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PS II down regulation as affected by the maximal activity of photorespiration in leaves of C₃ plants : Suppression of the activity of photorespiration under low light

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Introduction

It is not until the last decade that remarkable progress was made in the use of chlorophyll fluorescence to measure the quantum yield of PSII in intact leaves (Genty et al. 1989, Öquist and Chow 1992), although measurements of chlorophyll fluorescence had provided understandings of energy transfer and primary photochemical events in PSII. This development offered an opportunity for the assessment of the rate of total electron transport in photosynthetic apparatus. Quantitative studies have shown that electron flux through PSII is approximately accounted for by the activities of ribulose-1, 5-bisphosphate carboxylase/oxygenase (Rubisco) over a wide range of physiological conditions. Further, it has been shown that a depression of the activity of electron flow occurs in response to diminished sink demand of reductants by photosynthesis. However, it is also suggested that electrons not utilized by photosynthesis and photorespiration are consumed in the Water-water cycle. The coordination between the total electron flow and Rubisco reactions has been the subject of considerable attention, in relation to fluxes of electrons to other processes such as the Mehler reaction, nitrogen reduction and oxaloacetic acid reduction (Harbinson et al. 1990, Miyake and Yokota 2001). In this study, we analyzed control of total electron flow by limitation of Rubisco reactions in leaves of *N. tabacum*. It was found that total electron flux is suppressed by the down regulation of quantum yield of photosystem II when electron consumption in the photorespiratory pathway reaches saturation.

Materials and methods

Tobacco plants, *N. tabacum* Xanthi NC, grown for 5 to 7 weeks in a phytotron at 25 °C were used for the experiments. CO₂ concentration and partial pressure of water were measured using a transient photosynthesis system with a H₂O/CO₂ infra-red gas analyzer (LI-6400, Li-COR, USA). The flow rate of the flushing air was 670 ml min⁻¹. The air was stirred vigorously in a leaf chamber and boundary-layer conductance to the diffusion of water vapor was 1.42 mol H₂O m⁻²s⁻¹. Leaf temperature was maintained at 25 ± 1 °C and leaf-to-air vapor partial pressure was in the range 0.7 to 0.9 kpa. Actinic light was provided by a KL-1500 Schott light source (Schott, Germany). Neutral density filters were used to obtain light of different photon flux densities. The PAM 101 fluorescence measuring system (H. Walz, Germany) was employed to monitor modulated chlorophyll fluorescence. The experimental protocol of Genty et al. (1989) was basically followed. Fo was sensitized by a 1.6 kHz

measuring beam ($0.04 \mu\text{mol photon m}^{-2} \text{s}^{-1}$). Saturating pulses (800ms) of white light ($4,500 \mu\text{mol photon m}^{-2} \text{s}^{-1}$) were provided by a KL-1500 Schott light source (Schott, Germany) at intervals of 60s. The quantum yield of Photosystem II electron transport was calculated from $\Phi_{\text{PSII}} = (F_m' - F_s) / F_m'$ (Genty et al. 1989).

Results

Simultaneous measurements of CO₂ uptake and chlorophyll fluorescence in non-photorespiratory conditions

Fig. 1 shows the results of simultaneous measurements of CO₂ uptake and chlorophyll fluorescence performed in non-photorespiratory conditions using leaves of *N. tabacum* Xanthi NC. To inhibit the activity of photorespiration, CO₂ concentration was increased to either 800 or 1,600 $\mu\text{mol mol}^{-1}$. As shown in Fig. 1, there was a proportional correlation between values of product $\Phi_{\text{PSII}} * \text{PFD}$ and the rates of electron transport dependent on CO₂ assimilation (J_{CO_2}) which was determined from the rate of gross photosynthesis (GPR) multiplied by four (i.e. 4GPR). In the absence of photorespiration, almost all the electrons from photosystem II are utilized by CO₂ assimilation. Therefore, the proportional correlation means that a value of product $\Phi_{\text{PSII}} * \text{PFD}$ is an indicator of the rate of total electron transport.

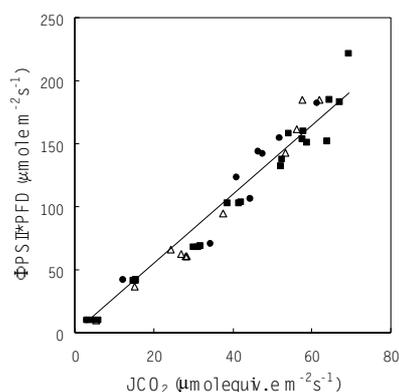


Fig. 1. A relationship between $\Phi_{\text{PSII}} * \text{PFD}$ and J_{CO_2} (= 4GPR) in non-photorespiratory conditions of $10 \text{ mmol mol}^{-1} \text{ O}_2$ and $800 \mu\text{mol mol}^{-1} \text{ CO}_2$ (circle), $10 \text{ mmol mol}^{-1} \text{ O}_2$ and $1,600 \mu\text{mol mol}^{-1} \text{ CO}_2$ (triangle), or $210 \text{ mmol mol}^{-1} \text{ O}_2$ and $1,600 \mu\text{mol mol}^{-1} \text{ CO}_2$ (square). PFD was changed from 13 to $1,094 \mu\text{mol m}^{-2} \text{s}^{-1}$. The regression line through the origin is $y = 2.74x$ ($r^2 = 0.95$).

Effects of atmospheric conditions on the rates of photosynthesis and total electron transport

Fig. 2 shows the results of the simultaneous measurements of CO₂ uptake and chlorophyll fluorescence performed in the atmospheric conditions in leaves of the tobacco plant. The rate of gross photosynthesis (GPR) increased almost linearly with increasing irradiance under light lower than about $160 \mu\text{mol photon m}^{-2} \text{s}^{-1}$, and approximately reached saturation under light of about $230 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 2a). The rates of photosynthesis GPR were lower in the atmospheric conditions than in the non-photorespiratory conditions, indicating that the atmospheric conditions were inhibitory to photosynthetic CO₂ assimilation (Fig. 2a). Although the inhibition of GPR was more apparent under high light, the inhibition was observed over a wide range of photon flux densities including low light.

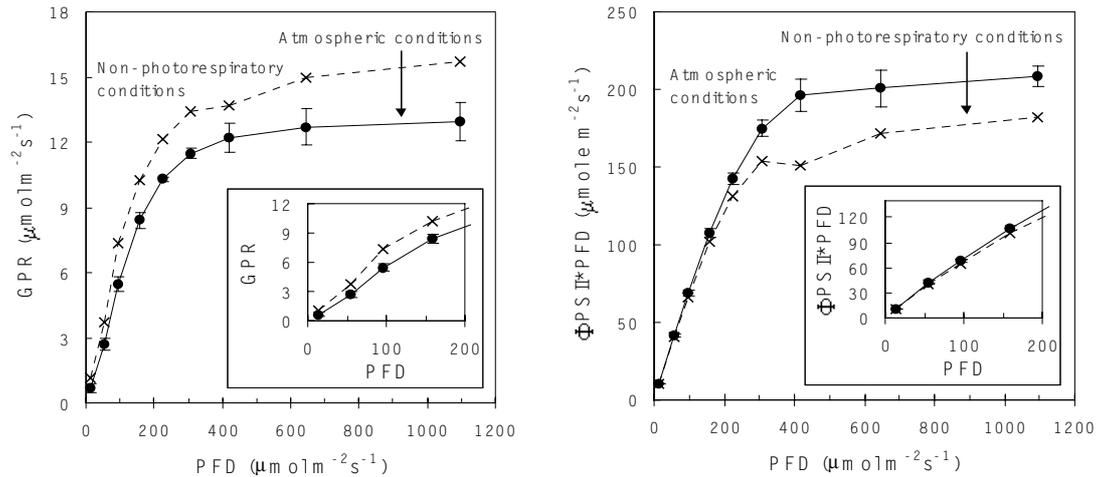


Fig. 2. Simultaneous measurements of CO_2 uptake and chlorophyll fluorescence in atmospheric conditions of $210 \text{ mmol mol}^{-1} \text{ O}_2$ and $350 \mu\text{mol m}^{-2} \text{ s}^{-1}$. **(a)** Changes in the rate of gross photosynthesis (GPR, closed circle) as a function of irradiance. Also shown are average values of GPR (\times) obtained from the experiments shown in Fig. 1 (i.e. The data for GPR were averaged across the non-photorespiratory conditions.). **(b)** Changes in value of product $\Phi\text{PSII}*\text{PFD}$ with irradiance (closed circle). \times , average values of the products $\Phi\text{PSII}*\text{PFD}$ in the non-photorespiratory conditions (Fig. 1). The error bars are \pm SD for at least three different experiments.

Comparisons of the values of $\Phi\text{PSII}*\text{PFD}$ between the non-photorespiratory conditions and the atmospheric conditions (Fig. 2b) reveals that the rate of total electron transport was enhanced by the atmospheric conditions under light higher than intermediate irradiance ($>230 \mu\text{mol m}^{-2} \text{ s}^{-1}$) which was nearly saturating for photosynthesis. However, such an enhancement was absent under low light ($<160 \mu\text{mol m}^{-2} \text{ s}^{-1}$).

Discussion

Suppression of the activity of photorespiration under low light

The oxygenation of RuBP by Rubisco competes with the carboxylation. The oxygenation of RuBP results in consumption of a large amount of photosynthetic energy in the subsequent metabolisms in the photorespiratory pathway. According to the accepted stoichiometry, release of CO_2 during photorespiratory carbohydrate oxidation consumes twice as much photosynthetic energy as uptake of CO_2 during carbon assimilation. The inhibition of the rate of photosynthesis (Fig. 2a) and the stimulation of total electron flux (Fig. 2b) under high light reflect the effects of oxygenation and thus indicate occurrence of photorespiration.

The activity of photorespiration is, however, thought to be suppressed under low light in the atmospheric conditions. Under low light which is limiting for photosynthesis, photorespiration would occur, since the rate of gross photosynthesis was diminished by the atmospheric conditions (Fig. 2a). On the other hand, total electron flow was almost the same between the atmospheric conditions and non-photorespiratory conditions, and the concomitant stimulation of total electron flux was not detected (Fig. 2b). This is inconsistent with the results obtained under high light, indicating a suppression of the activity of photorespiration. Since total electron flux was not affected by the air conditions under low light, total electron flux was

thought to be limited by light or irradiance. This limitation might cause the suppression of the activity of photorespiration.

Changes in the rates of electron transport as a function of irradiance

Total electron flux (J_e), the rate of electron transport depending on CO_2 assimilation (J_{CO_2}) and that coupled to photorespiration (J_{PR}) were determined for the data shown in Fig. 3. Under low light ($<160 \mu\text{mol m}^{-2} \text{s}^{-1}$), J_e and J_{CO_2} increased linearly with increasing irradiance. In this situation, J_{PR} was suppressed as mentioned above. Substantial increases in J_{PR} were detected under light with intermediate irradiance ($160 - 420 \mu\text{mol m}^{-2} \text{s}^{-1}$) which was nearly saturating for photosynthesis (J_{CO_2}). In this range of light intensity, J_e increased further with irradiance. Under high light ($>420 \mu\text{mol m}^{-2} \text{s}^{-1}$), J_{PR} completely reached saturation, and J_e also saturated.

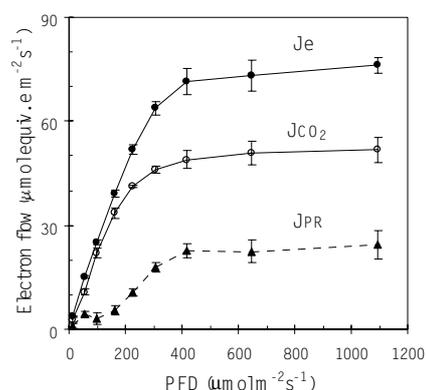


Fig. 3. Changes in the rate of total electron transport (J_e , closed circle), the rate of electron transport depending on photosynthetic CO_2 assimilation (J_{CO_2} , open circle) and the rate coupled to photorespiration (J_{PR} , closed triangle) with irradiance. Calculations of the rates of electron transport were made using the data shown in Fig. 2. J_{CO_2} was determined as four times the rate of gross photosynthesis (i.e. $J_{\text{CO}_2} = 4 (A + R_{\text{day}})$). J_e was estimated, on the basis of the result in Fig. 1, by dividing a corresponding value of $\Phi\text{PSII} \cdot \text{PFD}$ by 2.74 (i.e. $J_e = \Phi\text{PSII} \cdot \text{PFD} / 2.74$). J_{PR} was determined as a difference between J_e and J_{CO_2} . Experimental conditions were as in Fig. 2.

In conclusion, the rate of electron transport coupled to photorespiration (J_{PR}) was suppressed under low light. The increase in J_{PR} sustained the rise in total electron flux (J_e) under intermediate light. The saturation of J_{PR} caused the suppression of J_e probably due to down regulation of the quantum yield of photosystem II.

References

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