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Photosynthetic regulation under fluctuating light in field-grown *Cerasus cerasoides*: A comparison of young and mature leaves

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ABSTRACT

Photosystem I (PSI) is a potential target of photoinhibition under fluctuating light. However, photosynthetic regulation under fluctuating light in field-grown plants is little known. Furthermore, it is unclear how young leaves protect PSI against fluctuating light under natural field conditions. In the present study, we examined chlorophyll fluorescence, P700 redox state and the electrochromic shift signal in the young and mature leaves of field-grown *Cerasus cerasoides* (Rosaceae). Within the first seconds after any increase in light intensity, young leaves showed higher proton gradient (ΔpH) across the thylakoid membranes than the mature leaves, preventing over-reduction of PSI in the young leaves. As a result, PSI was more tolerant to fluctuating light in the young leaves than in the mature leaves. Interestingly, after transition from low to high light, the activity of cyclic electron flow (CEF) in young leaves increased first to a high level and then decreased to a stable value, while this rapid stimulation of CEF was not observed in the mature leaves. Furthermore, the over-reduction of PSI significantly stimulated CEF in the young leaves but not in the mature leaves. Taken together, within the first seconds after any increase in illumination, the stimulation of CEF favors the rapid lumen acidification and optimizes the PSI redox state in the young leaves, protecting PSI against photoinhibition under fluctuating light in field-grown plants.

1. Introduction

Plants use photosynthesis to convert light energy into chemical energy in the forms of ATP and NADPH, which are used for primary metabolism including the Calvin-Benson cycle and photorespiration. In linear electron flow (LEF), electrons derived from water splitting in photosystem II (PSII) are transported to $NADP^+$ via plastoquinone (PQ), the cytochrome b_6/f (Cyt b_6/f) complex, plastocyanin, and PSI. This electron transport is coupled to proton translocation and generates a proton motive force composed of a proton gradient (ΔpH) and a membrane potential (ΔΨ) [1]. Both ΔpH and ΔΨ drive equivalently ATP synthesis via chloroplast ATP synthase [2]. As a result, LEF produces simultaneously ATP and NADPH. The ATP/NADPH production ratio produced by LEF is calculated as 1.29 [3]. By comparison, the ATP/NADPH ratios required by the Calvin-Benson cycle and photorespiration are 1.5 and 1.75, respectively [4]. Therefore, LEF cannot satisfy the ATP/NADPH production ratio required by the primary metabolism, and a flexible mechanism is needed to provided additional ATP [5,6]. In cyclic electron flow (CEF), electrons from either NADPH or ferredoxin are cycled around PSI into the plastoquinone pool, which is coupled with the H^+ translocation from the stroma to the thylakoid lumen, generating ΔpH without producing NADPH. The CEF-dependent ΔpH formation helps additional ATP synthesis to regulate the ATP/NADPH production ratio [6,7], which is essential for sustaining photosynthetic CO_2 assimilation [8].

In addition, the ΔpH produced by CEF contributes to photoprotection for PSI and PSII [9–13]. Firstly, acidification of the thylakoid lumen down-regulates the quinone cycle in the Cyt b_6/f complex to slow down the electron transport rate from PSII to PSI, preventing over-reduction of PSI electron carriers [10,14–17]. This ΔpH-dependent PSI donor-side limitation is called photosynthetic control. In CEF mutants, the ΔpH formation was significant disturbed [18], resulting in over-reduction of PSI electron carriers [13,19]. The resulting reactive oxygen species generated within PSI cause PSI photoinhibition [13,20,21]. Secondly, ΔpH also activates the thermal energy dissipation of absorbed excess light energy in PSII, which can be monitored by measuring non-photochemical quenching (NPQ) of chlorophyll fluorescence [11,22,23]. Compared with the wild type plants of *Arabidopsis thaliana*

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and rice (*Oryza sativa*), *pgr5* mutants show significantly lower ΔpH and NPQ under high light, leading to stronger PSII photoinhibition under high light [9,11,24].

PSI is usually tolerant to constant high light in field-grown plants [25], excluding some shade-establishing plants [26–28]. However, under natural field conditions, plants usually experience extreme fluctuations of light intensity caused by cloud, sunflecks and shading [29]. Despite sunflecks and high light can increase the rate of CO_2 assimilation, the excess light energy increases the risk of photoinhibition [24]. A sudden increase in light intensity can drastically increases the absorbed light. Meanwhile, the electrons transported to PSII to PSI cannot be effectively consumed by the primary metabolism, leading to the accumulation of electrons in PSI electron carriers [30,31]. This over-reduction of PSI induces the generation of reactive oxygen species within PSI, thus causing oxidative damage to PSI [13,32,33]. By comparison, PSII activity is more tolerant to fluctuating light than PSI [13,24], and the photodamaged PSII can be quickly repaired [34]. As a result, PSI is the potential target of photoinhibition under fluctuating light. In opposite to PSII, photodamaged PSI cannot be repaired efficiently and is frequently fatal [10,35], owing to the negative effects of PSI photoinhibition on CO_2 assimilation and photoprotection [36,37]. Therefore, PSI photoinhibition should be alleviated in field-grown plants to enable normal growth under natural fluctuating light.

Fortunately, photosynthetic organisms have evolved several photoprotective mechanisms and alternative electron flows to protect PSI under fluctuating light. In nonflowering plants from cyanobacteria up to gymnosperms, photo-reduction of O_2 mediated by flavodiiron proteins (FDPs) is operational within the first seconds after any increase in light intensity [30,38,39]. FDPs accept electrons from PSI to O_2 and consume a significant fraction of the extra reducing power, thus avoiding over-reduction of PSI electron carriers [30,31]. Therefore, FDPs are the primary player enabling them growth under fluctuating light. However, FDPs are lost during evolution of angiosperms, and CEF has been regarded as the main player for PSI photoprotection under fluctuating light in them [10,13,19]. Upon a sudden increase in light intensity, the stimulation of CEF could favor the rapid formation of ΔpH [40], protecting PSI against photoinhibition at the donor and acceptor sides [13]. The *pgr5* mutant of *A. thaliana* died at the seedling stage when grown under fluctuating light [10]. When *pgr5* plants were first grown under constant light until development of the mature rosettes, fluctuating light caused much stronger PSI photoinhibition in *pgr5* plants than in wild type plants [10,13,24]. In these previous studies, *A. thaliana* and rice plants grown under constant light are usually used. However, the photosynthetic regulation under fluctuating light in field-grown plants is little known.

In field-grown plants, the survival of young leaves under natural fluctuating light is critical for plant growth. However, the photosynthetic regulation under fluctuating light in young leaves has not yet been clarified. Young leaves have lower photosynthetic capacity and photorespiration than mature leaves. Photorespiration is not only necessary for the regeneration of RuBP [41], but also an important electron sink to dissipate excess excitation energy [42–45]. Accordingly, young leaves should deal with more excess excitation energy under high light [46,47]. The excess excitation energy can induce the production of reactive oxygen species (ROS) within thylakoid membranes or in the chloroplast stroma, thus increasing the risk of PSI photoinhibition [20,26–28]. During steady state photosynthesis under constant high light, young leaves usually showed higher NPQ and P700 oxidation ratio to protect PSI and PSII against photoinhibition [46,48]. However, it is unclear how young leaves protect PSI against photoinhibition under fluctuating light in field-grown plants, which complicates our understanding of photosynthetic regulation under natural field conditions.

At present, many studies have investigated the photosynthetic regulation under fluctuating light in the model plants such as *A. thaliana* and rice. However, little is known about the photosynthetic regulation under fluctuating light in field-grown wild plants. In order to address this issue, we measured chlorophyll fluorescence, P700 redox state and the electrochromic shift signal under fluctuating light in the young and mature leaves of field-grown *Cerasus cerasoides* (Rosaceae). The aims of this study are: (1) to examine whether fluctuating light causes PSI photoinhibition in field-grown *C. cerasoides*; (2) to assess how young leaves of field-grown *C. cerasoides* protect PSI under fluctuating light.

2. Materials and methods

2.1. Plant materials and growth conditions

We used a deciduous angiosperm *Cerasus cerasoides* (D. Don) Sok. (Rosaceae) for experiments. *C. cerasoides* is native to Southern Tibet and Northwest Yunnan in China and has been cultivated for gardening. In this present study, *C. cerasoides* grown in open fields at the Kunming Botanical Garden, Yunnan, China (102°44′31″E, 25°08′24″N, 1950 m of elevation) were chosen. In order to compare photosynthetic characterizes in young and mature leaves, mature leaves flushed two months ago and young leaves flushed within two weeks were chosen for photosynthetic measurements. The young leaves showed significant lower leaf area and chlorophyll content than the mature leaves (Fig. S1).

2.2. P700 and chlorophyll fluorescence measurements

We used a Dual PAM-100 (Heinz Walz, Effeltrich, Germany) to simultaneously record PSI and PSII parameters at 25 °C [49]. After dark adaptation for 30 min, a saturating pulse was applied to measure the maximum fluorescence and the maximum change in P700, and then leaves were illuminated at a saturating light of 1809 μmol photons $m^{-2} s^{-1}$ for 5 min to measure PSI and PSII parameters during photosynthetic induction. Subsequently, leaves were illuminated at this high light for 10 min to activate photosynthetic electron sinks. Afterwards, leaves were illuminated at 59 μmol photons $m^{-2} s^{-1}$ for 5 min, then exposed to fluctuating light alternating between 1809 and 59 μmol photons $m^{-2} s^{-1}$. During this fluctuating light condition, PSI and PSII parameters were recorded.

The redox kinetics of P700 upon dark-to-light transition was measured during illumination at 1809 μmol photons $m^{-2} s^{-1}$. Before this measurement, leaves were dark-adapted for 30 min. The $P700^+$ signals (P) could vary between a minimum (P700 fully reduced) and a maximum level (P700 fully oxidized). The maximum, P_m, was determined by applying a saturation pulse (300 ms and 10,000 μmol photons $m^{-2} s^{-1}$) after pre-illumination with far-red light for 10 s. The P_m' was similarly obtained, except that actinic light was used instead of far-red light. Calculations of PSI parameters included the quantum yield of PSI photochemistry, $Y(I) = (P_m' - P) / P_m$; the quantum yield of PSI non-photochemical energy dissipation due to donor side limitation, $Y(ND) = P / P_m$; the quantum yield of non-photochemical energy dissipation due to acceptor side limitation, $Y(NA) = (P_m - P_m') / P_m$. The electron transport rate through PSI (ETRI) was calculated as ETRI = PPFD × Y(I) × 0.84 × 0.5.

PSII parameters were calculated as follows [50]: $Y(II) = (F_m' - F_s) / F_m'$ [51], $NPQ = (F_m - F_m') / F_m'$. F_m and F_m' represent the maximum fluorescence after dark and light adaptation, respectively. F_s is the light-adapted steady state fluorescence. Y(II) represents the quantum yield of PSII photochemistry, NPQ indicates the non-photochemical quenching in PSII. The electron transport rate through PSII (ETRII) was calculated as ETRII = PPFD × Y(II) × 0.84 × 0.5.

2.3. Electrochromic shift (ECS) analysis

The ECS signal was monitored as the change in absorbance at 515 nm, using a Dual PAM-100 equipped with a P515/535 emitter-detector module (Heinz Walz) [52]. After dark-adaptation for 30 min, the 515-nm absorbance change induced by a single turnover flash (ECS_{ST}) was measured. Subsequently, the actinic light (1809 μmol photons $m^{-2} s^{-1}$) was turned on, and ECS dark interval relaxation kinetics were recorded after transition from dark to the high light for 10 s and 5 min. Afterward, the actinic light was changed to 59 μmol photons $m^{-2} s^{-1}$ for 5 min, and then the ECS signal was measured after transition to 1809 μmol photons $m^{-2} s^{-1}$ for 10 s. Subsequently, leaves were repeatedly acclimated to 59 μmol photons $m^{-2} s^{-1}$ for 3 min, and then the ECS signal was measured after transition to 1809 μmol photons $m^{-2} s^{-1}$ for 120 s. We analyzed ECS dark interval relaxation kinetics ($DIRK_{ECS}$) as described by Kramer group [53–55]. The slow relaxation of the ECS signal was measured to calculate the proton gradient (ΔpH) [56]. All ΔpH levels were normalized against the magnitude of ECS_{ST} [21,33,57,58]. This normalization accounted for variations in leaf thickness and chloroplast density among the leaf samples.

2.4. Photoinhibitory treatments

In the present study, light from a 635 nm light-emitting diode (LED) equipped in Dual-PAM-100 was used as actinic light for photoinhibitory treatments. After dark adaptation for 30 min, the initial values of F P_m were measured. Subsequently, leaves were exposed to fluctuating light alternating between 59 and 1809 μmol photons $m^{-2} s^{-1}$ every 20 s for 20 min. Afterward, leaves were dark-adapted for 20 min and the residual values of P_m were measured.

2.5. Statistical analysis

The results were displayed as mean values of at least five independent measurements. One-Way ANOVA test was used at $\alpha = 0.05$ significance level to determine whether significant differences existed between different treatments.

3. Results

3.1. P700 redox kinetics upon abrupt illumination of dark-adapted leaves

The young leaves showed much lower P_m than the mature leaves (Fig. 1A), while F_v/F_m differed slightly (Fig. 1A). In order to examine the fast regulation of PSI redox state in the mature and young leaves of *C. cerasoides* upon dark-to-light transition, we determined the P700 redox kinetics upon the illumination of dark-adapted leaves to actinic light (1809 μmol photons $m^{-2} s^{-1}$) (Fig. 1B). In the young leaves, a rapid re-oxidation of P700 was observed in the young leaves (Fig. 1C). However, this rapid re-oxidation of P700 was completely missing in the mature leaves (Fig. 1C), similar to the P700 redox kinetics in *A. thaliana* [33,38].

3.2. Changes in ΔpH, PSI and PSII parameters after onset of light

Next, we examined the changes in ΔpH, PSI and PSII parameters after transition from dark to the high light of 1809 μmol photons $m^{-2} s^{-1}$. Interestingly, the young leaves built up a sufficient ΔpH in 30 s (Fig. 2A). By comparison, the mature leaves could not generate a sufficient ΔpH for photosynthetic control within the first 30 s after transition from dark to light (Fig. 2A). Concomitantly, the young leaves showed much higher Y(ND) (PSI donor side limitation) and lower Y(NA) (PSI acceptor side limitation) than the mature leaves (Fig. 2B and C), indicating that PSI was highly oxidized in the young leaves but was over-reduced in the mature leaves. The large differences in Y(ND) and Y(NA) between the mature and young leaves were only present in the first minutes after the light was switched on. After photosynthetic induction for 5 min, the value of ΔpH significantly increased in the mature leaves, which was accompanied with a high level of Y(ND) and a low value of Y(NA) (Fig. 2B and C). These results

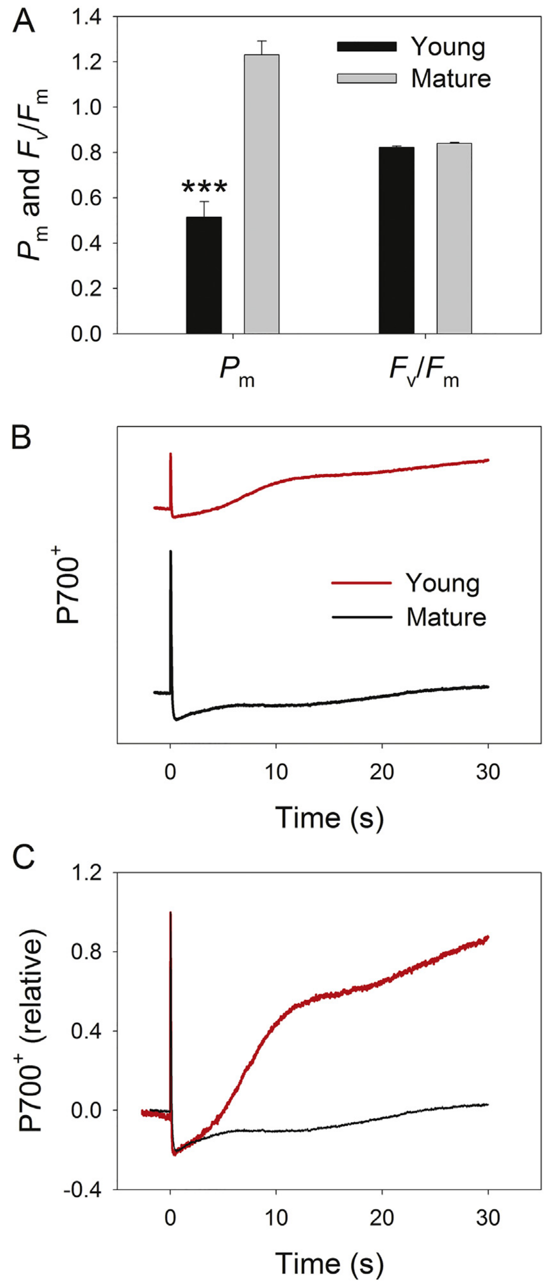

Fig. 1. (A) The maximum quantum yield of PSII and maximum photo-oxidizable P700 in the young and mature leaves. (B) Redox kinetics of P700 upon dark-to-light transition in the young and mature leaves. (C) Redox kinetics of P700 upon dark-to-light transition in the young and mature leaves (relative to the maximum P700 signal). The kinetics of redox changes were measured in vivo upon exposure of dark-adapted sample to actinic light (1809 μmol photons $m^{-2} s^{-1}$).

indicated that in the field-grown angiosperm *C. cerasoides*, the PSI redox state was significantly correlated to the ΔpH formation. The non-photochemical quenching (NPQ) in PSII was gradually induced during photosynthetic induction in both young and mature leaves (Fig. 2D). Furthermore, young leaves showed stronger NPQ than mature ones (Fig. 2D).

After the high light was switched on, ETRI increased to a high level within the first 30 s in the young leaves, and then declined to the minimal value at 60 s (Fig. 3A). Subsequently, ETRI gradually increased to the stable value (Fig. 3A). By comparison, in the mature leaves, ETRI rapidly increased within the first 60 s and then slightly increased during

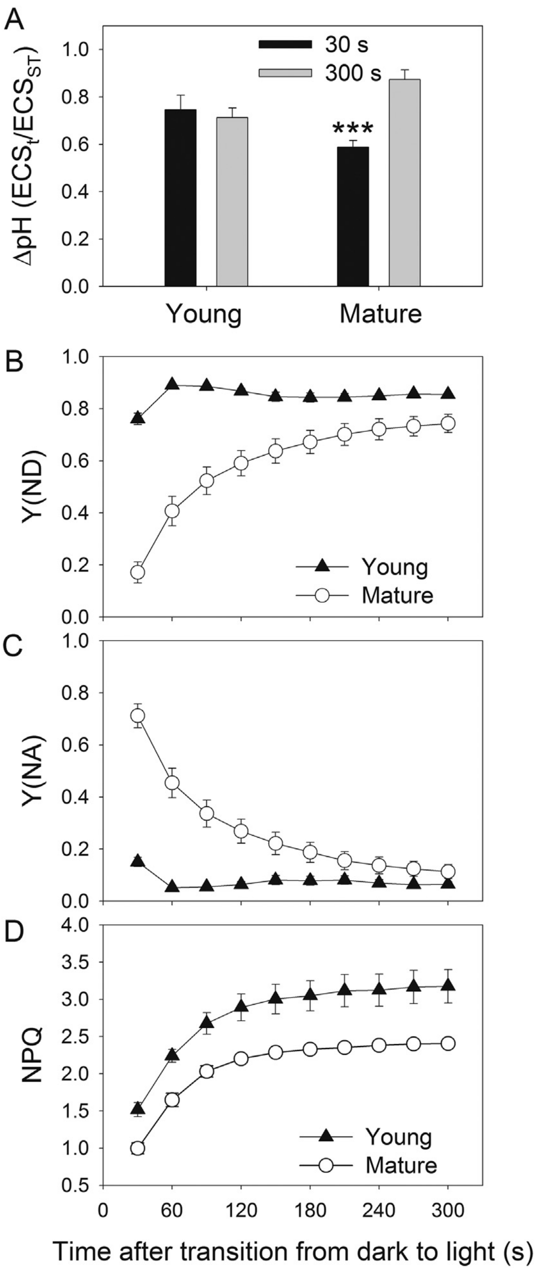

Fig. 2. (A) Changes in proton gradient (ΔpH) across the thylakoid membranes after transition from dark to actinic light (1809 μmol photons $m^{-2} s^{-1}$). Asterisk indicates significant difference between 30 s and 300 s. (B–D) Changes in Y(ND), Y(NA) and NPQ after transition from dark to actinic light (1809 μmol photons $m^{-2} s^{-1}$). Y(ND), the PSI donor side limitation; Y(NA), the PSI acceptor side limitation; NPQ, non-photochemical quenching in PSII. Values are means ± SE (n = 5).

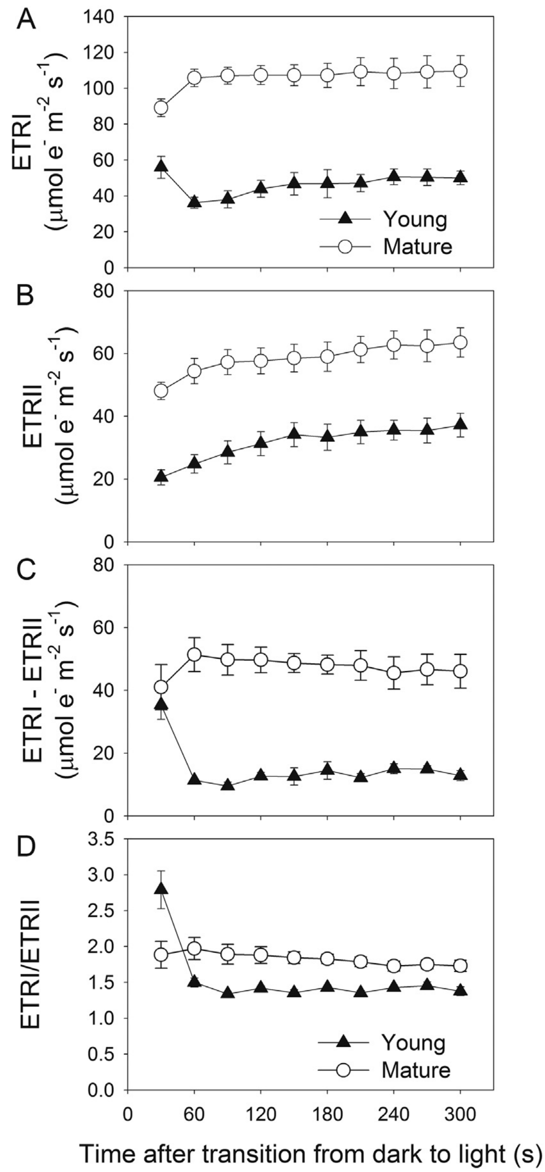

Fig. 3. Changes in ETRI (A), ETRII (B), ETRI–ETRII (C) and ETRI/ETRII (D) after transition from dark to actinic light (1809 μmol photons $m^{-2} s^{-1}$). ETRI, photosynthetic electron transport rate through PSI; ETRII, photosynthetic electron transport rate through PSII. Values are means ± SE (n = 5).

further illumination (Fig. 3A). ETRII gradually increased over time in both young and mature leaves, and the mature leaves showed much higher ETRII than the young leaves (Fig. 3B). Interestingly, in the young leaves, the value of ETRI–ETRII first increased in a high level after transition from dark to light for 30 s and then rapidly decreased (Fig. 3C). There results indicated the elevated CEF activation within the first 30 s in the young leaves. In contrast, this stimulation of CEF was not observed in the mature leaves (Fig. 3C). After illumination at the high light for 5 min, the mature leaves showed much higher CEF than the young leaves (Fig. 3C). The kinetics of ETRI/ETRII upon dark-to-light transition significantly differed between the young and mature leaves. In the young leaves, ETRI/ETRII rapidly increased to 2.8 after transition from dark to light for 30 s, and then rapidly decreased to the stable value approximately being 1.4 (Fig. 3D). In the mature leaves, ETRI/ETRII value was maintained at 1.8 over time (Fig. 3D). These results indicated that upon dark-to-light transition, young and mature showed significantly different kinetics of CEF activation.

3.3. Changes in ΔpH, PSI and PSII parameters under fluctuating light

We next examined the change in ΔpH after transition from 59 (low light) to 1809 μmol photons $m^{-2} s^{-1}$ (high light). Both young and mature leaves could not build up a sufficient ΔpH for photosynthetic control within the first 10 s after transition from low to high light, especially in the mature leaves (Fig. 4A). Consistently, the young leaves showed much higher Y(ND) than the mature leaves within the first 10 s after transition from low to high light (Fig. 4B). As a result, at this time, the mature leaves showed much higher Y(NA) than the young leaves (Fig. 4C), indicating the severe over-reduction of PSI electron carriers in the mature leaves. After transition from low to high light for 10 s, NPQ

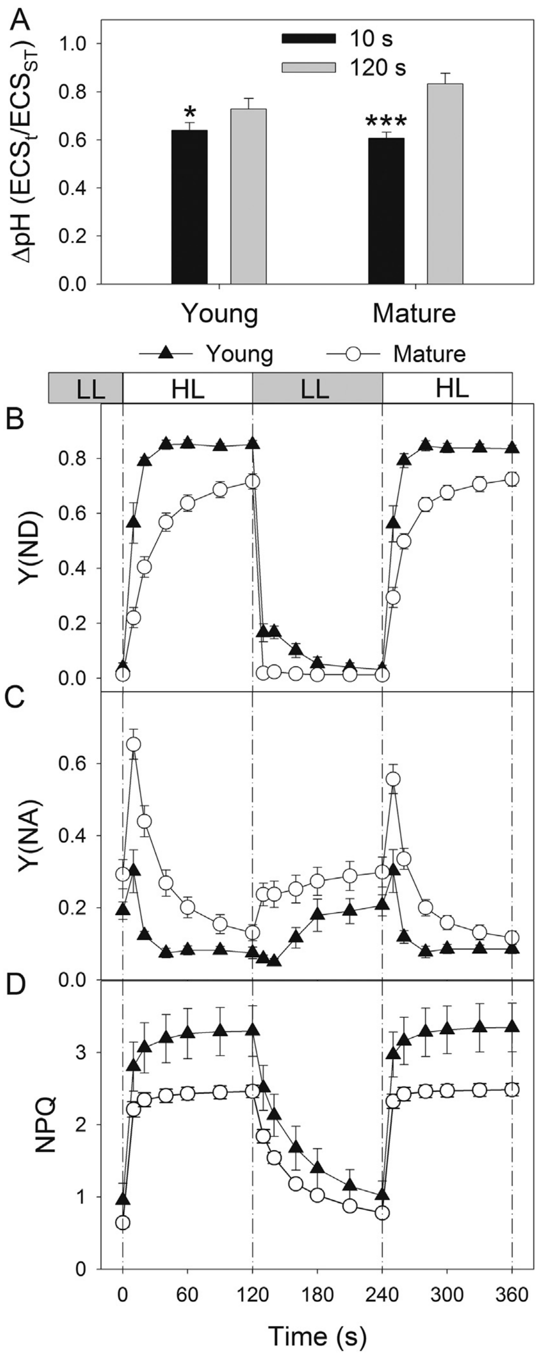

Fig. 4. (A) Changes in proton gradient (ΔpH) across the thylakoid membranes after transition from 59 μmol photons $m^{-2} s^{-1}$ (low light) to 1809 μmol photons $m^{-2} s^{-1}$ (high light). The values of ΔpH were measured after transition from 59 to 1809 μmol photons $m^{-2} s^{-1}$ for 10 s and 120 s. Asterisk indicates significant difference between 10 s and 120 s. (B–D) Changes in Y(ND), Y(NA) and NPQ in fluctuating light alternating between 59 and 1809 μmol photons $m^{-2} s^{-1}$. Values are means ± SE (n = 5).

was rapidly induced in both the young and mature leaves (Fig. 4D). These results implied the different responses of PSI redox state and NPQ upon transition from low to high light. Owing to the severe over-reduction of PSI, the mature leaves showed significantly stronger PSI photoinhibition than the young leaves (as indicated by the P_m values) (Fig. 5).

After transition from low to high light for 10 s, ETRI in the young leaves first increased to a high level, then rapidly decreased a stable value (Fig. 6A), while in the mature leaves it rapidly increased to a

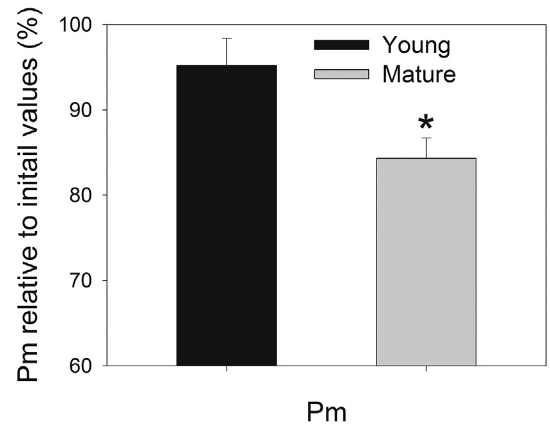

Fig. 5. Effect of fluctuating light on PSI photoinhibition. Dark-adapted leaves were exposed to fluctuating light alternative between 59 and 1809 μmol photons $m^{-2} s^{-1}$ for 20 min. After the fluctuating light treatment, the leaves were incubated in the dark for 20 min, and then Pm values were measured. Their relative values are shown against the values before the treatment. Asterisk indicates significant difference between the young and mature leaves. Values are means ± SE (n = 5).

stable value (Fig. 6A). Meanwhile, ETRII rapidly increased to the stable values in both the young and mature leaves (Fig. 6B). The maximum value of ETRII in the young leaves was much lower than that in the mature leaves (Fig. 6B). Interestingly, ETRI – ETRII in the young leaves first increased to a high level and then rapidly decreased to the stable value (Fig. 6C). This rapid stimulation of CEF was not observed in the mature leaves. Therefore, the young and mature leaves showed different kinetics of CEF after transition from low to high light. Furthermore, we found that, upon a sudden increase in light intensity, the ETRI – ETRII was positively correlated to Y(NA) in the young leaves (Fig. 7A). The highest activation of CEF was accompanied with the highest value of Y(NA), suggesting that the over-reduction of Y(NA) triggered the activation of CEF in the young leaves. In contrast, this significant correlation between Y(NA) and CEF was not observed in the mature leaves (Fig. 7B).

4. Discussion

Plants usually experience fluctuations of light under natural field conditions [29]. A sudden increase in light intensity can immediately affect the light absorption and electron transfer from PSII. However, the regulation of primary metabolism has slower kinetics. As a result, the ATP and NADPH produced by LEF cannot be consumed immediately by carbon assimilation, generating a dangerous imbalance between production of excited states and consumption of the reducing power [30]. The resulting accumulated excitation energy leads to the generation of reactive oxygen species within PSI, causing selective photoinhibition of PSI [13,30,31,39]. Once PSI photoinhibition occurs, the total photosynthetic electron flow and CO_2 assimilation are depressed [36,37,59,60], restricting plant growth [30,31]. Therefore, all oxygenic photosynthetic organisms must have photoprotective mechanisms and alternative electron flows to protect PSI against photoinhibition under fluctuating light [61–63]. In nonflowering plants, FDP mutants showed severe PSI photoinhibition and impaired plant growth when exposed to fluctuating light [30,31,39]. The FDP-mediated photoreduction of O_2 functions as an electron sink downstream of photosystem I for the first seconds after any increase in light intensity [30,38]. Therefore, FDPs is seminal in PSI photoprotection under fluctuating light in cyanobacteria up to gymnosperms [64]. However, FDPs were lost in angiosperms during evolution, and CEF around PSI is crucial for PSI photoprotection under fluctuating light in angiosperms [10,13,19,38]. Many studies have examined the role of CEF in photoprotection under fluctuating

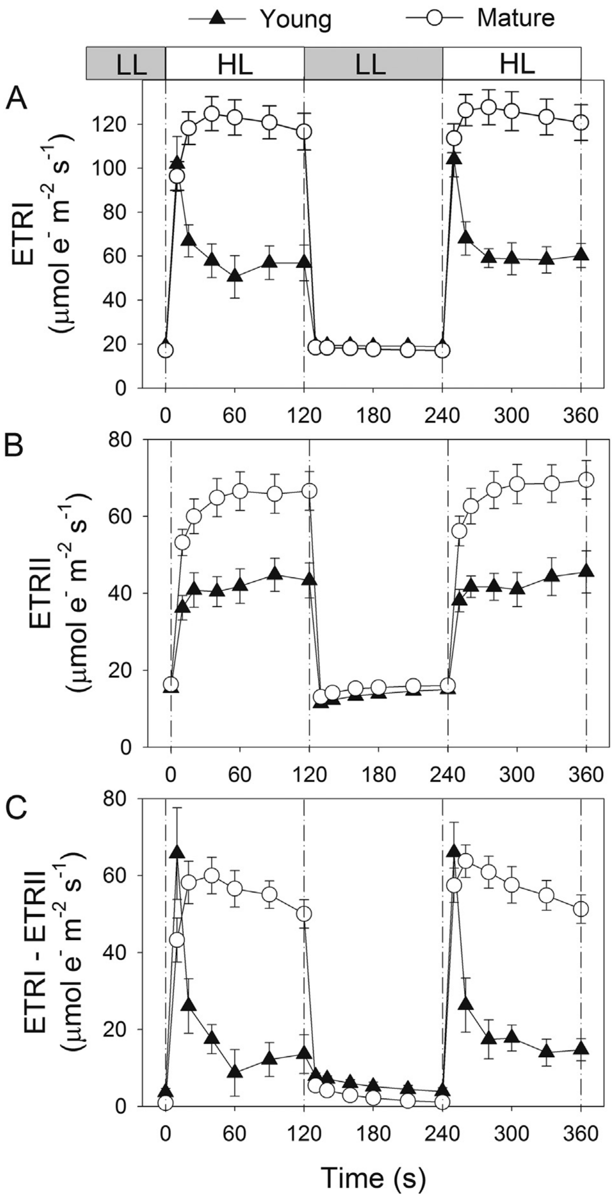

Fig. 6. Changes in ETRI (A), ETRII (B) and ETRI–ETRII (C) in fluctuating light alternating between 59 and 1809 µmol photons $m^{-2} s^{-1}$. Values are means ± SE (n = 5).

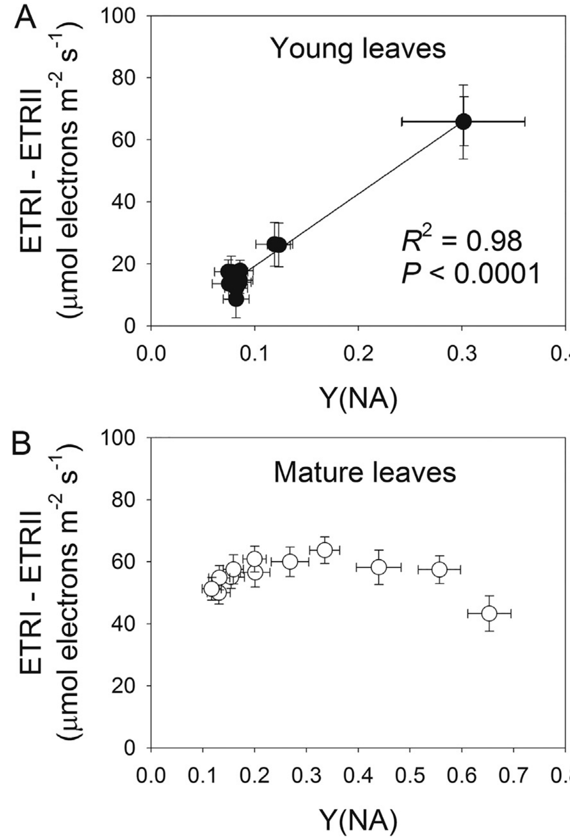

Fig. 7. The relationships between Y(NA) and ETRI–ETRII after transition from 59 to 1809 µmol photons $m^{-2} s^{-1}$. All data were used from Figs. 4 and 6.

light for *A. thaliana* and rice grown under constant light. However, the photosynthetic regulation under fluctuating light in field-grown angiosperms is little known. Furthermore, these previous studies focused on the photoprotective mechanisms in mature leaves of angiosperms. It is unclear how young leaves protect PSI against fluctuating light under natural field conditions.

In this article, we found that in the field-grown angiosperm *C. cerasoides*, the P700 redox kinetics upon dark-to-light transition differed significantly between the young and mature leaves (Fig. 1C). The young leaves showed rapid re-oxidation of P700 in 10 s. By comparison, this fast re-oxidation of P700 was not observed in the mature leaves, similar to the phenomenon in *A. thaliana* [38]. In angiosperms, lumen acidification is well known as a major component for regulation of PSI redox state [16,21,63]. Within the first 30 s after transition from dark to light, the mature leaves could not build up a sufficient ΔpH (Fig. 2A), resulting in the over-reduction of PSI (Fig. 2C). Meanwhile, the young leaves were capable of generating a sufficient ΔpH (Fig. 2A), preventing over-reduction of PSI (Fig. 2C). Furthermore, in the young leaves, CEF was highly stimulated within the first 30 s after transition from low to high light (Fig. 3C and D). As we known, CEF triggers proton translocation and generates a ΔpH across the thylakoid membranes, which initiates down-regulation of plastoquiol oxidation at the Cyt b_6/f complex, controlling electron flow from PSII to PSI. As a result, in the young leaves the elevated CEF activation helped the rapid oxidation of P700 during dark-to-light transition. Furthermore, the decreased PSII activity, as well as suppressed electron flow from PSII, can lead to the normal oxidation of P700 in the *pgr5* mutant of *A. thaliana* [12,17]. The lower ETRII values during photosynthetic induction pointed out the lower PSII activity in the young leaves (Fig. 3B). Consequently, the lower electron pressure from PSII can affect the P700 redox kinetics upon dark-to-light transition in the young leaves. Therefore, in the young leaves of field-grown *C. cerasoides*, the lower ETRII and stimulation of CEF cooperated to regulate the fast re-oxidation of P700 upon dark-to-light transition.

Upon a sudden transition from low to high light, angiosperms usually cannot build up a sufficient ΔpH to activate photosynthetic control at the Cyt b_6/f complex [32,33,40,58], making PSI highly reduced. The resulting ROS cause PSI photoinhibition [13]. Similarly, in the mature leaves of field-grown *C. cerasoides*, the low ΔpH upon a sudden increase in light led to over-reduction of PSI (Fig. 4A and C) and thus PSI photoinhibition (Fig. 5). In contrast, PSI was more tolerant to fluctuating light in the young leaves (Fig. 5). Within the first 10 s after the increase in light intensity, the young leaves showed elevated activation of CEF around PSI (Fig. 6C), which increased the total photosynthetic electron flow that supports proton translocation into the lumen, favoring the rapid formation of ΔpH. As a result, the young leaves generated a relatively high level of ΔpH, although it was slightly lower than the optimal value (Fig. 4A). Consequently, the electron flow from PSII to PSI could be effectively regulated via the ΔpH-dependent photosynthetic control at the Cyt b_6/f complex. In addition, young leaves showed significantly lower ETRII upon transition from low to high light (Fig. 6B). The lower PSII activity decreased excess excitation energy in PSI [12,66]. Taken together, in the young leaves the co-operation of ETRII and CEF alleviated over-reduction of PSI upon a sudden transition from low to high light.

When compared with the mature leaves, an interesting aspect of young leaves lies in the observation that the level of CEF activation under fluctuating light depended on the reduction state of PSI (Fig. 7A), similar to the findings in *A. thaliana* [40]. Specifically, upon a sudden transition from low to high light, the over-reduction of P700 acted as a signal to activate CEF, which in turn contributed to ΔpH formation and alleviates over-reduction of PSI electron carriers. This elevated activation of CEF was different from the activation of CEF by hydrogen peroxide [67], in which H_2O_2-induced increase in CEF appeared with a half time of about 20 min. After acclimated to high light for 2 min, the young leaves generated a sufficient ΔpH (Fig. 4A), making PSI highly oxidized (Fig. 4B). Under such condition, the CEF activation decreased to the stable level (Fig. 6C). This decrease in CEF activation was also essential for optimizing the trade-off between photoprotection and light use efficiency. If the CEF was highly activated all the time in the young leaves, the lumen of thylakoid would become more acidic. As reported in previous studies, over-acidification of thylakoid lumen not only depresses LEF and CO_2 assimilation but also results in the photoinhibition of PSII [13,57,68]. Therefore, in the young leaves the change in CEF after transition from low to high light plays an important role in optimizing the trade-off between photoprotection and CO_2 assimilation via regulation of ΔpH.

An additional beneficiary effect of the transient CEF stimulation is a result of its contribution to the ATP synthesis. Upon a sudden increase in light intensity, the enhanced rates of Rubisco carboxylation and oxygenation require a higher ATP/NADPH being approximately 1.6 [4]. However, the ATP/NADPH ratio produced by LEF is calculated as 1.29 [3], based on the structure of chloroplast ATP synthase [69]. As a result, LEF cannot satisfy the ATP/NADPH ratio required by primary metabolism. In contrast to LEF, CET generates ΔpH without producing NADPH. The CEF-dependent ΔpH formation contributes to additional ATP synthesis to satisfy the ATP/NADPH production ratio required by CO_2 assimilation and photorespiration [6,7,70,71]. This adjustment of the ATP/NADPH production ratio provides sufficient acceptors, Fd and $NADP^+$, for LEF, sustaining electron sinks downstream of PSI and alleviating over-reduction of PSI electron carriers [13]. Therefore, the transient CEF stimulation in the young leaves likely protects PSI under fluctuating light via acceptor-side regulation.

In conclusion, we found that in the field-grown angiosperm *Cerasus cerasoides*, young leaves were more tolerate to PSI photoinhibition under fluctuating light than mature leaves. In the young leaves, despite the lower photosynthetic capacity and photorespiration increase the risk of PSII photoinhibition, the lower PSII activity decreased electron pressure from PSII to PSI. Furthermore, upon a sudden increase in light intensity, a high reduction state of PSI induced a transient elevated CEF activation in the young leaves. The resulting rapid ΔpH formation alleviated over-reduction of PSI at donor and acceptor sides. Therefore, the cooperation of PSII activity and CEF protects PSI under fluctuating light in the young leaves. By comparison, in the mature leaves PSI was highly reduced after any increase in light intensity, leading to the production of reactive oxygen species within PSI, causing PSI photoinhibition under fluctuating light. These results highlighted the different responses of PSI to fluctuating light between young and mature leaves. Because the mechanisms of photosynthetic regulation under fluctuating light can be affected by the leaf developmental stages, molecular breeding of plants with higher photosynthesis should take into consideration the PSI photoprotection at different developmental stages.

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Transparency document

The Transparency document associated with this article can be found, in online version.

Declaration of competing interest

The authors declare no conflict of interest.

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