Commentary

Photoinhibition and Photoprotection under Environmental Stresses

Luca Vitale

National Research Council (CNR), Department of Biology, Agriculture and Food Science (DiSBA), Institute for Agricultural and Forest Systems in the Mediterranean (ISAFoM), Naples, Italy.

Abstract | Plants are often exposed in their habitat to multiple abiotic and biotic stresses that limit growth and productivity; however, plants are able, to some extent, to cope with limiting environmental conditions by means of different mechanisms that contribute to their adaptive success in different habitats.

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Correspondence | Luca Vitale, Institute for Agricultural and Forest Systems in the Mediterranean (ISAFoM), Naples, Italy; **E-mail** | luca.vitale@cnr.it
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Plants are often exposed in their habitat to multiple abiotic and biotic stresses (*e.g.* high light intensity, low or high temperatures, water shortage, salinity, diseases, etc.) that hamper growth and productivity; however plants are able, to some extent, to cope with limiting environmental conditions by means of different mechanisms that contribute to their adaptive success in different habitats.

Photosynthesis, the most important biological process on Earth, could be greatly impacted by environmental stresses and constraints. By photosynthesis, solar energy is used to convert CO_2 into different organic compounds that are required for plant growth and reproduction (primary metabolism) and for plant/environment interactions (secondary metabolism). Under optimal environmental conditions, the photosynthetic performance is high. By contrast, stressful environmental factors (*i.e.* high light intensity, cold or heat, water shortage or nutrient deficiency) may limit CO_2 fixation and lead to significant reduction of photosynthetic efficiency, and increased photooxidation damages.

From all the light energy absorbed by photosynthetic pigments, only a small fraction of light is used in photosynthesis. The remaining light excess is potentially detrimental for photosynthesis because it might lead to photoinhibition and/or photooxidation. The photoinhibition of photosynthesis (i.e. the reduction in photosynthetic efficiency) may result in chronic photoinhibition - related mainly to the damage of protein D1 within the PSII- or in dynamic photoinhibition that represents a regulatory mechanism to avoid photodamage (Vitale et al., 2012). Environmental constraints can also accelerate the production of reactive oxygen species (ROS) that increase the photooxidation damages for DNA, proteins, and lipids. In order to avoid or cope with the excess light, plants have evolved with several adaptive mechanisms.

Avoiding Strategies

The movement of leaf and chloroplast is an adaptive and rapid response that regulates light interception and absorption on diurnal basis (Aren et al., 2008; Davis and Hangarter, 2012). Paraheliotropism, the movement of leaves to avoid or minimize exposure to light, is a reversible alteration in leaf orientation, due to volume changes in the tissues of pulvinus located

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at the base of leafs or leaflets. By such movements, plants optimize the interception and absorption of light. Environmental stresses, however, such as water stress, high light intensity and temperatures increase the paraheliotropic leaf movements that reduce the radiative load of light on the leaf surface.

Light-induced changes in the distribution and orientation of chloroplasts inside cell have also been observed in the majority of plants. Under low light conditions, chloroplasts accumulate perpendicular to the incident light to optimize light absorption, and under high light conditions, chloroplasts aggregate parallel to the incident light to minimize light absorption and reduce photooxidation.

Tolerance Strategies

The light unused in photosynthesis has to be dissipated to avoid photodamages and photooxidation.

Thermal dissipation of light is a fundamental photoprotection mechanism in plants. It occurs mainly in PSII antennae and involves xanthophylls cycle, particularly zeaxanthin associated with conformational changes in the antennae complex (Niyogi et al., 2004). The excess of absorbed light can also be dissipated by non-assimilatory photochemistry, mainly photorespiration and water-water cycle (D'Ambrosio et al., 2006). At moderately high temperatures and water stress, photorespiration is a fundamental photoprotection mechanism. In C3 plants for example, the photorespiration reduces the photosynthetic efficiency, dissipating the light excess and reducing the synthesis of ROS. The water-water cycle, on the other hand, is a combination of biochemical reactions catalyzed by different 'scavengers' enzymes that operate in chloroplast. The actions of different scavenger enzymes reduce the photooxidative damages of ROS, produced under constraining conditions. Moreover, water-water cycle maintains an electron flow within the photosynthetic apparatus, even when CO_2 fixation is limited or inhibited, contributing to an effective photoprotection at low temperatures.

Finally, plants have also evolved with the ability to pre-acclimate shaded leaves to light stress, a process known as *high light systemic acquired acclimation* (HL-SAA). A systemic signal is rapidly transmitted from high-lighted exposed to distal shaded leaves, resulting in improved tolerance to oxidative stress (Karpinski et al, 1999). Several messengers, such as ROS and non-ROS signals, and signaling pathways, *e.g.* ABA- and MEcPP-mediated signaling, have been recently described (Cutler et al., 2010; Xiao et al., 2012).

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