> plants. A high CO<sub>2</sub> and low O<sub>2</sub> atmospheric concentration favours the carboxylase action, whereas a high O<sub>2</sub> and low CO<sub>2</sub> concentration favours the oxygenase action. Therefore due to the existence of photorespiration, photosynthesis is inhibited by oxygen. When the release of CO<sub>2</sub> by photorespiration equals CO<sub>2</sub> fixation by photosynthesis, a concentration of CO<sub>2</sub> is reached called the CO<sub>2</sub> compensation point. When the light is extinguished, continued CO<sub>2</sub> production from photorespiration results in a post illumination burst (PIB).

The enzymic pathways for CO<sub>2</sub> production from oxygen fixation are known as the photosynthetic carbon oxygen cycle (PCO). It involves the coordinated activities of the chloroplast, peroxisome and the mitochondria as well as transport of the compounds through the cytoplasm between these organelles and it is shown below;

The cost of fixing one molecule of O<sub>2</sub> is 9.5ATP equivalents and in the presence of photorespiration, the consumption of ATP and reducing equivalents per CO<sub>2</sub> fixed (5.375 mol ATP and 3.5 mol NADPH) is higher than in the absence of photorespiration (3mol ATP and 2 mol NADPH). Therefore photorespiration results in considerable loss of fixed carbon and utilization of energy, which subsequently decreases the productivity and yield. CAM and C<sub>4</sub> plants have developed a supplementary system of fixation of CO<sub>2</sub> into C<sub>4</sub> acids. In both plants the decarboxylation of these C<sub>4</sub> acids elevates the CO<sub>2</sub> concentration in the vicinity of Rubisco to enhance carboxylation and suppress oxygenation. Therefore here photorespiration occurs, in some conditions but is greatly reduced. Although in C<sub>3</sub> plants the rate of the carboxylase reaction is four times that of the oxygenase reaction under atmospheric conditions, why C<sub>3</sub> plants haven't evolved a mechanism for CO<sub>2</sub> concentration like C<sub>4</sub> and CAM plants is an interesting point. It seems a wasteful reaction and maybe with the increasing CO<sub>2</sub> concentration of the atmosphere it may diminish photorespiration and make CO<sub>2</sub> concentrating mechanism more important. Or, photorespiration may have a necessary purpose in the plant. For example the PCO cycle generates metabolites, such as glycine, serine or one-carbon units for other processes in plants. It is also involved in stress protection, including light stress and therefore elicits protection against photoinhibition. The focus of this essay will be to evaluate the effectiveness of photorespiration as a mechanism for protecting against photoinhibition.

Photoinhibition is a reversible process that reduces the efficiency at which absorbed light is used during the light dependent reactions of photosynthesis. It can be split into two types; dynamic photoinhibition; the rapidly reversible decrease in PSII efficiency involving dissipation of the energy of excess photons in the antennae and chronic photoinhibition; the slowly reversible decrease in PSII efficiency involving loss of reaction center function.

Non-assimilatory electron transport via oxygenase photorespiration stimulates photon utilization and thereby mitigates chronic photoinhibition under natural conditions this was observed when transgenic tobacco plants were studied having twice the normal amount of GS2 (plastidic glutamate synthase – a key enzyme in photorespiration) had an improved capacity for photorespiration and an increased tolerance to high light intensity, where as those with a reduced amount of GS2 had a diminished capacity for photorespiration and were photoinhibited more severely by high light intensity compared with control plants.

An additional reaction found to mitigate chronic photoinhibition is the Mehler reaction (the water-water cycle), arguably an additional type of photorespiration whereby the photoreduction of O<sub>2</sub> at PSI occurs. This photoreduction produces superoxide radicals (O<sub>2</sub><sup>-•</sup>), which disproportionate to H<sub>2</sub>O<sub>2</sub> and O<sub>2</sub> with the aid of superoxide dismutase. The H<sub>2</sub>O<sub>2</sub> is rapidly detoxified to water by the ascorbate peroxidase pathway. Since the electron flow from water in PSII to water in PSI occurs in this process, it has been termed the water–water cycle The water–water cycle not only scavenges free radicals and peroxide, but also generates a pH gradient (ΔpH) across the thylakoid membranes when little electron transport acceptors are available in PSI. This ΔpH enhances non-radiative dissipation of light energy as observed by non-photochemical quenching. Therefore, the water–water cycle is considered to function to dissipate the energy of excess photons also.

The extent to which these reactions prevent photoinhibition has been investigated by various groups.

Chilling induced photoinactivation occurs as a result of low temperatures, which limit the light and CO<sub>2</sub> saturated photosynthetic capacity of leaves in many plant species because the proportion of absorbed light that is excess to photochemistry is increased. Investigations into grapevine leaves found them relatively resistant to low temperature-induced net photo inactivation of PSII, implying highly efficient energy dissipation mechanisms. These include photorespiration, the water-water cycle as mentioned and the xanthophylls cycle. (The xanthophylls cycle is mediated by the particular group of carotenoids, violaxanthin, antheraxanthin and zeaxanthin. Under conditions of low irradiance violaxanthin functions as an antenna pigment by transferring energy to chlorophyll a. With increasing irradiance, violaxanthin is biochemically transformed into zeaxanthin, via the intermediate antheraxanthin, a reaction reversed in the dark. Zeaxanthin and antheraxanthin together with a low pH within the photosynthetic membrane, facilitate the harmless dissipation of excess excitation energy directly within the light-harvesting antennae.) Investigation into the photo inactivation of PSII in these leaves found that non-photochemical energy dissipation involving xanthophylls and fast D1 repair (the PSII subunit destroyed in photo inhibition) were the main protective processes reducing the rate of photoinactivation. The total absorbed light dissipated via xanthophylls mediated processes were up to 75% of the total absorbed radiation in grapevine. It was additionally found that O<sub>2</sub> reduction via photorespiration and the water-water cycle is negligible at low temperatures. When the water-water cycle and photorespiration were suppressed by low O<sub>2</sub> partial pressure the rate of photoinactivation failed to increase indicating that both processes contributed little to photoprotection under low temperature and high light conditions. The water-water cycle was more temperature dependent than photorespiration and was reduced to negligible proportions below 15°C. Therefore photorespiration is not an effective mechanism for protecting against photoinhibition at low temperatures. However, it is more efficient at high temperatures. Under water stress, where the supply of CO<sub>2</sub> to the chloroplasts is restricted in the light because of stomatal closure, the generation of CO<sub>2</sub> in the green cells by photorespiration maintains carbon in the intermediates of the Calvin cycle. Otherwise because of insufficient diffusion of external CO<sub>2</sub> into the leaves there would be excess photons. However, although in this incidence photorespiration is increased relative to carbon assimilation, it is decreased in absolute terms. The photorespiration path uses energy even at low photon flux densities thus lowering C assimilations and so the whether it has a unique protective function can be doubted and in this respect it seem a not particularly effective mechanism for protecting against photoinhibition as can not be regulated. However, it is at low Co<sub>2</sub> concentrations and high O<sub>2</sub> concentrations when its energy dissipation qualities are required.