Chapter 6

Photoinhibition and Photoprotection under Nutrient Deficiencies, Drought and Salinity

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Summary

Some of the more frequent abiotic stresses in plants are limited availability of nutrients and water, as well as salinity. All these situations occur both in natural habitats and in crops. Stressed plants often experience decreases in photosynthetic rates, whereas they still harvest sunlight. Environmental stresses such as those may decrease the efficiency with which solar energy is harvested and used by plants in photosynthetic reactions. This feature is what the scientific community has often called photoinhibition. Some researchers tacitly assume that photoinhibition may result from photodamage, whereas others believe that it is more the integration of a series of regulatory and protective adjustments. The aim of this review is to summarize the current knowledge concerning photoinhibition- and photoprotection-related processes under nutrient deficiencies, drought, and salinity stress, and to discuss the role that photoinhibition could play under such environmental stresses.

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I. Introduction

The terminology concerning photoinhibition in plants is still a matter of debate and cause of misunderstandings (Adams et al., Demmig-Adams et al., this volume). For instance, in environmental and agronomic forums it is still very common to translate and understand any reference to photoinhibition as a damage-type occurrence, with little or no consideration to the possible photoprotective sides of those processes.

The aim of the present paper is to summarize the current knowledge on photoinhibition and photoprotection occurring under the most common nutrition-related abiotic stresses in plants. This includes deficiencies of Fe, N, and other elements, and also drought and elevated salinity. We have considered as photoinhibition-related those situations where one or several of the following observations have been made: i) a decrease in quantum yield of photosynthesis, ii) decreases in F_v/F_m ratios after dark adaptation, iii) changes in D1 protein amount or turnover rate, and iv) a permanent "lock-in" of the xanthophyll cycle pigments in the de-epoxidized state. We have considered as photoprotection-related observations those reporting non-permanent changes in xanthophyll cycle-mediated thermal dissipation, elicitation of antioxidative systems, and decreases in leaf Chl concentrations. In this latter case, however, it should be taken into account that the role of smaller antenna size in photoprotection seems to be small (Baroli et al., 2003).

II. Iron (Fe) Deficiency

Iron is part of many plant components, and therefore is required for plant growth. Iron is abundant in the earth's crust, but under oxygenic conditions and at the pH values prevailing in many environments, the existing Fe(III) equilibrium concentrations are far lower than those required for plant growth (Marschner, 1995). As a consequence, Fe deficiency is a common abiotic stress that affects many photosynthetic organisms (Terry and J. Abadía, 1986; Geider and La Roche, 1994; Straus, 1994). Species affected range from sea phytoplankton (Behrenfeld et al., 1996) to high value crops in arid and semiarid environments (Mortvedt, 1991). Iron deficiency is a potential problem in Calcisol soils, that cover approximately 800 million ha worldwide (FAO, 1988). Since the most visual effect of Fe deficiency in plants is the yellowing of young leaves, Fe deficiency is usually named Fe chlorosis (from the Greek word "chloros", yellow-green). Iron chlorosis is one of the yield limiting factors for some crops. A good example is fruit tree crops in Mediterranean environments, since growers not using Fe fertilization face major fruit yield and quality losses (Álvarez-Fernández et al., 2003) and also marked reductions in orchard longevity (Sanz et al., 1992).

A. Effects of Fe Deficiency on Photosynthesis

Approximately 80% of the plant Fe is located in the chloroplast, where it is a constituent of a number of photosynthetic machinery components, including cytochromes, Fe-S centers, and others (Terry and J. Abadía, 1986). When Fe is in low supply, the amount of photosynthetic membranes per chloroplast decreases. This is accompanied by decreases in all membrane components, including electron carriers of the photosynthetic electron transport chain (Terry and J. Abadía, 1986 and references therein) and the thylakoid pigments Chls and carotenoids (Morales et al., 1990, 1994; J. Abadía and A. Abadía, 1993). Because of these changes, thylakoids from Fe-deficient plants show characteristics of a "diluted" photosynthetic membrane (Terry and J. Abadía, 1986). Iron deficiency also decreases RuBP carboxylation capacity, both through reduced Rubisco enzyme activation (Taylor and Terry, 1986) and down-regulation of gene expression (Winder and Nishio, 1995). The Fe deficiency-mediated decreases in light harvesting, electron transport, and carbon fixation capacities seem to be well coordinated (Winder and Nishio, 1995).

As a consequence of all these changes, Fe deficient leaves have low photosynthetic rates and can dissipate in this way a limited amount of energy. The decreases in leaf pigment concentrations occurring with Fe deficiency may provide some protection through decreases in light harvesting capacity (see below). Pigment

Abbreviations: A – antheraxanthin; C_a – external CO_2 concentration; Chl – chlorophyll; C_i – substomatal CO_2 concentration; D – fraction of light absorbed by PS II that is dissipated thermally in the antenna; ETR – electron transport rate; NPQ – non-photochemical quenching; P – fraction of light absorbed by PS II that is used in photochemistry; Pc – fraction of P that Rubisco uses for RuBP carboxylation; Po – fraction of P that Rubisco uses for RuBP oxygenation; PPFD – photosynthetic photon flux density; PS I – Photosystem I; PS II – photosystem II; Rubisco – ribulose-1,5-*bis*phosphate carboxylase oxygenase; RuBP – ribulose *bis*phosphate; V – violaxanthin; X – fraction of light absorbed by PS II that is neither used in photochemistry nor dissipated thermally in the antenna; Z – zeaxanthin.