論文の内容の要旨

論文題目　Responses of the photosynthetic electron transport system to fluctuating light

（変動光に対する光合成電子伝達系の応答）

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Light energy absorbed by chloroplasts drives photosynthesis. When absorbed light is in excess, the thermal dissipation systems of excess energy are induced and the photosynthetic electron flow is regulated, both contributing to suppression of reactive oxygen species production and photodamages. Various regulation mechanisms of the photosynthetic electron flow and energy dissipation systems have been revealed. However, most of such knowledge has been obtained by the experiments conducted under controlled conditions with constant light, whereas natural light condition is drastically fluctuated. To understand photosynthesis in nature, we need to clarify not only the mechanisms that raise photosynthetic efficiency but those for photoprotection in fluctuating light. Although these mechanisms appear to be well balanced, regulatory mechanisms achieving the balance are little understood.

To assess roles of the cyclic electron flow around PSI (CEF-PSI) and O_2-dependent alternative pathways including the water-water cycle in fluctuating light (FL), I grew the wild type and *pgr5* mutant of *Arabidopsis thaliana* in continuous light at 100 µmol photon m^{-2} s^{-1} of photosynthetically active photon flux density (PPFD) for 8 h per day, and measured chlorophyll fluorescence and P700 absorbance changes in their leaves in the FL alternating between 240 (HL) and 30 µmol photon m^{-2} s^{-1} (LL) every 2 min. At 20% O_2, the photochemical quantum yield of PSII, Y(II), decreased, in particular in *pgr5*, soon after the start of the fluctuating light treatment (Fig. 1). PSI of the *pgr5* plants was markedly photoinhibited by this treatment for 42 min (Fig. 2A). Slight PSI photoinhibition was also observed in the wild type (Fig. 2A). I measured energy sharing between PSII and PSI and estimated the electron transport rates through PSII, ETR(II), and through

PSI, ETR(I). *pgr5* showed larger energy allocation to PSI. In contrast to the wild type, the ratios of ETR(I) to ETR(II) in the *pgr5* plants were higher in LL but lowered in HL at 20% O_2 due to the acceptor-side limitation on PSI. At 2.7 or 0% O_2, the CEF-PSI of the *pgr5* plants was enhanced, the acceptor-side limitation of PSI was released, and PSI photoinhibition was not observed (Fig. 2C and E). The results suggest that the light fluctuation is a potent stress to PSI and that the CET-PSI is essential to protect PSI from this stress.

To assess the effects of short-term fluctuating light on photoinhibition of both PSII and PSI, and on regulation of the photosynthetic electron transport system, I measured chlorophyll fluorescence and P700 parameters of *A. thaliana* grown in the continuous light in three FL alternating between the HL for 2 min and LL for 2min, the FL-240/30 (HL at 240 and LL at 30 μmol photons m^{-2} s^{-1}), FL-1200/30 (HL at 1200 and LL at 30 μmol photons m^{-2} s^{-1}) and FL-1200/240 (HL at 1200 and LL at 240 μmol photons m^{-2} s^{-1}). All of the FL caused PSI photoinhibition, but the degree was similar during three FL treatments (Fig. 3). In response to the FL-1200/30, ETR(II) and ETR(I) kept pace with the changes in light intensity (Fig. 4A and F). In these FL, photoprotective systems, such as the energy dissipation in the PSII antenna system (Fig. 4B) and the down-regulation of electron flow by the photosynthetic control at the cytochrome b_6/f complex (Fig. 4G), functioned to regulate the linear electron flow. However, the activities of these systems were insufficient in the FL-240/30. Thus, ETR(II) and ETR(I) in HL phases in the FL-240/30 decreased stepwise with the cycle (Fig. 4A and F). These results suggest that differences in modes of light fluctuation have distinct effects on regulation of the photosynthetic electron transport system. I examined the roles of photosynthetic alternative electron flows in response to the FL. The over-expression line of PGR5 showed the marked tolerance to the FL. In addition, continuous measurements of the changes in the electrochromic pigment shift showed that the rate of H^+ effluxes via the H^+-ATPase in chloroplasts did not decrease with the cycles. This may explain why PSI photoinhibition did not enhance PSII photoinhibition in the FL. I suggest that the alternative electron flows, especially the PGR5-mediated cyclic electron flow around PSI, contribute significantly to the compensation of electron flow through PSI, and consequently keep the whole electron transport safely.

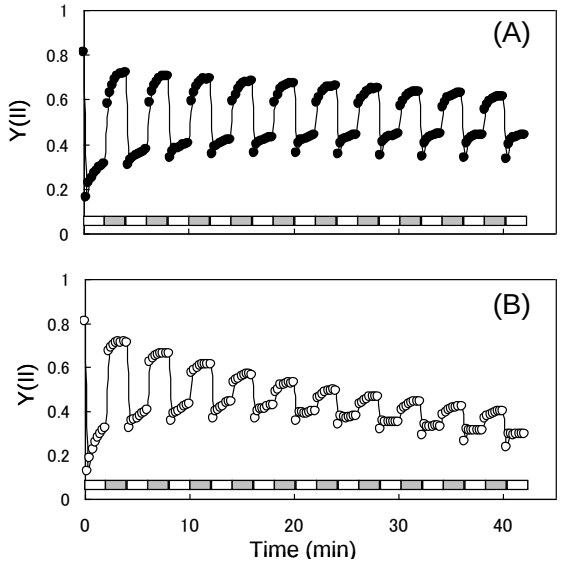

Figure 1. Response of photochemical quantum yield of PSII (Y(II)) of the wild type (A) and *pgr5* (B) plants to the fluctuating light. The light alternating between HL at 240 μmol photons m^{-2} s^{-1} for 2 min (open bars) and LL at 30 μmol photons m^{-2} s^{-1} for 2 min (grey bars) was applied to the leaf after the dark treatment for 30 min. Measurements were made at 20% O_2 and 390 ppm CO_2. The each data point represents the mean (n = 5 to 6).

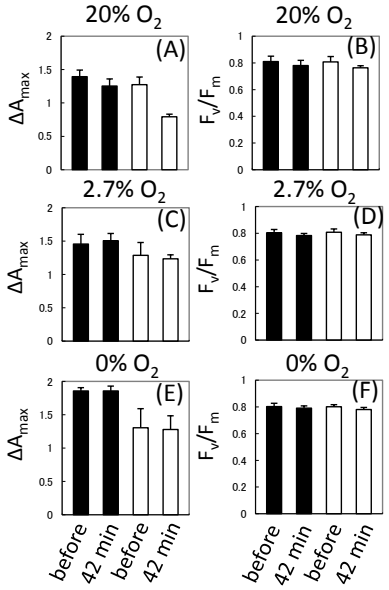

Figure 2. Effects of the fluctuating light treatments on ΔA_{max} and F_v/F_m at 20 (A and B), 2.7 (C and D) and 0% (E and F) O_2 concentrations in wild type (black bar) and *pgr5* (white bar). Following the light treatments for 42 min and dark treatment for 30 min, functions of the PSI and PSII reaction centers were determined as ΔA_{max} (A,C and F) and F_v/F_m (B, D and F). Measurements were made at 390 ppm CO_2. Error bars represent the SD (n = 4 to 8).

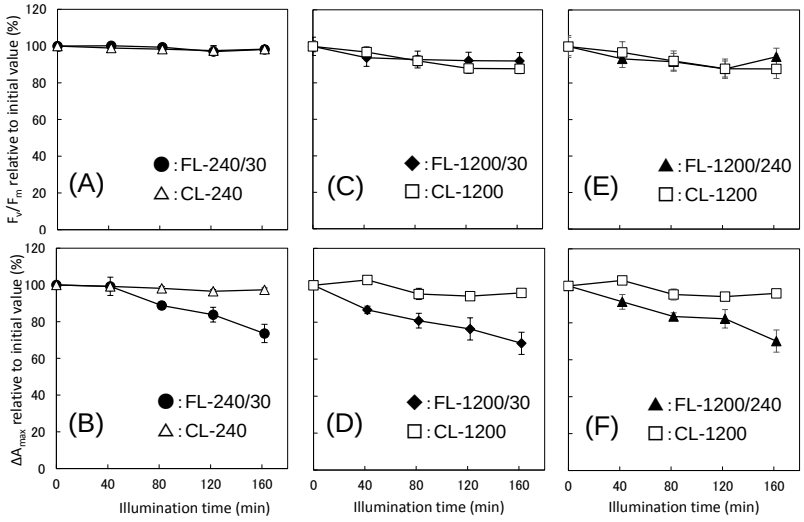

Figure 3. Effects of the fluctuating light (closed symbol) and continuous light (open symbol) on photoinhibition of PSII (A, C and E) and PSI (B, D and F) in the leaves of the col-0 plants in the absence of lincomycin. Three fluctuating light regimes included the FL-240/30 (circle), FL-1200/30 (diamond) and FL-1200/240 (triangle). Two continuous light were CL-240 (triangle) and CL-1200 (square). Following the light treatments for 42, 82, 122 and 162 min, the fractions of the functional PSII and PSI reaction center, F_v/F_m and ΔA_{max}, respectively, were determined after dark adaptation for 30 min. Data were normalized to the initial values measured in the dark before light treatments. Measurements were made in room air. The values represent the mean ±SD (n = 4 - 6).

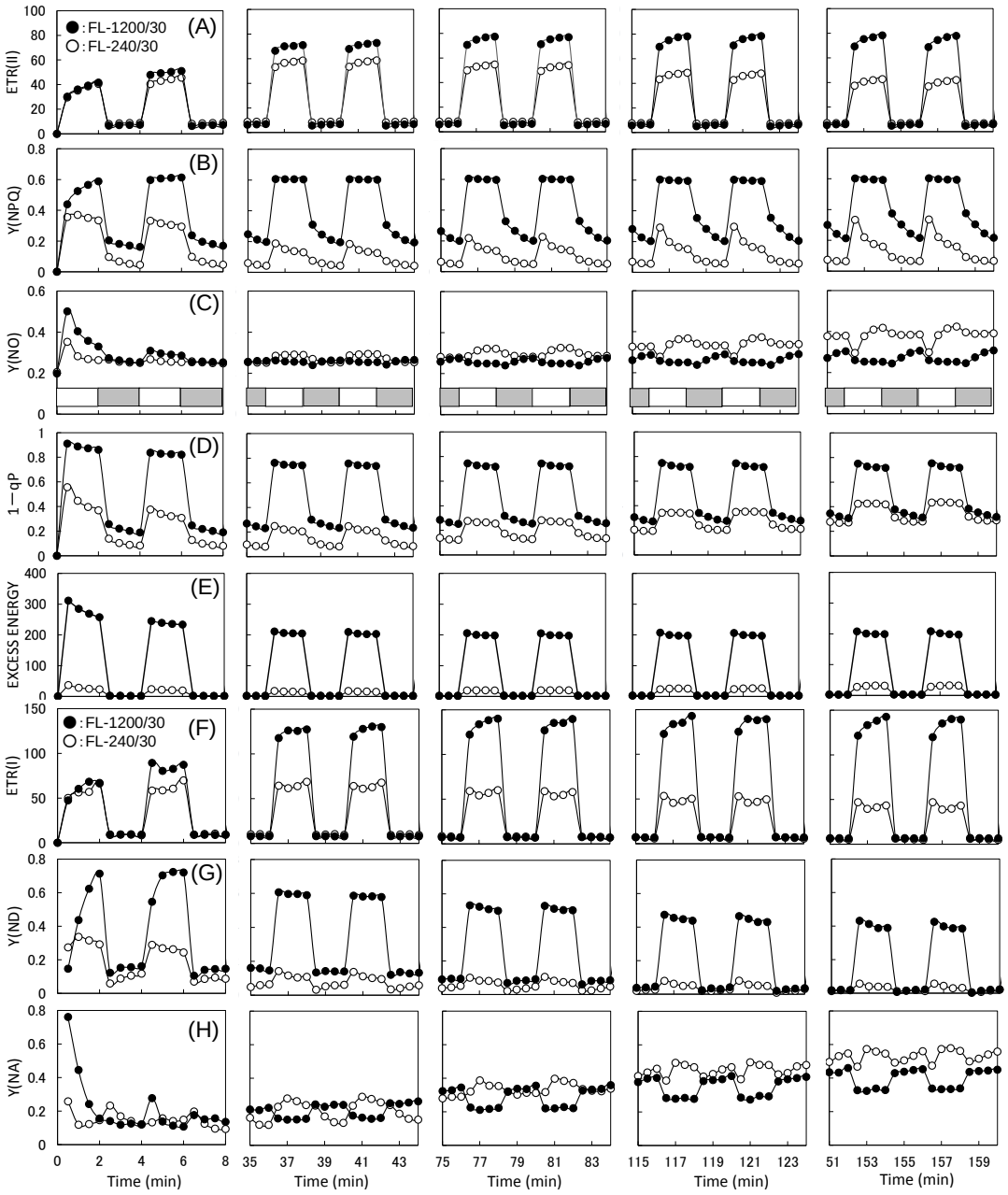

Figure 4. Changes in the PSII and PSI parameters in the FL-1200/30 (closed symbol) and FL-240/30 (open symbol) for 162 min. The light treatments were applied to the leaves after the dark treatment for 30 min. PSII parameters; ETR(II) (A), Y(NPQ) (B), Y(NO) (C), 1－qP (D), Excess energy (E). PSI parameters; ETR(I) (F), Y(ND) (G), Y(NA) (H). Data for 8 min were depicted from five parts during the light treatment for 162 min. White bar; HL phase, grey bar; LL phase. Measurements were made in ventilated room air. The values represent the mean (n = 4 - 6).