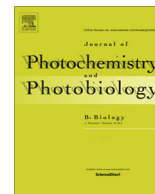




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## Photosynthetic proton and electron transport in wheat leaves under prolonged moderate drought stress

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### ABSTRACT

In conditions of long-lasting moderate drought stress, we have studied the photoprotective responses in leaves of wheat (*Triticum aestivum* L., cv. Katya) related to the photosynthetic electron and proton transport. The dark-interval relaxation kinetics of electrochromic bandshift (ECS) indicated a decrease of electric and an increase of osmotic component of the proton motive force in drought stressed leaves, but neither the total proton motive force (pmf) nor the thylakoid proton conductance ( $gH^+$ ) were affected. We observed the enhanced protection against overreduction of PSI acceptor side in leaves of drought stressed plants. This was obviously achieved by the rapid buildup of transthylakoid pH gradient at relatively low light intensities, directly associated to the steep increase of NPQ and the down-regulation of linear electron transport. It was further accompanied by the steep increase of redox poise at PSII acceptor side and PSI donor side. The early responses related to thylakoid lumen acidification in drought-stressed leaves could be associated with the activity of an enhanced fraction of PSI not involved in linear electron flow, which may have led to enhanced cyclic electron pathway even in relatively low light intensities, as well as to the drought-induced decrease of IP-amplitude in fast chlorophyll fluorescence kinetics.

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### 1. Introduction

Water deficiency causes multiple negative effects and triggers the complex of responses at different levels. The main direct effects of drought are associated with the decrease of CO<sub>2</sub> supply for carboxylation caused by stomatal and mesophyll limitation [1–3], associated with a decrease in energetic efficiency due to up-regulation of photorespiration [4], or with direct negative non-stomatal effects on metabolic pathways [5,6]. Moreover, the oxidative stress can seriously affect the leaf's photosynthetic machinery, mostly as a result of the interaction between drought and excessive light or under multiple stress conditions [7,8].

The photosynthetic machinery disposes with the flexibility thanks to the existence of different “safety valves” and mechanisms allowing to dissipate the excess of excitation energy and to ensure the output ratio of ATP/NADPH that matches the demands of plant metabolism [9,10]. The central process in higher

plants is non-photochemical quenching, by which the excess light energy is harmlessly dissipated as heat [11]. Non-photochemical quenching is induced by a low thylakoid lumen pH and a high  $\Delta pH$  that are generated by photosynthetic electron transport, especially under excess light conditions. The low pH of thylakoid lumen activates qE by protonating the protein PsbS [12] and by activating violaxanthin deepoxidase, which converts violaxanthin to antheraxanthin and zeaxanthin in the xanthophyll cycle [13]. There is also evidence for dissipation of excess energy in the reaction center of PSII [14]. Energy from linear electron flow can be in part redirected to photorespiration [15] or the water–water cycle [16], which also contribute to transthylakoid  $\Delta pH$ , as they keep the linear electron transport relatively high; this can be particularly important in drought stress [17]. Anyway, the proton circuit of photosynthesis can be modulated also, by the activity of cyclic electron flow around photosystem I, which can be up-regulated in stress conditions [18–20]. The process was shown to be essential as it contributes to photoprotection and balancing ATP/NADPH production ratio [21]. Although the contribution of cyclic electron transport (CET) to the buildup of transthylakoid  $\Delta pH$  and ATP synthesis has been questioned by some authors [22], the protective effects of PSI cyclic electron pathway was clearly documented [23].

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In this paper, we will try to contribute with our data on the responses measured at the level of electron and proton transfer in thylakoids in wheat leaves. In addition to decrease in electron transport rate, there are many studies showing the specific stress effects on electron transport processes based on chlorophyll fluorescence records, such as an increase of PSII heterogeneity associated with accumulation of  $Q_B$  non-reducing PSII reaction centers [24–26] and enhancing alternative electron pathways [27]. Moreover, the molecular studies indicated also decrease in expression and activity of ATP synthase [5,28], *cyt b6/f* [28] or other functional proteins [29]. Here, we have applied the combination of *in vivo* analyses of proton transfer using measurements electrochromic bandshift (ECS), together with analyses of slow and fast chlorophyll fluorescence and P700 kinetics, associated mainly with the electron transport related processes. Each of these particular signals is rich in information, and by combining together, they illustrate the interplay of individual photosynthetic responses and pathways, well balanced to protect the sensitive sites of the photosynthetic apparatus in conditions of long-term drought stress. More specifically, we will demonstrate the major role of enhanced PSI cyclic electron flow in the regulation of linear electron transport to reduce the over-reduction of PSI acceptor side, and thus reduce the risk of oxidative stress in chloroplasts.

## 2. Material and methods

### 2.1. Cultivation of plants

Plants of winter wheat (*Triticum aestivum* L.), cv. Katya were grown individually in pots (0.5 l) with the standard peat substrate. The pots were regularly irrigated and occasionally fertilized using liquid fertilizer with micronutrients. The cultivation and experiment were carried out in a growth chamber with artificial light provided by fluorescent tubes (Osram Fluora) with maxima in red and blue spectral region (the incident PAR at leaf level  $\sim 200 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ , photoperiod 14 h light/10 h dark, temperature 19–24 °C).

### 2.2. Drought stress treatment and measuring protocol

Drought stress was induced after the last leaf appeared. All pots were watered daily, and water was supplied to 70% of soil water capacity in control plants and 20% of soil water capacity in stressed plants. Measurements were taken from the leaves of drought-stressed plants (hereinafter referred as “Drought”) on the 10th to 14th day. All measurements were taken from the last leaf (the flag leaf on the wheat main stem). The simultaneous measurements of  $\text{CO}_2$  assimilation with chlorophyll fluorescence (ChlF), simultaneous measurements of P700 and ChlF and in some samples also measurements of electrochromic bandshift were performed on the same leaf. Between the different measurements, the plants were exposed to ambient light for at least half an hour to eliminate the effect of previous measurements. The same leaf was then used for determination of the water status.

### 2.3. Measurements of the leaf water status

Water status in wheat flag leaf was measured both as the relative water content (RWC) by gravimetric method and as the leaf water potential (WP) by the psychrometric method using micro-voltmeter Psypro with chamber C-52 (Wescor, USA), as described elsewhere [27].

### 2.4. Simultaneous measurements of gas exchange and chlorophyll fluorescence

The measurements were carried out using a Licor 6400 gasometer (Licor, USA) with simultaneous measurement of ChlF. After dark

adaptation (20 min in the dark box and 3 min in measuring head) the  $F_0$  and  $F_m$  values were determined, and the actinic light provided by LED light unit ( $1000 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ ) was switched on, at leaf temperature 20 °C, reference  $\text{CO}_2$  content 380 ppm, and ambient air humidity. Every 2 min, the gas exchange rate was measured, followed by saturation pulse and far-red pulse for  $F_0'$  determination. The values recorded after the steady state was reached are presented here (after at least 30 min of illumination in measuring head). The values of gas exchange parameters ( $\text{CO}_2$  assimilation rate –  $A_{\text{CO}_2}$ ; stomatal conductance –  $g_s$ ; internal  $\text{CO}_2$  concentration –  $c_i$ ) were calculated directly by the software of gas analyzer; the calculation ChlF parameters will be described below.

### 2.5. Simultaneous measurements of P700 redox state and chlorophyll fluorescence

The state of PSI and PSII photochemistry was measured with a Dual PAM-100 (Walz, Germany) with a ChlF unit and P700 dual wavelength (830/875 nm) unit, as described by Klughammer and Schreiber [30]. Saturation pulses ( $10,000 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ ), intended primarily for the determination of ChlF parameters were used also for the assessment of P700 parameters. Prior the measurements, the analyzed plants were exposed to ambient light in a growth chamber for at least 30 min; immediately before the measurements, plants were dark adapted for 20 min in a dark box, and for app. 2 min in the measuring head. After determination of  $F_0$ ,  $F_m$  and  $P_m$ , the light intensity similar to ambient ( $174 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ ) was used to start up the photosynthetic processes. After a steady-state was reached, a rapid light curve was triggered (light intensities 14, 30, 61, 103, 134, 174, 224, 347, 539, 833, 1036, 1295, 1602  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ ; 30 s at each light intensity) with saturation pulse and far-red pulse for  $F_0'$  determination after 30 s at each light intensity. Before the calculation of ChlF parameters, the ChlF records were corrected for PSI fluorescence by the method of Pfündel [31]. For the calculation of ChlF parameters, the following basic values were used:  $F$ ,  $F'$  – fluorescence emission from dark- or light-adapted leaf, respectively;  $F_0$  – minimum fluorescence from dark-adapted leaf (PS II centers open);  $F_m$ ,  $F_m'$  – maximum fluorescence from dark- or light-adapted leaf respectively (PS II centers closed);  $F_0'$  – minimum fluorescence from light-adapted leaf; PAR – the intensity of photosynthetic active radiation (in  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ ). The ChlF parameters were calculated as follows [32]: the maximum quantum yield of PSII photochemistry,  $F_v/F_m = (F_m - F_0)/F_m$ ; the actual quantum yield (efficiency) of PSII photochemistry,  $\Phi_{\text{PSII}} = (F_m - F')/F_m'$ ; electron transport rate at PSII (calculated assuming the equal distribution of light energy between PSI and PSII and the leaf absorbance 0.84):  $\text{ETR}_{\text{PSII}} = 0.84 \times 0.5 \times \text{PAR} \times \Phi_{\text{PSII}}$ ; non-photochemical quenching,  $\text{NPQ} = (F_m - F_m')/F_m'$ ; the redox poise of the primary electron acceptor of PSII,  $Q_A^-/Q_A \text{ total} = 1 - qP = 1 - [(F_m' - F')/(F_m' - F_0')]$ . For the calculation of P700 parameters, the following basic values were used:  $P$  – P700 absorbance at given light intensity;  $P_m$ ,  $P_m'$  – maximum P700 signal measured using saturation light pulse following after short far-red pre-illumination in dark- or light-adapted state. The P700 parameters were calculated as follows [30]: effective quantum yield (efficiency) of PS I photochemistry at given PAR,  $\Phi_{\text{PSI}} = (P_m' - P)/P_m$ ; electron transport rate at PSI (calculated assuming the equal distribution of light energy between PSI and PSII and the leaf absorbance 0.84),  $\text{ETR}_{\text{PSI}} = 0.84 \times 0.5 \times \text{PAR} \times \Phi_{\text{PSI}}$ ; oxidation status of PSI donor side, i.e. the fraction of P700 that is oxidized at given state,  $P700^+/P700 \text{ total} = \Phi_{\text{ND}} = P/P_m$ ; reduction status of PSI acceptor side, i.e. the fraction of overall P700 that is oxidized in a given state by saturation pulse due to a lack of electron acceptors,  $\Phi_{\text{NA}} = (P_m - P_m')/P_m$ . During all measurements, ChlF and P700 kinetics was recorded (each 30 ms; during saturation pulses each 0.3 ms).

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