# Photoinhibition and Zeaxanthin Formation in Intact Leaves: A Possible Role of the Xanthophyll Cycle in the Dissipation of Excess Light Energy—Commentary

**Demmig B, Winter K, Krüger A, Czygan FC** (1987) Photoinhibition and zeaxanthin formation in intact leaves: a possible role of the xanthophyll cycle in the dissipation of excess light energy. Plant Physiol **84:** 218–224

Plants grown in low light and then shifted to high light show lasting reductions in their photosynthetic efficiency and rates of light-saturated photosynthesis; this observation is termed the photoinhibition of photosynthesis. Photoinhibition is relevant not only to plants in changing light conditions but also to those growing under any conditions that limit photosynthesis and growth. Thus, for example, during water stress, which causes a limitation of $CO_2$ uptake by reducing stomatal apertures, incoming light energy easily exceeds the ability of the leaf to perform $CO_2$ fixation and photoinhibition will occur. In the mid 1980s, photoinhibition was a relatively new finding, with clear implications for agriculture and plant ecology, yet there was little mechanistic understanding of the process. It was already clear that excess light could decrease photosynthesis by bleaching chlorophyll and/or damaging photosynthetic enzymes, a process termed photodamage. Photodamage was the favored hypothesis explaining photoinhibition, because most crop plants demonstrate bleaching under photoinhibiting conditions. Today, photodamage remains a valid explanation for photoinhibition, with one critically important caveat: plants also take active measures to prevent photodamage, a process termed photoprotection. For example, evergreens can enter a photoprotected state, with strongly down-regulated photochemical efficiency, for the entire duration of a harsh winter.

Barbara Demmig (now Demmig-Adams) and her postdoctoral mentor, Stanford's Olle Björkman, published several articles in 1987 proposing a lasting photoprotective dissipation of excess excitation energy as harmless heat in photoinhibited evergreen leaves. However, Barbara and Olle could not yet provide a mechanistic explanation for dissipation: exactly how was dissipation activated in response to high light? The *Plant Physiology* article commemorated here provided a tremendous conceptual breakthrough in photosynthesis research by giving us a one-word answer to that question: zeaxanthin.

Zeaxanthin is one of three carotenoid pigments of thylakoid membranes that make up the xanthophyll cycle. During the cycle, violaxanthin is converted to zeaxanthin in a light-dependent and reversible manner. High light causes the accumulation of zeaxanthin, and darkness results in the reappearance of violaxanthin. While still at Stanford, Barbara saw the possibility of a connection between zeaxanthin and dissipation, but she did not have the technical ability to measure carotenoids and explore that connection.

Then, Barbara started a new position at the Lehrstuhl für Botanik II of the Universität Würzburg, Germany, in the laboratory of Professor Klaus Winter. As luck would have it, Klaus' lab was next door to that of pharmacology Professor Franz-Christian Czygan, who had considerable experience with the separation and measurement of carotenoids. Ms. Almuth Krüger was a technician in that laboratory who performed most of the carotenoid analyses. Barbara's plant experiments generated numerous samples for Almuth's analysis, resulting in the clear demonstration of an inverse correlation between zeaxanthin concentrations and photosynthetic efficiency, clearly implicating zeaxanthin in dissipative photoprotection.

Twenty-four years later, the hypothesis placing zeaxanthin in a central role for dissipative photoprotection, over short (minute to minute), medium (diurnal), and long (seasonal) time scales, in nearly every photosynthetic organism, has weathered numerous experimental tests and enjoys tremendous explanatory power in studies ranging from biophysics to community ecology.

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