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Mini Review

Plant Responses to Water Deficit and Photoinhibition

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Mini-Review

Light and oxygen are essential to the CO_2 Assimilation rate (A) and carbohydrates synthesis for life on Earth [1]. However, they can also damage cell membranes, especially the thylakoids, where electron transport produces ATP and NADPH2 [2]. High photosynthetic photon flux density (PPFD) above 600 to 800 µmol m^{-2} s^{-1}, in the presence of O_2 (a strong oxidant), can cause damage to photosystem II (PS II) in the thylakoid membranes of chloroplasts [3]. This metabolic phenomenon is the light-induced decrease in photosystems activity called photoinhibition, and it can lead to a reversible or irreversible photooxidative damage to the photosynthesis apparatus [4]. The PS II reaction center cannot absorb the excessive energy of high PPFD. Thus, it is transferred with electrons to O_2, producing reduced oxygen species (singlet oxygen, hydrogen peroxide, hydroxyls, and other radicals), called reactive oxygen species (ROS). The ROS can cause damage to lipids and proteins of the cell membranes, as the thylakoids and, ultimately, cause leaf death [3]. Photoinhibition occurs when high PPFD is associated with other environmental stresses, such as drought. Nevertheless, even during the day, an increase in air temperature and a reduction of RH% can happen due to high PPFD at midday, even in C4 plants, such as corn [4]. Under high PPFD, the photosynthetic apparatus's capacity to use the absorbed energy is reduced because of the diminution of A due to the ambient stresses. However, water photolysis is maximal due to high PPFD [3]. The electrons liberated by photolysis cannot be incorporated into the photosystem because its components stay reduced with the lower use of NADPH2 at the end of electron transport when A is lowered by the stress (Figure 1). Thus, the free-electron reacts with O_2 forming Reactive Oxygen Species (ROS), causing oxidation of lipids and proteins of the membrane reducing its activity and the electron transport [4].

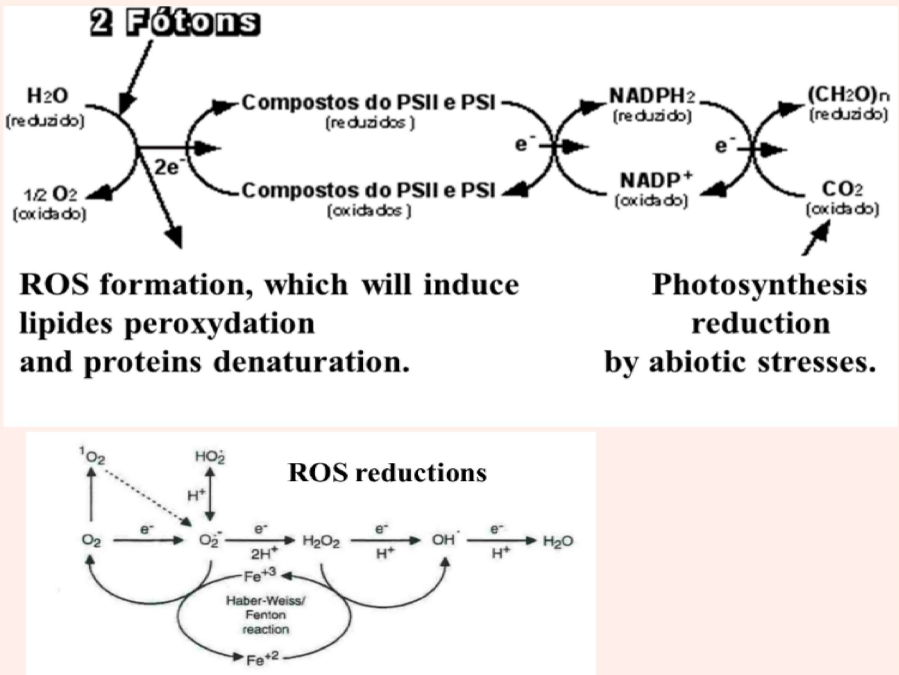

Figure 1: Oxy-reductive reactions of the photosystem electron transport producing NADPH2 to reduce CO_2 to carbohydrates; and ROS formation using free electrons from the water photolysis.

In the field, drought is generally associated with a high PPFD due to a clear sky, and photoinhibition an oxidative stress will occur even under moderate water stress, as shown in (Figure 1) [5]. Water deficit affects several physiological responses, varying in intensity among the species, its growth stages, and cultivation conditions [6]. There is a reduction in A under mild water deficiency, but the causes of this reduction are still under debate. Some authors state that there is only a limitation of CO_2 substrate, a diffusional limitation due to stomatal closure under mild stress [5]. Nevertheless, at the onset of drought, there is stomata closure and a reduction of cell growth and protein synthesis and thus carbohydrate synthesis [6]. However, studies from the 1970' showed a diffusional and a metabolic effect on A, due to loss of integrity of cell membranes (Figure 2), even under mild stress [7].

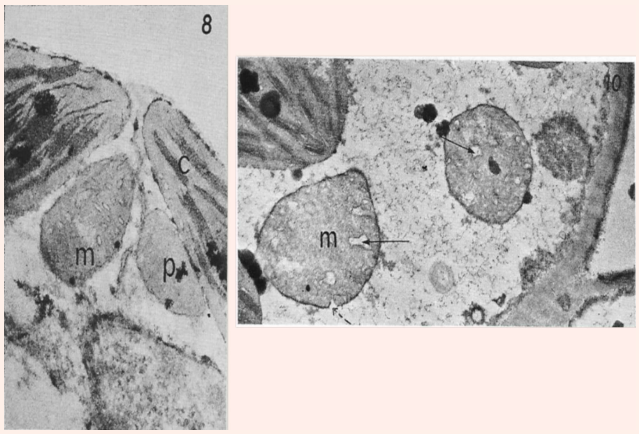

Figure 2: Under mild water deficit (high water potential [Ψw]), chloroplast and mitochondria membranes were affected by oxidation, and lipids droplets were seen (Data from Vieira da Silva, 1976).

This metabolic effect is probably triggered by Photoinhibition [8]. In addition to this effect, RuBP regeneration in the Calvin cycle is reduced, probably due to a lower chloroplastic ATPase activity caused by the reduced electron transport or lower cytoplasmic inorganic phosphorus (Pi) availability for ATP synthesis [8, 9]. Pi is exchanged by triose-P from the chloroplast through the phosphate antiporter translocators [9]. Therefore, a foliar spray of mono ammonium phosphate (MAP) can increase the cytoplasmic Pi content and reduce drought's photoinibitory effect [9]. A mild water deficit was imposed in an experiment with common bean two days after the foliar Pi spray (MAP). A was evaluated during eight days of water stress and three days after recovery. After rehydration, the A and gs of one genotype supplied with Pi were higher than those of non-Pi-supplied plants [9]. These results revealed an up-regulation of A (Ac)'s recovery after water deficit with a foliar spray of Pi, but it was genotype-specific (Table 1).

Table 1: O_2 evolution (Ac) of bean genotypes Ouro Negro and A320, both suffering maximum water stress and after recovery, in non-Pi-supplied or Pi-supplied plants. Pi-supplied leaves were sprayed with 10 g P L^{-1} and non-Pi-supplied leaves with 2.64 g N L^{-1}.

Genotype	Pi Foliar Spray	Water Stressed	After Recovery
A320	non-supplied	17.00 c	19.33 c
	Pi supplied	18.55 c	26.97 ab
Ouro Negro	non-supplied	21.45 bc	27.76 ab
	Pi supplied	26.08 ab	32.40 a

Data represent the mean value of three replicates. In columns, mean values followed by different letters show the statistical difference by the Student Neuman Keul's test ($p<0.05$) (Data from Santos et al., 2006).

As stated before, photo oxidative damage occurs when sunlight cannot be fully utilized because the photosynthetic electron transport is saturated [3]. This effect can be evaluated by measuring the maximum quantum yield of PS II, i.e., the ratio of variation in maximal fluorescence emission (Fv/Fm) obtained with the chlorophyll a fluorescence equipment, as shown in (Figure 3). Therefore, another study with water deficit imposition in *Phaseolus vulgaris* L. genotypes was conducted with two experiments: one under a mean PPFD of 500µ mol m^{-2} s^{-1} and the other under a mean 850 µmol m^{-2} s^{-1} of PPFD. The results of both experiments were compared, and a more significant decrease in the maximum quantum yield of photosystem II (Fv/Fm) under mild water stress and high PPFD than under low PPFD (Figure 3).

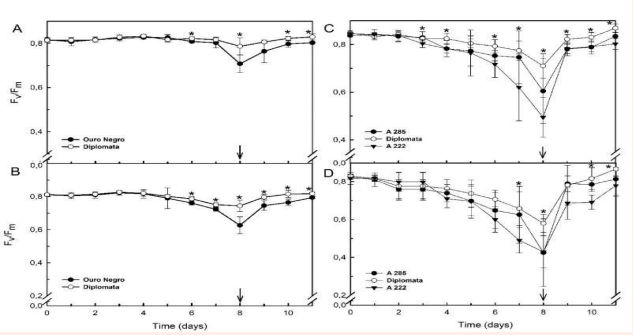

Figure 3: The maximum quantum yield of photosystem II (Fv/Fm) of two cultivars under lower mean values of PPFD around 550 µmol m^{-2} s-1: Ouro Negro and Diplomata, measured at dawn and after sunset (A) and (B), respectively; and three cultivars under higher mean values of PPFD around 850 µmol m^{-2} s-1: A 285, Diplomata and A 222 (C) and (D) at dawn and after sunset, respectively. The arrow shows the day of rehydration, and the asterisk represents significant differences (Data from Macedo et al., 2019).

The chlorophyll a fluorescence parameter Fv/Fm, under lower PPFD, was reduced only under severe water deficit. However, Fv/Fm and other chlorophyll a fluorescence parameters were reduced from the beginning of the drought in the second experiment under the higher PPFD (Figure 3). For example, the non-photochemical quenching (NPQ) values, i.e., energy dissipation to avoid photoinhibition, were almost double in the second experiment compared with the first. The high NPQ indicated a higher energy dissipation, primarily by heat [2, 3], to avoid more intense photoinhibition in the second experiment [5]. Therefore, a metabolic effect of water deficit on A, due to oxidative stress under high PPFD, as occurs in nature during drought, is evident (Figure 3), showing a diffusional and metabolic effect even during the onset of drought.

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