

Buchanan B B. Role of light in the regulation of chloroplast enzymes.
Annu. Rev. Plant Physiol. 31:341-74, 1980.
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The review summarizes evidence for the role of light in regulating enzymes of carbon dioxide assimilation and related processes in photosynthesis. The contributions of the different regulatory signals invoked (changes in pH, ion gradient, sulphydryl groups) were analyzed to provide a general picture of how light fulfills its newly identified regulatory function. [The *SCI*® indicates that this paper has been cited in more than 485 publications.]

Light, Thioredoxin, and Chloroplasts

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It has been known for four decades that light functions in photosynthesis by supplying the assimilatory power, ATP and NADPH, for carbon dioxide assimilation (historically known as the "dark" reactions). At the time my review was written, 1980, the view that light plays another role in photosynthesis, notably in regulating carbon assimilation, was neither widely known nor widely accepted. My review was the first comprehensive effort to present this concept and summarize the evidence for it. This is one reason why the article is widely cited.

As described in my review, the first evidence that light plays a role in regulating carbon dioxide assimilation came from experiments in the mid-1960s which showed that certain enzymes of the reductive pentose phosphate cycle are activated by illumination of intact leaves (I. Ziegler, Technische Universität München) and chloroplast preparations (our laboratory, University of California at Berkeley). Experiments on light/dark transition with algal cells during this period were also interpreted as evidence for light activation of key enzymes of the cycle (J.A. Bassham, also University of California at Berkeley). A number of subsequent reviews have summarized the evidence in support of this posttranslational regulatory role for light, which applies also to enzymes outside the area of carbon assimilation.¹ The wide inclusion of this type of regulation in contemporary text-

books of biology and biochemistry attests to the acceptance of this view.

In fulfilling its regulatory role in photosynthesis, light absorbed by chlorophyll is converted to signals—including changes in pH, ion gradient, sulphydryl groups, and concentrations of divalent cations and metabolite effectors¹—that collectively "inform" selected enzymes that the light is on so that the major biosynthetic and degradatory pathways can be appropriately directed. In this way, the cell can use available resources to increase growth and survival under a range of environmental conditions.

In the case of sulphydryl changes, the light signal is transmitted from chlorophyll containing membranes via ferredoxin (an iron-sulfur protein that transports energetic electrons) and ferredoxin-thioredoxin reductase (an iron-sulfur enzyme with a catalytically active disulfide group) to one of two thioredoxins—a family of small proteins universally distributed in nature. Through changes in the hydrogen status of its own sulphydryl groups, thioredoxin brings about reversible changes in the sulphydryl status and hence the activity of target enzymes. The fact that my review was the first to describe the then newly identified regulatory role of thioredoxin also accounts for its citation record.

Two developments in the thioredoxin area, both unforeseen in 1980, warrant comment. In the first case, thioredoxin has been found to promote the growth of animal cells¹⁻³—a finding that may open the door for a new method of treatment of retrovirus-related disorders.⁴ In the other development, thioredoxin has been identified as a signal in seed germination.^{5,6} Following reduction by NADPH and NADP-thioredoxin reductase, thioredoxin acts to control germination by (i) neutralizing the activity of a disulfide protein that specifically inhibits an enzyme central to starch breakdown, and (ii) solubilizing and unfolding storage proteins, thereby permitting their breakdown and use by the developing seedling. These experiments have also provided a new thioredoxin-based technology that seems promising for the improvement of flour⁷ and potentially other seed products.

1. Buchanan B B. Regulation of CO₂ assimilation in oxygenic photosynthesis: the ferredoxin/thioredoxin system. Perspective on its discovery, present status and future development. *Arch. Biochem. Biophys.* 288:1-9, 1991.
2. Wollman E E, d'Auriol L, Rimsky L, Shaw A, Jacquot J P, Wingfield P, Graber P, Dessarps F, Robin P & Galibert F. Cloning and expression of a cDNA for human thioredoxin. *J. Biol. Chem.* 263:15506-12, 1988.
3. Tagaya Y, Maeda Y, Mitsui A, Kondo N, Matsui H, Hamuro J, Brown N, Arai K, Yokota T, Wakasugi H & Yodoi J. ATL-derived factor (ADF), an IL-2 receptor/Tac inducer homologous to thioredoxin: possible involvement of dithiol-reduction in the IL-2 receptor induction. *EMBO J.* 8:757-64, 1989.
4. Matsutani H, Nakamura H, Ueda Y, Kitaoka Y, Kawabe T, Iwata S, Mitsui A & Yodoi J. ADF (adult T cell leukemia-derived factor)/human thioredoxin and viral infection: possible new therapeutic approach. *Adv. Exp. Med. Biol.* 319:265-74, 1992.
5. Kobrehel K, Wong J H, Balogh A, Kiss F, Yee B C & Buchanan B B. Specific reduction of wheat storage proteins by thioredoxin *h. Plant Physiol.* 99:919-24, 1992.
6. Jiao J, Yee B C, Wong J H, Kobrehel K & Buchanan B B. Thioredoxin-linked changes in regulatory properties of α -amylase/subtilisin inhibitor protein. *Plant Physiol. Biochem.* (In press.)
7. Wong J H, Kobrehel K, Nimbona C, Yee B C, Balogh A, Kiss F & Buchanan B B. Thioredoxin and bread wheat. *Cereal Chem.* 70:113-4, 1993.

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