Postprint: Adaptation of Pinellia ternata Photosystem to Diurnal Variations in Light and Temperature

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Date: 2020-08-03T00:00:00+00:00

Abstract

To investigate the adaptive mechanism of the photosystem of Pinellia ternata to diurnal variations in light intensity and temperature, this study simulated environmental conditions of low temperature (10–18 °C), moderate temperature (20–28 °C), and high temperature (28–38 °C) under the same diurnal variation of light intensity (0–1 600 mol · m-2 · s-1) for three consecutive days, while simultaneously measuring chlorophyll fluorescence parameters of photosystem II (PSII) and photosystem I (PSI). The adaptation of the photosynthetic system of P. ternata to diurnal variations in light intensity and temperature was studied through changes in the photosynthetic activity and electron transport capacity of PSII and PSI. The results showed that: (1) PSII minimum fluorescence (Fo') and PSII reaction center excitation energy capture efficiency (Fv' /Fm') decreased with increasing light intensity; the increase in light intensity was the main cause of reduced photosystem activity, and low temperature further contributed to the decrease in photosystem activity; (2) Increases in light intensity and temperature enhanced PSI acceptor-side non-photochemical energy dissipation efficiency [Y(ND)] while reducing PSI donor-side non-photochemical energy dissipation efficiency [Y(NA)]; increased light intensity did not cause substantial excitation pressure on the donor side but led to the accumulation of significant excitation pressure on the acceptor side, whereas lower temperatures decreased acceptor-side activity, resulting in higher excitation pressure accumulation on the donor side; (3) Photoinhibition and photodamage caused by high light (light intensity >900 mol · m-2 · s-1) led to reductions in the actual photochemical quantum yield of PSII [Y(II)] and the actual photochemical quantum yield of PSI [Y(I)], with low temperature further exacerbating the decline in Y(II) and Y(I); (4) The increase in electron transport rate of PSI [ETR(I)] under high light initiated cyclic electron flow (CEF), and the elevated CEF stabilized the electron transport rate of PSII [ETR(II)] under high temperature while protecting PSII

from light-induced damage; (5) Although the non-photochemical quenching coefficient (NPQ) increased with light intensity during the 3-day treatment, the lower NPQ under low temperature compared with high temperature resulted in the quantum yield of non-regulated energy dissipation of PSII [Y(NO)] remaining at the highest level, manifesting obvious photoinhibition. These results demonstrate that low temperature reduces the adaptability of P. ternata to high-light environments, whereas high temperature enhances the adaptability of the photoreaction system to high light by strengthening NPQ and accelerating CEF generation to reduce photoinhibition, thereby accelerating electron transport in the light reactions and maintaining the stability of the photoreaction system. Therefore, low temperature stress exacerbates damage to the photosystem of P. ternata, and appropriate temperature elevation can enhance the adaptability of the photoreaction system to high light.

Full Text

Preamble

Adaptation of Pinellia ternata Photoreaction System to Diurnal Changes of Light and Temperature

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Abstract

To investigate the adaptation mechanisms of *Pinellia ternata* photosystems to diurnal variations in light intensity and temperature, this study simulated three consecutive days of low temperature (10–18 °C), moderate temperature (20–28 °C), and high temperature (28–38 °C) conditions under identical diurnal light intensity patterns (0–1,600 μmol · m^{-2} · s^{-1}). Chlorophyll fluorescence parameters of Photosystem II (PSII) and Photosystem I (PSI) were measured to examine how photosynthetic activity and electron transport capacity of PSII and PSI respond to these diurnal changes. The results demonstrated: (1) Minimal fluorescence of PSII (Fo') and excitation energy capture efficiency of PSII reaction centers (Fv' /Fm') decreased with increasing light intensity, with light intensity being the primary factor reducing photosystem activity, while low temperature further exacerbated this reduction; (2) Increasing light intensity and temperature elevated PSI acceptor-side heat dissipation efficiency [Y(ND)]

while reducing donor-side heat dissipation efficiency [Y(NA)], indicating that light intensity increased excitation pressure at the acceptor side without causing substantial pressure at the donor side, whereas low temperature reduced acceptor-side activity and caused higher excitation pressure at the donor side; (3) High light (>900 μmol · m^{-2} · s^{-1}) induced photoinhibition and photodamage in *P. ternata*, reducing actual photochemical quantum yields of PSII [Y(II)] and PSI [Y(I)], with low temperature further aggravating these reductions; (4) Increased electron transport rate of PSI [ETR(I)] under high light initiated cyclic electron flow (CEF), and higher CEF stabilized PSII electron transport rate [ETR(II)] at high temperatures while protecting PSII from light damage; (5) Although non-photochemical quenching coefficient (NPQ) increased with light intensity throughout the three-day treatment, low temperature resulted in consistently lower NPQ, leaving the quantum yield of non-regulated energy dissipation in PSII [Y(NO)] at the highest level and demonstrating pronounced photoinhibition compared to high temperature. These findings indicate that low temperature reduces *P. ternata*' s adaptability to high-light environments, whereas high temperature enhances adaptation by increasing NPQ and accelerating CEF, thereby accelerating electron transport and maintaining stability of the photoreaction system while reducing photoinhibition. Consequently, low temperature stress aggravates damage to the *P. ternata* photoreaction system, while appropriate temperature elevation can enhance the adaptability of the photoreaction system to high light.

Keywords: *Pinellia ternata*, light, temperature, photoreaction system, chlorophyll fluorescence parameters

Introduction

Pinellia ternata (Thunb.) Breit. is a medicinal plant in the Araceae family whose dried tubers are widely used in traditional medicine, exhibiting broad market demand and application prospects with high research value (Gao et al., 2019). Numerous studies have demonstrated that high temperature and intense light constrain photosynthesis in *P. ternata*, subsequently affecting growth and development and reducing yield and quality (Xue et al., 2007; Zheng, 2008; Zhang, 2015). In photosynthetic mechanisms, the photoreaction system—primarily Photosystem II (PSII) and its oxygen-evolving complex (OEC), ATP synthesis, and carbon assimilation—represents the most temperature- and light-sensitive sites (Nishiyama et al., 2006; Murata et al., 2007), with the photoreaction system being the most significantly affected component (Gururani et al., 2015). Since temperature and light restrict *P. ternata* growth and development, investigating the adaptation of its photoreaction system to these factors is essential.

Light and temperature are critical environmental factors affecting plant photosynthesis. Short-term high light exposure causes chloroplasts to capture excessive light energy (Szymańska et al., 2017), leading to accumulation of harmful excitation energy and reactive oxygen species (ROS) in photosynthetic mem-

branes that damage PSII (Takahashi & Badger, 2011). Under long-term high light stress, limitations in CO_2 assimilation cause over-reduction of Photosystem I (PSI), resulting in PSI damage (Li et al., 2009). Plants employ photoprotective strategies to reduce excitation energy under high light stress: to minimize energy accumulation at PSII, plants dissipate excess energy as heat through non-photochemical quenching (NPQ) (Gururani et al., 2015; Ruban, 2016). In electron transport, plants can limit electron transfer from PSII donors to PSI through redox feedback mechanisms that reduce cytochrome b_6f complex activity, thereby preventing PSI over-reduction (Joliot & Johnson, 2011). Activation of cyclic electron flow (CEF) accelerates electron efflux from PSI acceptors, preventing PSI over-reduction and protecting PSI from photodamage (Shikanai, 2014).

In low temperature environments, reduced Rubisco enzyme activity and blocked tricarboxylic acid (TCA) cycle impair ATP and NADPH reduction capacity (Eberhard et al., 2008), increasing thylakoid lumen proton concentration and accelerating water-water cycles and ROS production. ROS causes oxidative damage to photoreaction systems and inhibits repair of photosynthetic proteins, reducing photosynthetic electron transport rates and suppressing PSII activity (Falcone et al., 2004; Tyystjärvi, 2013; Sawicki et al., 2016; Khanal et al., 2017). Appropriate high temperatures accelerate photorespiration and photosynthetic carbon assimilation rates, promoting photoreaction processes (Wahid et al., 2007). However, high temperature-induced proton efflux from thylakoid membranes may disrupt coupling between ATP synthesis and electron transport, while increased CEF can compensate for this proton efflux, enabling continued ATP synthesis (Schrader et al., 2004; Allakhverdiev et al., 2008).

In studies of *P. ternata* photosynthetic physiology, Jin et al. (2006) reported that diurnal changes in net photosynthetic rate exhibited a bimodal pattern, with light intensity variation being a primary influencing factor. Xue et al. (2010) found that continuous high temperature stress reduced photosynthetic rate and electron transport rate in *P. ternata*, with long-term high temperature stress causing PSII damage. Exogenous Ca^{2+} and proline can alleviate high temperature-induced inhibition of photosynthesis and PSII damage, thereby improving yield (Yang et al., 2014; Su et al., 2015). Although previous research has examined *P. ternata*' s environmental adaptation characteristics and photosynthetic mechanisms, studies on the combined effects of different temperatures and light intensities remain limited, particularly regarding adaptation to diurnal variations in light and temperature.

This study simulated three consecutive days of low temperature (LT), moderate temperature (MT), and high temperature (HT) conditions under identical diurnal light intensity patterns (0–1,600 $\mu mol \cdot m^{-2} \cdot s^{-1}$). Using Dual-PAM-100, we measured chlorophyll fluorescence parameters of PSII and PSI to analyze the adaptation characteristics of *P. ternata*' s photoreaction system to diurnal light and temperature changes, investigating the photosynthetic physiological adaptation mechanisms to these environmental factors.

1. Materials and Methods

1.1 Plant Material and Cultivation

Healthy *P. ternata* corms approximately 1 cm in diameter were selected and soaked in carbendazim solution (1,000× dilution) for 20 minutes before planting. The substrate consisted of red soil and organic matter mixed at a 1:1 volume ratio. Six kilograms of this mixture were placed in each pot (30 cm height, 15 cm inner diameter), with 21 pots prepared total. On May 1, 2018, 15 selected corms were evenly sown in each pot and covered with 2 cm of organic matter. Pots were placed in a shaded nursery at Yunnan Agricultural University' s teaching farm, constructed with *P. ternata* shade netting providing 60% transmittance. Uniform field management was implemented, and after seedling emergence, thinning was conducted to maintain 20 plants per pot. The experimental site at Yunnan Agricultural University is located in Panlong District, Kunming (102°45 E, 25°08 N) at 1,966 m elevation, with an annual mean temperature of 15.10 °C and annual precipitation of 1,000 mm, featuring distinct wet and dry seasons.

1.2 Experimental Treatments

1.2.1 Light Intensity Measurement To characterize diurnal light intensity patterns at the cultivation site, a Li-190R quantum sensor and Li-1500 light quantum recorder (Li-Cor, USA) were used to collect photosynthetically active radiation (PAR) data every 10 seconds from 6:00 to 18:00. On June 13, 2018, diurnal PAR changes were measured on a clear day at the Yunnan Agricultural University teaching farm [Figure 1: see original paper].

1.2.2 Treatment Implementation Based on light intensity measurements, simulated diurnal variation experiments began on October 1, 2018, in growth chambers. For each temperature treatment, five pots of uniformly growing *P. ternata* plants (average height >15 cm) were placed in growth chambers. Artificial climate chambers and LED lights controlled temperature and light intensity to simulate one-day temperature and light variations, with 12-hour day and night periods. Chlorophyll fluorescence parameters were measured every 2 hours during the day. After 12 hours of night treatment, parameters were measured at 6:00 on the following day. During measurement, uniformly developed leaves from the uppermost layer were randomly selected, with one leaf per pot measured on the middle leaflet, avoiding the main vein. Under identical diurnal light conditions, three temperature environments were simulated: low temperature (LT), moderate temperature (MT), and high temperature (HT), each applied continuously for three days. Specific light and temperature settings are shown in Table 1 .

1.3 Chlorophyll Fluorescence Measurements

Following the methods of Kramer et al. (2004), a Dual-PAM-100 chlorophyll fluorometer (Walz, Germany) was used to measure chlorophyll fluorescence parameters and P700 absorbance changes. During growth chamber treatment, actinic light was activated and both measurement systems were balanced. After fluorescence signals stabilized (4–5 minutes), minimal fluorescence under light (Fo), maximal fluorescence under light (Fm), steady-state fluorescence (Fs), and maximal quantum yield of P700 under light (Pm) were determined. Parameter definitions and calculations follow Kooten & Snel (1990) and Genty et al. (1989):

- Maximum photochemical efficiency: Fv' /Fm' = (Fm' - Fo')/Fm'
- Non-photochemical quenching coefficient: NPQ = (Fm - Fm')/Fm'
- Quantum yield of non-regulated energy dissipation at PSII: Y(NO) = F/Fm
- Electron transport rate through PSII: ETR(II) = Y(II) × PPFD × 0.85 × 0.5
- Electron transport rate through PSI: ETR(I) = Y(I) × PPFD × 0.85 × 0.5
- Actual photochemical quantum yield of PSII: Y(II) = (Fm' - Fs)/Fm'
- Actual photochemical quantum yield of PSI: Y(I) = (Pm' - P)/Pm
- Donor-side heat dissipation efficiency of PSI: Y(ND) = P/Pm
- Acceptor-side heat dissipation efficiency of PSI: Y(NA) = (Pm - Pm')/Pm
- Cyclic electron flow rate: CEF = ETR(I) - ETR(II)

1.5 Data Analysis

Data were processed using Microsoft Excel 2013. One-way ANOVA was performed using SPSS 19.0. Values are presented as means ± standard deviation. SigmaPlot 10.0 was used for figure preparation.

2. Results

2.1 Adaptation of PSII Activity to Diurnal Light and Temperature Variations

Fo' represents minimal fluorescence of PSII under light. In this experiment, Fo' measured daily at 6:00 represented PSII initial fluorescence (Fo) after overnight dark adaptation. Across the three-day treatment, Fo' in all temperature treatments initially decreased, then gradually increased before stabilizing [FIGURE:2A–C]. The LT treatment consistently showed higher Fo' than the other treatments, particularly after nighttime exposure to 10 °C. On day 3, MT treatment showed a slight increase in Fo' compared to days 1 and 2, while HT treatment showed the opposite trend [Figure 2C: see original paper].

Fv' /Fm' represents effective photochemical quantum yield of PSII under actinic light, reflecting excitation energy capture efficiency of reaction centers.

Measurements at 6:00 also represented maximum PSII photochemical conversion efficiency (Fv/Fm) after dark adaptation. Among the three temperature treatments, varying low temperature had the greatest impact on Fv' /Fm' [Figure 2F: see original paper]. With increasing light intensity, Fv' /Fm' in all three temperature treatments decreased rapidly, indicating that light intensity was the primary factor affecting Fv' /Fm' [Figure 1D: see original paper]. As treatment duration increased, temperature effects became more pronounced. On days 2 and 3, Fv' /Fm' decreased with increasing light intensity in all treatments, but LT-treated Fv' /Fm' remained at the lowest level from 6:00 on day 2 and continued decreasing at the same time points across three days [Figure 2E: see original paper]. HT and MT treatments maintained stable Fv' /Fm' levels during the same periods. These results demonstrate that low temperature caused Fv' /Fm' reduction, particularly on days 2 and 3 when values fell below 0.8, whereas HT and MT treatments stabilized around 0.8. After three days of treatment, increasing light intensity was the main cause of Fo' elevation and Fv' /Fm' reduction, with low temperature further exacerbating these changes.

2.2 PSI Adaptation to Diurnal Light Under Different Temperatures

Y(NA), the quantum yield of non-photochemical energy dissipation at PSI caused by acceptor-side limitation, is an important indicator of PSI photodamage or photoinhibition. MT and HT treatments reached maximum Y(NA) at 8:00 on day 1 [Figure 3A: see original paper], indicating that increasing light caused substantial excitation pressure accumulation at the acceptor side. However, with prolonged treatment, HT-treated Y(NA) remained at the highest level, while LT-treated Y(NA) decreased at 10:00 on day 1 and subsequently remained at the lowest level. MT-treated Y(NA) consistently fell between LT and HT levels. These results suggest that HT treatment may have caused PSI photoinhibition or damage due to increased acceptor-side excitation pressure.

Y(ND), the quantum yield of non-photochemical energy dissipation at PSI caused by donor-side limitation, increased from 8:00 to 12:00 on day 1 in all treatments [Figure 3D: see original paper], correlating with increased light intensity. However, Y(ND) remained highest under low temperature and lowest under high temperature, showing an opposite pattern to Y(NA) [Figure 3E: see original paper]. Elevated Y(ND) indicated substantial excitation pressure accumulation at the donor side under LT treatment. By days 2 and 3, temperature treatments showed greater divergence, with Y(ND) consistently higher under low temperature [Figure 3F: see original paper] and progressively lower under high temperature. These Y(NA) and Y(ND) patterns reveal that enhanced light primarily increased acceptor-side excitation pressure, while temperature changes over three days mainly affected donor-side pressure—low temperature intensified donor-side excitation pressure, whereas high temperature alleviated it.

2.3 Effects of Diurnal Light and Temperature on Quantum Yields of PSII and PSI

Throughout the three-day treatment, PSII quantum yield Y(II) was consistently lower under low temperature than under the other treatments [FIGURE:4A–C]. Y(II) decreased rapidly after 6:00 each day as light intensity increased. On days 2 and 3, significant differences in Y(II) among temperature treatments became apparent [FIGURE:4B, C], with LT-treated Y(II) remaining lowest and approaching zero on day 3, suggesting PSII closure or damage [Figure 4C: see original paper]. MT-treated Y(II) and Y(I) also showed declining trends on days 2 and 3, likely due to photoinhibition from excessive light exposure. HT-treated Y(II) remained at normal levels until showing a declining trend after 14:00 on day 3 [Figure 4C: see original paper].

PSI photochemical efficiency Y(I) showed a pattern of initial decrease followed by increase across all three days [Figure 4D: see original paper]. HT-treated Y(I) remained at high levels, with an increasing trend on days 2 and 3 [FIGURE:4E, F]. LT-treated Y(I) reached maximum levels at 6:00 on days 2 and 3, then remained lowest thereafter. MT-treated Y(I) remained stable across three days, following a diurnal pattern of decreasing then increasing with light changes. HT-treated Y(I) consistently remained highest, maintaining stable levels except at 16:00 on days 2 and 3, when the 38 °C treatment caused a temporary decline that recovered under 35.5 °C. These results demonstrate that temperature affected Y(II) and Y(I) under identical light conditions, with appropriate temperature elevation enhancing both quantum yields.

2.4 Effects of Diurnal Light and Temperature on Linear Electron Transport and Cyclic Electron Flow

Relative electron transport rate through PSII [ETR(II)] reflects linear electron transport activity. From day 1, all temperature treatments maintained relatively high linear electron transport capacity, with ETR(II) increasing with temperature [Figure 5A: see original paper]. HT treatment consistently showed highest linear electron transport capacity, peaking at 14:00 when light intensity was strongest from 12:00–14:00. LT-treated ETR(II) increased on day 1 but remained lowest on days 2 and 3 [FIGURE:5B, C], indicating low temperature inhibition of linear electron transport. MT-treated ETR(II) remained relatively stable, with minimal impact from the three-day treatment.

Relative electron transport rate through PSI [ETR(I)] reflects both linear and cyclic electron transport capacity. Over three days, ETR(I) showed similar patterns to ETR(II) [FIGURE:5D–F]. Cyclic electron flow rate (CEF) followed daily light intensity patterns [Figure 5I: see original paper] but showed substantial variation among treatments. Low temperature CEF remained similar and lowest throughout [FIGURE:5I–K]. Moderate temperature CEF showed slight increases after 14:00 on day 3, while high temperature CEF peaked daily at 16:00. On days 2 and 3, moderate and high temperature CEF increased signif-

icantly and remained higher than other treatments. Under high temperature, *P. ternata* maintained high ETR(I) and ETR(II) while higher CEF further enhanced high temperature adaptation. Low temperature PSII and PSI activity reduction likely decreased linear electron transport rates, and the lack of CEF involvement may have further contributed to photoinhibition under low temperature.

2.5 Increased NPQ Enhances High Temperature Adaptation Under Variable Light

NPQ represents the capacity to dissipate excess light energy as heat, reflecting photoprotective ability. Throughout the three-day treatment, HT-treated leaves maintained highest NPQ [FIGURE:6A–C], while LT-treated leaves showed lowest NPQ. Compared to low temperature, moderate temperature also maintained relatively high NPQ. On day 1, NPQ under low temperature showed an increasing trend [Figure 6A: see original paper], but after rising at 8:00 on day 2, it rapidly decreased [Figure 6B: see original paper] and remained lowest thereafter, with slight recovery at 16:00 when temperature peaked on days 2 and 3 [Figure 6C: see original paper]. This indicates temperature effects on NPQ. With increasing light intensity, HT-treated *P. ternata* maintained high NPQ, demonstrating enhanced heat dissipation for self-protection under high temperature.

Y(NO), the quantum yield of non-regulated energy dissipation at PSII, is an important indicator of photodamage. On day 1, LT-treated Y(NO) remained high, decreasing at 18:00 [Figure 6D: see original paper], but increased to near 1 after 10:00 on day 2 [Figure 6E: see original paper] and maintained this level on day 3 [Figure 6F: see original paper]. This indicates insufficient photochemical energy conversion and photoprotective regulation (e.g., heat dissipation) under low temperature [FIGURE:6B, C], preventing complete dissipation of absorbed light energy and causing severe PSII photoinhibition or damage. MT-treated Y(NO) also increased but less dramatically than LT treatment, returning to normal levels after one day. HT-treated Y(NO) remained lowest, indicating minimal photoinhibition under high temperature.

3. Discussion

3.1 High Light and Low Temperature Conditions Aggravate PSII Photoinhibition and Photodamage in *P. ternata*

High light causes photoinhibition in plants, and temperature stress 叠加 intensifies this effect, causing PSII photodamage (Khanal et al., 2017). Photoinhibition increases Y(NO), an indicator of photoinhibition or photodamage (Kalaji et al., 2016). In higher plants, Fv' /Fm' measured under dark adaptation is approximately 0.8, with PSII inhibition causing Fv' /Fm' reduction (Björkman & Demmig, 1987). PSII inactivation, damage, or altered energy dissipation cause Fo' elevation (Kalaji et al., 2014). In this study, Y(NO) changes indicated severe PSII photoinhibition in *P. ternata* under high light (>900 $\mu mol \cdot m^{-2} \cdot s^{-1}$)

and low temperature. LT-treated Fv' /Fm' fell below 0.8 at 6:00 on days 2 and 3 [FIGURE:2E, F], indicating that low temperature aggravated high light-induced photoinhibition. Elevated Fo' under LT and MT treatments [Figure 2C: see original paper] may reflect severe PSII damage. Studies on chrysanthemum (*Dendranthema morifolium*) also demonstrated Fo' elevation under combined low temperature and high light (Liang et al., 2010). Conversely, research on *Bletilla striata* (Wang et al., 2018) and long-term 37 °C treatment on *P. ternata* (Xue et al., 2010) showed high temperature-induced Fo' elevation and Fv' /Fm' reduction. However, this study found that high temperature stabilized Fo' and Fv' /Fm' , likely due to shorter high temperature exposure (maximum 38 °C for only 2 hours) and repair of potentially damaged PSII during the 28 °C night period in the diurnal treatment. These results demonstrate that high light causes photoinhibition in *P. ternata*, with low temperature exacerbating this effect and causing photodamage.

3.2 High Light and Low Temperature Conditions Reduce Photoreaction System Activity in *P. ternata*

Y(II) and Y(I) reflect actual primary light capture efficiency of PSII and PSI, respectively, serving as relative indicators of photosynthetic electron transport rates (Kalaji et al., 2014). Throughout the three-day treatment, LT-treated *P. ternata* maintained lowest Y(II) and Y(I). The significant Y(II) reduction [FIGURE:4C, F] indicated strong inhibition of leaf photoreactions under low temperature (Bailey et al., 2008). The significant elevation of Y(NO), an indicator of PSII photodamage, corresponded with Y(II) reduction, showing that PSII damage decreased electron transport rates. Reduced Y(II) under low temperature further decreased linear electron transport rates ETR(I) and ETR(II) [FIGURE:4E; FIGURE:5B]. The consistently highest donor-side Y(ND) under low temperature prevented electron transfer from PSII to PSI, representing the primary cause of ETR(I) and ETR(II) reduction [Figure 3F: see original paper]. Meanwhile, consistently lowest acceptor-side Y(NA) under low temperature also indicated PSI inhibition. Although high temperature increased Y(NA) [Figure 3C: see original paper], which should reduce linear electron transport, ETR(I) and ETR(II) remained highest under high temperature, correlating with consistently high Y(I). Ballottari et al. (2007) reported that PSI exhibits greater stability than PSII, and rapid electron transport under high temperature suggests that increased Y(NA) did not result from photodamage. Higher Y(II) under high temperature increased Y(I), which elevated excitation pressure at PSI acceptors. *P. ternata* enhanced PSI heat dissipation Y(NA) to avoid photodamage and maintain primary light capture efficiency. Low temperature-induced photoreaction system damage reduced Y(I) and Y(II), and decreased Y(NA) further inhibited photoreaction system activity. High temperature maintenance of high Y(I) may relate to CEF activation, while lower Y(ND) promoted PSII activity and enhanced linear electron transport rates.

3.3 NPQ and CEF Activation Enhance *P. ternata*' s Adaptation to High Temperature and High Light

NPQ effectively dissipates excess light energy (Ruban, 2016). Chen et al. (2008) demonstrated that heat dissipation capacity in wheat (*Triticum aestivum* L.) increased with light intensity and temperature, showing a linear relationship with light intensity. Hu et al. (2010) found that high temperature promoted NPQ increase. In this study, NPQ increased with light intensity, following diurnal patterns consistent with Feng et al. (2002) [Figure 6B: see original paper]. High temperature maintained consistently high NPQ in *P. ternata* leaves, enhancing PSII protection under high light and stabilizing Fv' /Fm' . High NPQ under high temperature ensured high linear electron transport rates [Figure 5C: see original paper], whereas reduced NPQ under low temperature aggravated PSII damage, increased Y(NO), and manifested as obvious photodamage, subsequently reducing linear electron transport rates ETR(I) and ETR(II).

Excessive light energy capture by chloroplasts under high light causes PSII inhibition (Szymańska et al., 2017). Short-term high light protection involves NPQ increase to prevent PSII damage and reduce ROS production (Gururani et al., 2015; Ruban, 2016). Long-term high light acclimation involves CEF activation to protect photoreaction systems (Huang et al., 2012). Under high temperature, *P. ternata* enhanced CEF to promote trans-thylakoid proton gradient establishment [Figure 5K: see original paper], which strengthened PSII NPQ, stabilized the oxygen-evolving complex, and protected PSII from photoinhibition, maintaining Y(NO) at the lowest level. Proton gradient establishment activated ATP synthase, stabilizing the ATP/NADPH ratio and ensuring high TCA cycle activity under high temperature (Rumeau et al., 2007). High CEF under high temperature also alleviated over-reduction of PSI electron acceptors, reducing superoxide anion production at PSI (Huang et al., 2012) and preventing PSI photoinhibition. Therefore, increased NPQ and CEF activation are primary mechanisms enabling *P. ternata* to adapt to diurnal high temperature and high light, stabilizing both PSII and PSI.

Low temperature inhibits Rubisco and blocks the TCA cycle (Khanal et al., 2017), reducing ATP and NADPH reduction capacity and increasing water-water cycles and ROS production in thylakoid lumens (Sawicki et al., 2016). This study found that reduced heat dissipation and cyclic electron flow caused PSII and PSI inhibition and damage. Prolonged low temperature suppresses PSII center D1 protein repair rates, further reducing PSII activity [Figure 2F: see original paper] (Wahid et al., 2007). Low temperature may also reduce thylakoid membrane lipid fluidity (Falcone et al., 2004), affecting membrane protein conformation, weakening interactions between cytochrome b_6/f complex and plastoquinone/plastocyanin, and reducing thylakoid electron transport capacity –likely the main reason for reduced electron transport under LT treatment. Although high temperature increases thylakoid membrane fluidity and may cause proton efflux, disrupting ATP synthesis-electron transport coupling (Schrader et al., 2004), short-term 38 °C treatment did not damage the photoreaction sys-

tem. Increased cyclic electron flow around PSI compensated for proton efflux, enabling continued ATP synthesis (Allakhverdiev et al., 2008). Thus, appropriate high temperature maintained stability of *P. ternata*' s photoreaction system under high light.

High light inhibits *P. ternata* photoreactions, and low temperature exacerbates this photoinhibition. Long-term low temperature damages leaf photoreaction systems and reduces high light adaptability. Appropriate temperature elevation promotes NPQ and CEF, accelerates photoreaction electron transport, maintains photoreaction system stability, and reduces photoinhibition, thereby enabling *P. ternata* photoreaction systems to adapt to high light environments. In cultivation, shade structures should be established to reduce high light-induced photoinhibition, and greenhouse facilities can be employed for large-scale cultivation to better control light intensity and temperature.

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Note: Figure translations are in progress. See original paper for figures.