Chapter 9

Molecular Analysis of Photoprotection of Photosynthesis

Hou-Sung Jung and Krishna K. Niyogi*
Department of Plant and Microbial Biology,
University of California, Berkeley, CA 94720-3102, USA

Summary

Plants have diverse defense mechanisms against high light stress. Plants can reduce absorption of light energy through chloroplast avoidance and antenna size reduction. However, the capacity of the avoidance and the antenna size reduction for protection is limited, so that plants often absorb more energy than they can use. Therefore, plants need mechanisms to deal with this excess absorbed light energy, such as harmless thermal dissipation by feedback de-excitation. The transthylakoid pH gradient, xanthophyll cycle, PsbS, and other light-harvesting complex proteins are required for this thermal dissipation. In addition, alternative electron transport allows electrons to pass to acceptors other than CO_2, thereby relieving overreduction of electron transport components in high light conditions. To detoxify reactive oxygen species that are inevitably produced during high light stress, plants have antioxidants including carotenoids, ascorbate, and tocopherols. In spite of these photoprotective mechanisms, photodamage may still occur, and efficient repair of damaged systems could be a photoprotective mechanism. In this chapter, recently published molecular genetics studies on each step of photoprotection have been reviewed. Genes

*Author for correspondence, email: niyogi@nature.berkeley.edu

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required for each defense mechanism that have been identified thus far are introduced, and cloned genes that can possibly be related to photoprotection are discussed.

I. Introduction

In nature, photosynthesis is indispensable for sustaining much of the life on earth. Photosynthesis begins with light energy absorption and its conversion into chemical energy. During this reaction, ATP and NADPH are produced, and oxygen is also generated from H_2O as a byproduct. This converted chemical energy is then used to assimilate CO_2 into carbohydrates.

By definition, photosynthesis requires light energy. The light energy is collected mainly by chlorophylls in light-harvesting complexes (LHCs). After absorbing the light energy, a chlorophyll becomes excited to its singlet excited state and then transfers the absorbed energy in one of several ways including photochemistry indicated by photochemical quenching of chlorophyll fluorescence. The energy is delivered to reaction centers of photosystems, where it drives the initial charge separation reactions of photosynthesis (photochemistry). Besides photochemistry, fluorescence emission, de-excitation by thermal dissipation, and decay through triplet state are the other ways by which excited chlorophylls return to ground state.

The light energy, however, is not always a good thing, because too much light may cause damage in plants. When plants receive more light than they can utilize, the lifetime of singlet excited chlorophyll extends, and the chance of returning to ground state through triplet state chlorophyll is increased. This pathway can dissipate excess energy (Foyer and Harbinson, 1999; Niyogi, 2000); however, the generated triplet chlorophyll can transfer its energy to oxygen so that singlet oxygen is produced. Singlet oxygen is a harmful type of reactive oxygen species (ROS) that can cause degradation of membrane and protein structure of photosystems (Barber and Andersson, 1992; Melis, 1999).

Plants have various levels of photoprotective mechanisms (Fig. 1) (Barber and Andersson, 1992; Long et al., 1994; Niyogi, 1999). First of all, plants can protect themselves from excess light by avoiding absorption of the high light. Second, plants can reduce the amount of absorbed energy by thermal dissipation. Third, electrons can be transported through alternative pathways to relieve excitation pressure (Asada, 1999; Ort, 2001). Plants also have antioxidants to detoxify ROS (Bartley and Scolnik, 1995; Smirnoff, 2000). Finally, plants can efficiently repair damaged photosystems. Each mechanism plays a role depending on how strong the incident light is. In most cases, these mechanisms are well coordinated to protect plants from not only just steady high light, but also sudden light intensity changes, such as strong sunshine between clouds.

To understand the photoprotective mechanisms in detail, molecular analysis has been used to identify and characterize the function of various genes in photoprotection. Most of these genes have been identified in plant model systems including Synechocystis, *Chlamydomonas*, and especially *Arabidopsis*, using forward and reverse genetics (Golan et al., 2004). Forward genetics begins with a mutant phenotype and then proceeds to identification of the affected gene; reverse genetics starts with a gene sequence followed by generation and characterization of knockout mutants.

In this chapter, we present a review of the molecular analysis of photoprotection including descriptions of mutants and cloned genes involved in photoprotection. We have tried to focus on recently identified factors for photoprotection as well as to update some results concerning previously known factors.

Abbreviations: ELIP – early light-induced protein; ETR – electron transport rate; FNR – ferredoxin-NADP$^+$ reductase; FQR – ferredoxin-plastoquinone oxidoreductase; HPT – homogentisate phytyltransferase; HSP – heat shock protein; LHC – light-harvesting complex; Mg-ProtoIX – Mg-protoporphyrin IX; NDH – NADPH/NADH dehydrogenase; NPQ – nonphotochemical quenching; OHP – one-helix protein; PQ – plastoquinone; PS II – photosystem II; ROS – reactive oxygen species; SEP – stress-enhanced protein; Φ_{PSII} – PS II efficiency (quantum yield of Photosystem II)

II. Avoiding High Light Absorption

Avoidance of high light absorption can be a photoprotective mechanism because it can simply reduce the input of light energy (Fig. 1). Although plants are sessile, they are able to adjust the amount of energy absorption through chloroplast movement and antenna size reduction in chloroplasts.

A. Chloroplast Avoidance Movement

In limiting light, plant chloroplasts move to the periclinal walls that are perpendicular to the incident light