J Plant Res (2016) 129:379–395
DOI 10.1007/s10265-016-0816-1

JPR SYMPOSIUM

Responses of the Photosynthetic Systems to Spatio-temporal Variations in Light Environments: Scaling and Eco-devo Approaches

Photosynthetic response to fluctuating environments and photoprotective strategies under abiotic stress

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Received: 20 January 2016 / Accepted: 6 March 2016 / Published online: 29 March 2016

Abstract Plants in natural environments must cope with diverse, highly dynamic, and unpredictable conditions. They have mechanisms to enhance the capture of light energy when light intensity is low, but they can also slow down photosynthetic electron transport to prevent the production of reactive oxygen species and consequent damage to the photosynthetic machinery under excess light. Plants need a highly responsive regulatory system to balance the photosynthetic light reactions with downstream metabolism. Various mechanisms of regulation of photosynthetic electron transport under stress have been proposed, however the data have been obtained mainly under environmentally stable and controlled conditions. Thus, our understanding of dynamic modulation of photosynthesis under dramatically fluctuating natural environments remains limited. In this review, first I describe the magnitude of environmental fluctuations under natural conditions. Next, I examine the effects of fluctuations in light intensity, CO_2 concentration, leaf temperature, and relative humidity on dynamic photosynthesis. Finally, I summarize photoprotective strategies that allow plants to maintain the photosynthesis under stressful fluctuating environments. The present work clearly showed that fluctuation in various environmental factors resulted in reductions in photosynthetic rate in a stepwise manner at every environmental fluctuation, leading to the conclusion that fluctuating environments would have a large impact on photosynthesis.

Keywords Alternative pathway · Electron transport · Fluctuating environment · Photoinhibition · Photoprotection · Photosynthesis

Introduction

Researches on regulations of steady-state photosynthesis in response to variations in light intensity (Evans et al. 1993; Ögren and Evans 1993; Yamori et al. 2010a), CO_2 concentration (Farquhar et al. 1980; Yamori et al. 2005; Yamori and von Caemmerer 2009), temperature (Yamori et al. 2005, 2006, 2010b), and humidity (Bunce 1997; Lu et al. 2015; Rawson et al. 1977) have been extensively examined under controlled laboratory conditions. Predicting the environmental responses of the steady-state photosynthetic rate is central to many models of changes in the future global carbon cycle and terrestrial biosphere (Bernacchi et al. 2013; Groenendijk et al. 2011; Zhu et al. 2004). However, plants in natural environments must cope with highly dynamic and unpredictable conditions during the day. Models of steady-state photosynthesis tend to overestimate photosynthesis under fluctuating light (Naumburg and Ellsworth 2002; Timm et al. 2004). To improve models of dynamic photosynthesis under fluctuating environmental conditions, a better understanding of the responses of photosynthesis to fluctuating environments is needed.

Light intensity is the most variable factor in natural environments; during the day, it changes on the order of seconds, minutes, or hours because of changes in leaf angle, cloud cover, and overshadowing canopy. Leaves could receive 50–300 sunflecks per day (some shorter than 10 s) in the understory (Pearcy 1988; Pfitsch and Pearcy 1989). Sunflecks longer than 120 s represent only 5 % of the total number but contribute more than 75 % of total daily light,

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and therefore such sunflecks in forest understories would be more important for photosynthesis than the short ones. Previous researches on photosynthetic responses to fluctuating light have focused on their mechanisms and interspecific variations (Pearcy 1990; Pearcy and Way 2012). Photosynthetic responses to sunflecks differ among and within species depending on sunfleck duration, frequency, and intensity (Chazdon and Pearcy 1986; Leakey et al. 2004; Sims and Pearcy 1993; Watling et al. 1997; Yin and Johnson 2000). A sudden increase in light intensity typically leads to a hyperbolic increase in the leaf photosynthetic rate (e.g., Bai et al. 2008; Han et al. 1999; Pearcy 1990; Valladares et al. 1997). Because of biochemical and stomatal limitations, there is a time lag from onset of light to achievement of the maximum rate of photosynthesis (Allen and Pearcy 2000; Bai et al. 2008; Chen et al. 2011; Han et al. 1999; Pearcy 1990; Rijkers et al. 2000; Yamori et al. 2012, 2016a).

In contrast, the effects of fluctuations in temperature, CO_2 concentration, relative humidity, and leaf-to-air vapor pressure deficit (VPD, which combines temperature and relative humidity into a single value) on dynamic photosynthesis have not been examined (Kaiser et al. 2015; Way and Pearcy 2012). The leaves of many plants are thin and have only minimal heat capacity; when exposed to strong sunlight, they can warm up substantially above air temperature, especially when stomata are closed. Leaves with low transpiration rates (e.g., oak leaves) suffer frequent high-temperature episodes, during which leaf temperature can increase above air temperature by as much as 10–15 °C within 1 min (Hanson et al. 1999; Singsaas et al. 1999; Singsaas and Sharkey 1998). In cotton leaves, which have high transpirational cooling, the temperature repeatedly exceeded 40 °C and fluctuated by as much as 8–10 °C in a matter of seconds (Wise et al. 2004). Since leaf temperature and thus VPD often change in parallel with light intensity (Peak and Mott 2011; Schymanski et al. 2013), fluctuation of leaf temperature and VPD as well as light intensity would affect the photosynthetic rate.

CO_2 concentration at the leaf surface also fluctuates, since active photosynthesis could significantly reduce the CO_2 concentration in the air at the leaf surface. Subsequent air flow at the leaf surface could transiently restore it to near ambient. Thus, the frequency of fluctuations in CO_2 at the leaf surface would be highly variable and determined by photosynthetic rate and wind conditions.

Plant growth and yield depend largely on photosynthesis (Long et al. 2006; Yamori et al. 2016b; Zhu et al. 2010). Understanding not only steady-state photosynthetic characteristics but also non-steady-state photosynthetic characteristics under fluctuating environments is needed for improving dynamic photosynthesis models and for using biotechnological strategies to improve photosynthetic performance under natural conditions (Yamori 2013). In this review article, after introducing the magnitude of environmental fluctuations under natural conditions, the effects of fluctuations in light intensity, CO_2 concentration, leaf temperature, and relative humidity on dynamic photosynthesis has been analyzed in rice. Finally, photoprotective strategies that allow plants to maintain the photosynthesis under stressful fluctuating environments have been summarized. The present work clearly showed that various fluctuating environmental factors led to reductions in photosynthetic rate in a stepwise manner at every environmental fluctuation, resulting in photoinhibition. Thus, it is concluded that fluctuating environments have a large impact on photosynthetic performance and are stressful for plants.

Light-dependent reactions of photosynthesis

Light is absorbed by light-harvesting systems, which contain chlorophylls and carotenoids. The energy captured by the photosynthetic pigments is transferred to the reaction centers of photosystem I (PSI) and photosystem II (PSII) in the thylakoid membranes of chloroplasts (Fig. 1). Electrons derived from water splitting in PSII are ultimately transferred to $NADP^+$ via PSI, resulting in NADPH production. This process is known as linear electron transport (Fig. 1). This linear electron transport, in which electrons pass through the cytochrome (Cyt) b_6/f complex, generates a proton (H^+) gradient across the thylakoid membrane (ΔpH) (Allen 2003). Together with protons generated by the water-splitting complex, ΔpH induces the qE component of non-photochemical quenching (NPQ) of excitation energy. The ΔpH and transmembrane electrical potential ($\Delta\psi$) enable ATP production by ATP synthase (Fig. 1). In contrast to linear electron transport, cyclic electron transport around PSI depends solely on PSI; the electrons also pass through the Cyt b_6/f complex (Fig. 1). Cyclic electron transport around PSI can generate ΔpH and drives ATP synthesis without NADPH accumulation (Yamori and Shikanai 2016). Generated ATP and NADPH fuel the Calvin–Benson cycle and other metabolic pathways in the chloroplast stroma. Because of a concentration gradient, CO_2 diffuses from the air through the stomata and then through intercellular airspaces into cells and ultimately chloroplasts, where it is fixed into carbohydrates (Fig. 1).

Photosynthesis is sensitive to various environmental changes, because it needs to balance absorbed light energy with the energy consumed by various metabolic pathways. The rate of photosynthesis rises with the increase in light intensity until saturation (Fig. 2). Low light limits photosynthesis and thus plant growth, whereas excessive light

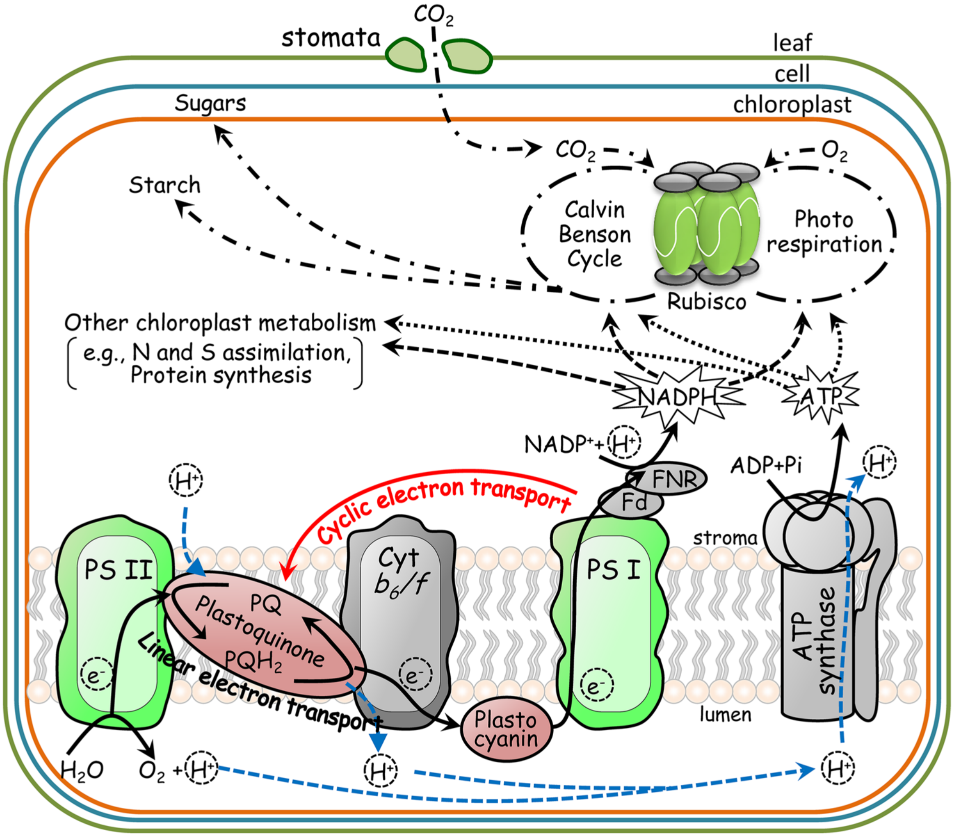


Fig. 1 Scheme of photosynthetic reactions in C_3 higher plants [modified from Yamori and Shikanai (2016)]. Light energy captured by chlorophyll and light-harvesting complexes drives electron transport, which is used to reduce $NADP^+$–NADPH. Electron transport drives proton (H^+) translocation from the stroma into the lumen, generating an H^+ electrochemical gradient and enabling ATP production. ATP and NADPH are used to fix CO_2 (photosynthesis) and to react with O_2 (photorespiration); both processes are catalyzed by Rubisco. In photosynthesis, ATP and NADPH are used in the Calvin–Benson cycle to produce triose phosphates for carbohydrate metabolism (i.e., sugar and starch). They are also used in a range of metabolic activities in the chloroplast (e.g., nitrogen and sulfur metabolism). The *solid black arrows* show electron transport in the thylakoid membranes, the *solid red arrow* shows cyclic electron flow around PSI, the *dotted blue arrows* show the movement of protons (H^+), and the *dashed/dotted black arrows* show metabolic pathways in which the ATP and NADPH are used. *PSII* photosystem II, *PQ* plastoquinone, *Cyt* b_6f cytochrome b_6/f complex, *PSI* photosystem I, *Fd* ferredoxin, *FNR* ferredoxin-NADP reductase, *Pi* inorganic phosphate (color figure online)

can cause photoinhibition of PSII, which results in reductions in photosynthetic rate (Aro et al. 1993; Takahashi and Badger 2011). PSII is very sensitive to light stress and is rapidly inactivated under strong light, a phenomenon that is referred to as PSII photoinhibition (Aro et al. 1993; Powles 1984). The light-induced photodamage to PSII and the repair of photodamaged PSII occur simultaneously. PSII photoinhibition becomes apparent when the photodamage rate exceeds the repair rate. Photosynthetic rate is also limited by other factors such as low or high temperature, low humidity, and low CO_2 concentration, where light intensity would be frequently in excess of that required for CO_2 assimilation, which can lead to photoinhibition (Fig. 2). Thus, photoinhibition is common even at light intensities that would be otherwise optimal (Murchie et al. 1999).

Dynamic photosynthetic responses to fluctuating environments

The rate of photosynthesis is determined by not only the rate of steady-state photosynthesis but also the speed of photosynthetic responses to fluctuating environments (Way and Pearcy 2012). In the present study, chlorophyll fluorescence, P700 redox state, and gas exchange were simultaneously measured in rice (*Oryza sativa* 'Hitomebore') plants exposed to fluctuating environments (for Materials and methods, see Fig. 3). Under constant conditions, the rates of CO_2 assimilation and electron transport around PSI (ETR I) and PSII (ETR II) were constant for 5 h, and the reduction level of the plastoquinone pool (1 − qL) and NPQ (an indicator of thermal dissipation of excess energy) were constant. Under fluctuating light,

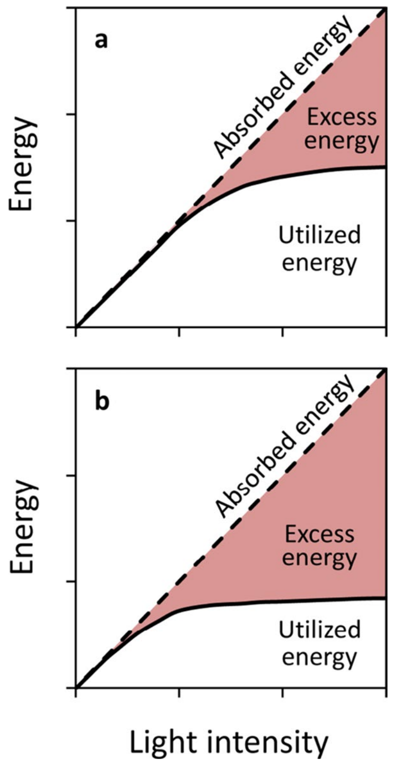


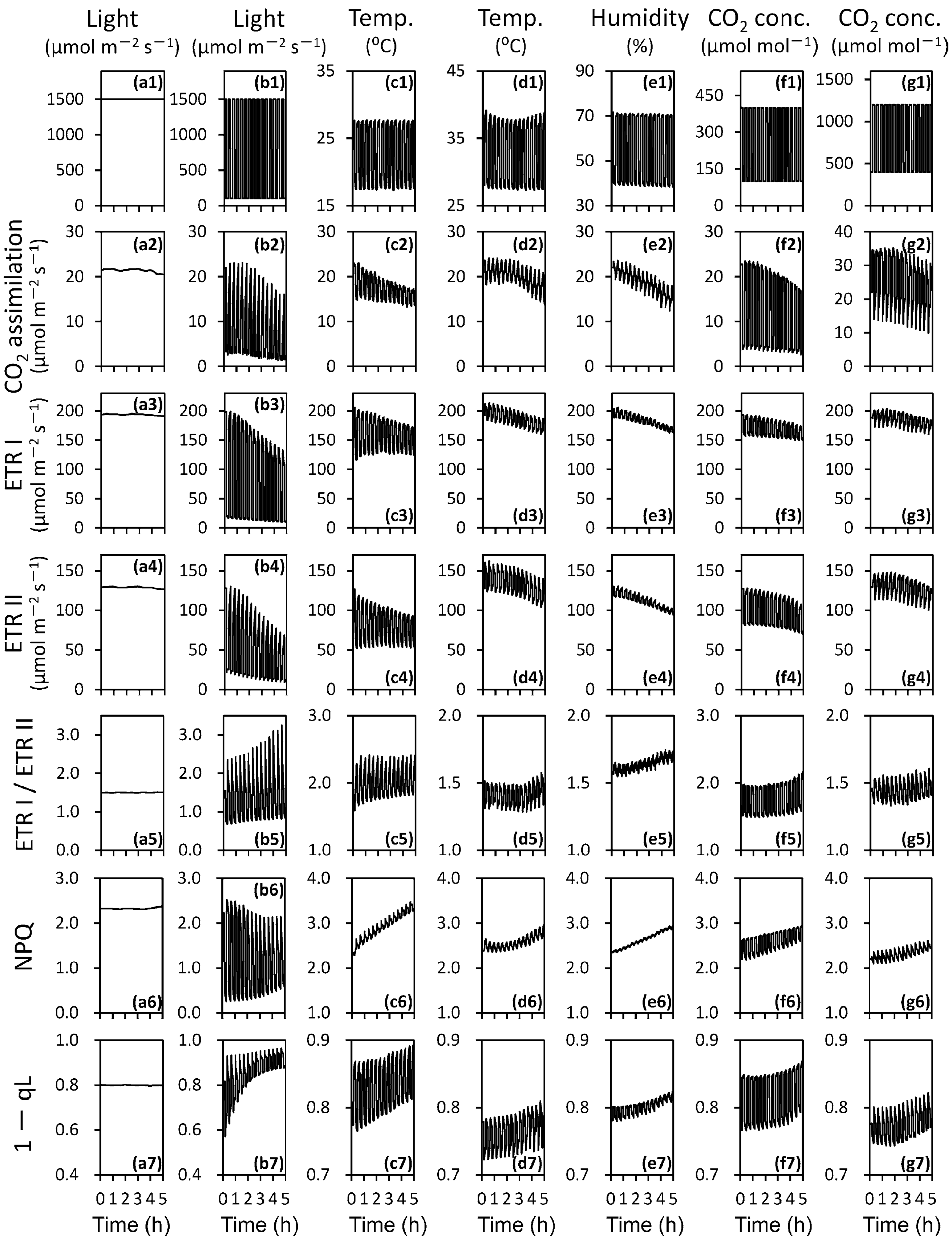
Fig. 2 Photosynthesis and photoinhibition in leaves. *Dashed line* represents light energy absorbed by plants, and *solid line* is the light response curve of photosynthesis. The difference between the amounts of energy absorbed and used in photosynthesis (*red areas*) represents excess energy that needs to be removed. **a** Favorable (non-stressful) conditions, **b** unfavorable conditions (e.g., low temperature or drought) (color figure online)

Fig. 3 Responses of photosynthetic parameters to constant and fluctuating conditions in rice (*O. sativa* ‘Hitomebore’). Plants were grown at 400 μmol mol^{-1} CO_2, relative humidity of 70 %, 28 °C, and 500 μmol photons m^{-2} s^{-1}. Measurements of chlorophyll fluorescence, P700 redox state and also gas exchange were performed simultaneously with a Dual-PAM-100 and a GFS-3000 measuring system (Walz, Effeltrich, Germany) in uppermost, fully expanded new leaves of 60–80 day old plants as described in Yamori et al. (2011). The rates of electron transport around PSI (ETR I) and around PSII (ETR II), the ETR I/ETR II ratio, CO_2 assimilation rate, the redox state of the plastoquinone pool (1 − qL), and non-photochemical quenching (NPQ) were simultaneously measured under the growth conditions with the following modifications: **a** constant light (1,500 μmol photons m^{-2} s^{-1}), **b** fluctuating light (100 μmol m^{-2} s^{-1} for 10 min and 1,500 μmol m^{-2} s^{-1} for 10 min), **c** fluctuating temperature (18 °C for 10 min and 28 °C for 10 min) with constant light (1,500 μmol photons m^{-2} s^{-1}), **d** fluctuating temperature (28 °C for 10 min and 38 °C for 10 min) with constant light (1,500 μmol photons m^{-2} s^{-1}), **e** fluctuating relative humidity (40 % for 10 min and 70 % for 10 min) with constant light (1,500 μmol photons m^{-2} s^{-1}), **f** fluctuating CO_2 concentration (100 μmol mol^{-1} for 10 min and 400 μmol mol^{-1} for 10 min) with constant light (1,500 μmol photons m^{-2} s^{-1}), **g** fluctuating CO_2 concentration (400 μmol mol^{-1} for 10 min and 1,200 μmol mol^{-1} for 10 min) with constant light (1,500 μmol photons m^{-2} s^{-1}). ETR I (or ETR II) was calculated by multiplying the quantum yield of PSI (or PSII) and the estimated energy absorption in PSI (or PSII) (=PPFD x 0.84 x 0.5), where 0.84 represents the leaf absorbance and 0.5 is the proportion of absorbed light energy allocated to PSI or PSII. Values are mean ± SE, $n = 3$ ▶

ETR I, ETR II, and CO_2 assimilation rate decreased and 1 − qL increased in a stepwise manner at every transition to low light, whereas NPQ was slightly suppressed during both the low-light and high-light phases (Fig. 3). After 5 h of fluctuating light, ETR I, ETR II, and CO_2 assimilation rate during both low- and high-light phases were decreased. Under fluctuating temperature (moderate–low or moderate–high), relative humidity (moderate–low), and CO_2 concentration (ambient–low or ambient–high), all the photosynthetic parameters (i.e., ETR I, ETR II, and CO_2 assimilation rate) decreased in a stepwise manner at every transition, whereas 1 − qL and NPQ gradually increased over 5 h (Fig. 3).

The maximum level of the P700 signal (P_m; full oxidation of P700) in the dark and the maximum quantum yield of PSII (F_v/F_m) were measured before and after exposure to constant or fluctuating conditions for 5 h (Fig. 4). Fluctuating CO_2 concentration, leaf temperature, and relative humidity significantly reduced F_v/F_m in comparison with constant conditions, indicating that PSII is susceptible to fluctuating environments (Figs. 4, 5). On the other hand, only fluctuating light significantly reduced P_m, indicating that PSI is more susceptible to fluctuating light than to constant high light or other fluctuating conditions (Figs. 4, 5). In fluctuating environments, the electron transport system accumulates excess reducing power, which cannot be dissipated as heat and may cause a strong reducing burst (Fig. 3), eventually leading to photoinhibition of PSI or PSII (Fig. 4). As a result, plants decreased their CO_2 assimilation rate via a reduction in ETR I and ETR II (Fig. 3). Thus, these experiments showed that fluctuating conditions are stressful for rice plants (Fig. 5).

Various components of photosynthesis respond to environmental fluctuations with very different time constants. For example, when light intensity is increased suddenly after a prolonged period of darkness or low light, photosynthetic rate increases gradually over the course of several minutes to tens of minutes and approaches a new steady-state level (e.g., Yamori et al. 2012). In this phase of photosynthetic induction, the initial reactions involved in electron transport respond to changes in light intensity immediately (for a review, see Pearcy 1990). During the first 1–2 min of light induction, the photosynthetic rate is limited by the build-up of metabolic pools, especially by RuBP regeneration (Sassenrath-Cole and Pearcy 1992; Way and Pearcy 2012). Light fluctuation within a few seconds would not have a drastic effect on the Calvin–Benson cycle, because the activation of enzymes under light and their inactivation in the dark take several minutes to tens of minutes (Buchanan 1980, 1991). Because light controls


Light (μmol m⁻² s⁻¹)
Light (μmol m⁻² s⁻¹)
Temp. (°C)
Temp. (°C)
Humidity (%)
CO2 conc. (μmol mol⁻¹)
CO2 conc. (μmol mol⁻¹)
(a1)
(b1)
(c1)
(d1)
(e1)
(f1)
(g1)
0
500
1000
1500
15
25
35
25
35
45
30
50
70
90
0
150
300
450
0
500
1000
1500
CO2 assimilation (μmol m⁻² s⁻¹)
(a2)
(b2)
(c2)
(d2)
(e2)
(f2)
(g2)
0
10
20
30
40
ETR I (μmol m⁻² s⁻¹)
(a3)
(b3)
(c3)
(d3)
(e3)
(f3)
(g3)
0
50
100
150
200
ETR II (μmol m⁻² s⁻¹)
(a4)
(b4)
(c4)
(d4)
(e4)
(f4)
(g4)
0
50
100
150
ETR I / ETR II
(a5)
(b5)
(c5)
(d5)
(e5)
(f5)
(g5)
0.0
1.0
1.5
2.0
3.0
NPQ
(a6)
(b6)
(c6)
(d6)
(e6)
(f6)
(g6)
0.0
1.0
2.0
3.0
4.0
1 − qL
(a7)
(b7)
(c7)
(d7)
(e7)
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0.4
0.6
0.7
0.8
0.9
1.0
0 1 2 3 4 5
Time (h)

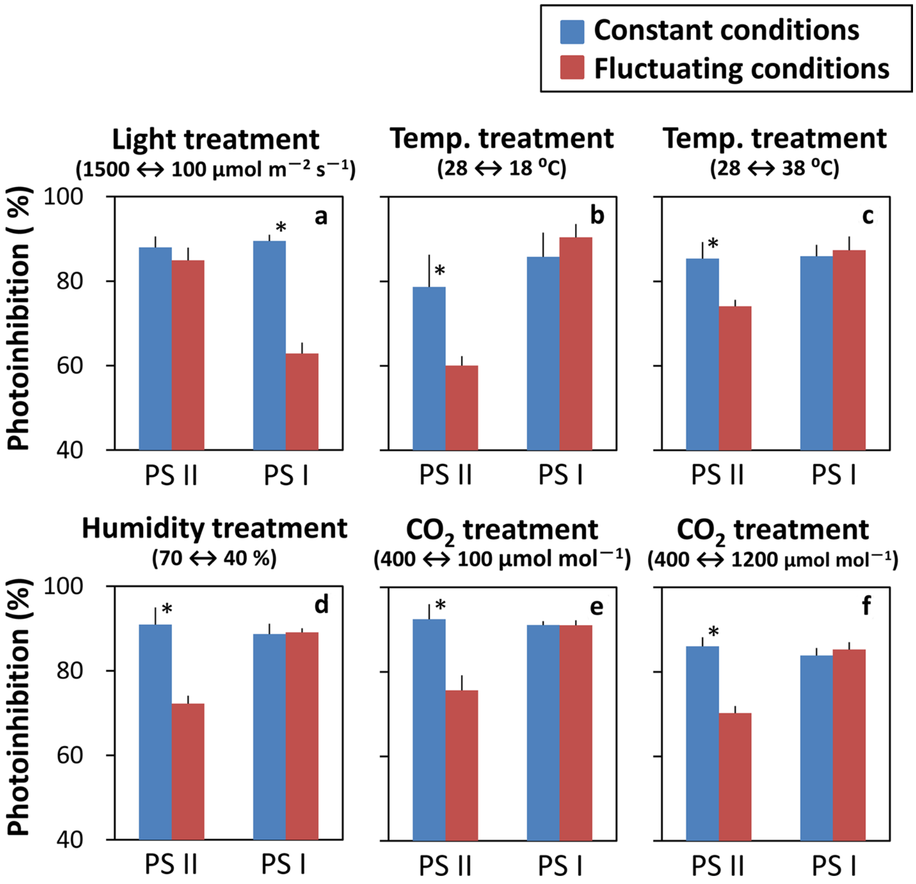

Fig. 4 Effect of fluctuating conditions on photoinhibition of PSI and PSII. The maximum level of the P700 signal of PSI (P_m, full oxidation of P700) and the maximum quantum yield of PSII (F_v/F_m) were measured with a Dual-PAM-100 and a GFS-3000 measuring system (Walz, Effeltrich, Germany) before and after exposure to constant or fluctuating conditions for 5 h. Values were measured after dark incubation for 30 min. Constant and fluctuating environments were as in Fig. 3. The extent of photoinhibition of PSI and PSII is relative to the initial P_m and F_v/F_m values (%). Values are mean ± SE, $n = 3$

the activity of a number of Calvin–Benson cycle enzymes and ATP synthase via the ferredoxin/thioredoxin system, the changes in light intensity within minutes may be critical for CO_2 assimilation in the Calvin–Benson cycle [which includes ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco), chloroplast fructose-1, 6-bisphosphatase (FBPase), sedoheptulose-1,7-bisphosphatase (SBPase), phosphoribulokinase (PRK)] (Kirschbaum and Pearcy 1988; Sassenrath-Cole and Pearcy 1992, 1994). Light fluctuation for several tens of minutes may affect stomatal conductance (Cardon and Berry 1992; Lawson et al. 2002; Morison 1998). Because these reactions affect photosynthesis as a whole, drastic fluctuations in light intensity can cause photoinhibition and reduce plant growth (Kono et al. 2014; Tikkanen and Aro 2012; Yamori et al. 2016a).

Temperature changes have a strong impact on photosynthetic reactions. The temperature response curve of photosynthetic rate is generally parabolic, often with an optimum at the growth temperature (for reviews, see Way and Yamori 2014; Yamori et al. 2014). A decrease in temperature by 10 °C (e.g., from 20 to 10 °C) will reduce the activity of Calvin–Benson cycle enzymes by 50 %. This usually reduces the demand for the reducing equivalent (NADPH) and causes subsequent accumulation of reductants. High temperatures reduce the activity of the Calvin–Benson cycle enzymes, especially Rubisco. The activation state of Rubisco is regulated by Rubisco activase (Portis 2003), which fails to maintain a high Rubisco activation state at high temperatures because of its thermolability (Crafts-Brandner and Salvucci 2000; Salvucci and Crafts-Brandner 2004). Thus, fluctuating temperature (moderate–low or moderate–high) in combination with high light could lead to over-reduction of the photosynthetic electron transport chain and eventually to photoinhibition.

Drought stress induces stomatal closure, which limits CO_2 transfer into leaves and limits photosynthesis (Chaves et al. 2009; Cornic 2000; Flexas and Medrano 2002). This limitation can decrease the activity of the Calvin–Benson cycle enzymes and result in over-reduction of the photosynthetic electron transport chain, similar to the effect of temperature. High CO_2 concentrations reduce stomatal conductance (Ainsworth et al. 2002; Ainsworth and Rogers 2007; Medlyn et al. 2001). In *Phaseolus vulgaris*, fluctuations in CO_2 concentration decreased CO_2 assimilation rate via a reduction in stomatal conductance (Cardon et al. 1994, 1995). Although changes in CO_2 concentration, temperature, and humidity may be more gradual than changes in light intensity, fluctuating conditions causing stomatal closure under high light can lead to photoinhibition.

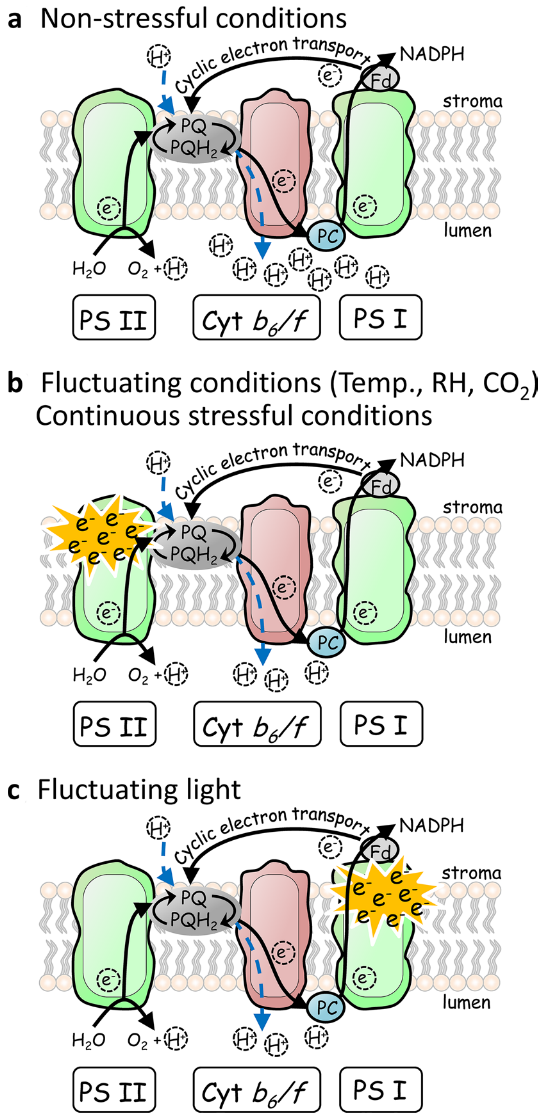

Fig. 5 Summary of photoinhibition under various environmental conditions. **a** Under non-stressful (favorable) conditions, photoinhibition does not occur. **b** Under constant light stress and various fluctuating conditions (temperature, relative humidity, or CO_2 concentration), the electron transport system accumulates excess reducing power which cannot be dissipated as heat, causing photoinhibition of PSII. **c** Under fluctuating light, strong reduction of the entire electron transport system for a couple of hours causes a strong reducing burst at the acceptor side of PSI, leading to PSI photoinhibition

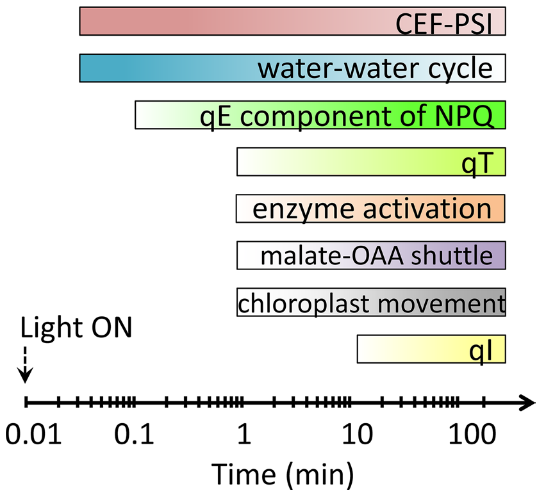

Fig. 6 Time scale of various photoprotective mechanisms to prevent photoinhibition [modified from Eberhard et al. (2008)]. CEF-PSI: cyclic electron transport around PSI, water–water cycle: Mehler-ascorbate peroxidase pathway, qE: energy-dependent quenching component of nonphotochemical quenching (NPQ) of absorbed light, qT: state transitions to balance the excitation of PSII and PSI, enzyme activation: activation of key enzymes in the Calvin–Benson cycle by thioredoxin, malate-OAA shuttle: malate–oxaloacetate shuttle, chloroplast movement: light-induced movement and arrangement of chloroplasts, qI: photoinhibitory processes

Photoinhibition of photosystems I and II

Photoinhibition may represent downregulation of the photosynthetic apparatus when harvested light energy exceeds energy that can be used by the chloroplast. In our experiments, fluctuating conditions other than light damaged PSII (Fig. 4). Many studies also have reported the sensitivity of PSII to photodamage, and PSII has an efficient and dynamic repair machinery (for reviews, see Aro et al. 1993, 2005). The damaged PSII proteins, primarily D1, are replaced with newly synthesized proteins after partial PSII disassembly (Takahashi and Badger 2011). ROS generated under various stresses inhibit PSII repair (Takahashi and Murata 2008). The dynamic control of active PSII reaction centers via a photoinhibition–repair cycle may rescue PSI from photodamage under high light (Tikkanen et al. 2014).

In contrast to PSII, PSI lacks efficient repair, and thus its recovery is extremely slow (Kudoh and Sonoike 2002). PSII photodamage increases linearly with light intensity, whereas PSI damage appears only when the electron flow from PSII exceeds the capacity of PSI electron acceptors. PSI has generally been regarded as more stable than PSII in vivo (Sonoike 2011). However, under natural conditions, PSI photodamage could be much more frequent than anticipated. PSI is potentially susceptible to fluctuating light even in wild-type Arabidopsis (Kono et al. 2014; Suorsa et al. 2012; Tikkanen et al. 2010) and rice (Figs. 4, 5; Yamori et al. 2016a). Selective photoinhibition of PSI by moderate light treatment of intact leaves at chilling temperatures occurs in several plant species, including cotton (Kornyeyev et al. 2003a, b), cucumber (Sonoike and Terashima, 1994; Terashima et al. 1994), and potato (Havaux and Davaud 1994). Thus, PSI is the primary site of photoinhibition in many plant species under certain conditions (e.g., fluctuating light or chilling temperature with moderate light intensity), and PSI photodamage could limit crop growth in temperate climates.

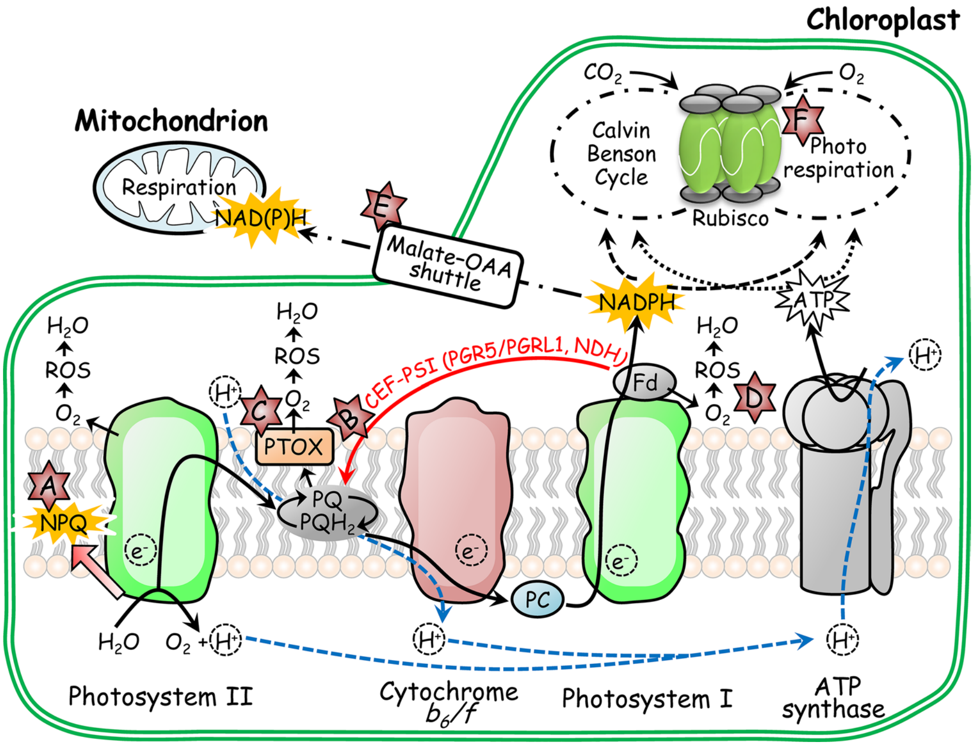

Fig. 7 Major photoprotective mechanisms that prevent photoinhibition. **a** The qE component of NPQ dissipates excess light energy absorbed by photosynthetic pigments (chlorophyll and carotenoids) as heat. **b** Cyclic electron transport around PSI (CEF-PSI) includes the PGR5/PGRL1-dependent and NDH-dependent pathways and helps to generate ΔpH across the thylakoid membrane. **c** Plastoquinol terminal oxidase (PTOX). Electrons are transferred from plastoquinol (PQH_2) via PTOX, which oxidizes plastoquinone (PQ) and reduces O_2–H_2O. **d** ROS scavenging through the water–water cycle: photoreduction of O_2–H_2O at the reducing side of PSI. O_2^- produced at PSI is scavenged by superoxide dismutase (SOD) and, subsequently by ascorbate peroxidase (APX), which consume NADPH. **e** Metabolic interactions between chloroplasts and mitochondria: the malate–oxaloacetate (OAA) shuttle. NADPH generated by electron transport in the chloroplast can be re-oxidized by the mitochondrial respiratory chain, in which NADPH is consumed by the reduction of OAA–malate; and some of the malate is exported from the chloroplast to the mitochondrion to synthesize ATP. Malate can also be oxidized back to OAA in the cytosol to produce NADH. **f** The photorespiration pathway. Photorespiration requires ATP and releases previously fixed CO_2

Photoprotective strategies to prevent photoinhibition

Rapid photosynthetic responses to fluctuating environments which operate on the proper timescale should determine their viability and survival under such stressful environment conditions. A number of photoprotective mechanisms over a wide range of time scales have been reported (Fig. 6); (1) photoprotection by avoiding exposure to light and (2) photoprotection by coping with excess light absorbed by photosynthetic pigments (Baena-Gonzalez and Aro 2002; Holt et al. 2004; Takahashi and Badger 2011). Below, I review various photoprotective strategies, with emphasis on photoprotection by coping with excess absorbed light.

Photoprotection by avoiding exposure to light at the leaf or chloroplast levels

Leaf movement, such as paraheliotropism, is an efficient strategy to reduce light interception and thus to avoid excess light energy absorption (Arena et al. 2008; Jiang et al. 2006; Ludlow and Bjorkman 1984; Pastenes et al. 2005), and also to reduce heat and transpirational water loss which confers the plant to protect against photoinhibition (Forseth and Ehleringer 1982; Gamon and Pearcy 1989). Paraheliotropism protects against photoinhibition in bean (Bielenberg et al. 2003; Pastenes et al. 2005), soybean (Jiang et al. 2006), and wild grape (Gamon and Pearcy 1989, 1990). Another type of leaf movement is leaf rolling, which protects leaves from dehydration because it reduces the effective leaf area and therefore transpiration. At the same time, leaf rolling protects leaves from photodamage (Corlett et al. 1994).

Chloroplasts alter their positions to optimize the use of light (Suetsugu and Wada 2007; Wada et al. 2003). Under strong light, they move from the cell surface to the side walls of cells. This so-called “avoidance response” protects against photoinhibition (Kasahara et al. 2002) because chloroplast movements decrease light interception by the photosynthetic apparatus and may reduce light absorptance by approximately 20 % (Brugnoli and Bjorkman 1992). Chloroplasts move at velocities above 1 μm min^{-1} (Kagawa and Wada 2004), and thus their avoidance response would be completed in approximately 20 min. Two photoreceptors for chloroplast movement, phototropin 1 (PHOT1) and phototropin 2 (PHOT2), have been identified in *Arabidopsis thaliana*. Only PHOT2 participates in the avoidance response, but both play a role in chloroplast accumulation in illuminated cell areas under low light to maximize light absorption for photosynthesis (Wada et al. 2003).

Photoprotection by coping with excess light absorbed by photosynthetic pigments

Several photoprotective processes involving in the photosynthetic electron transport have been proposed (Fig. 7).

Thermal energy dissipation of absorbed excess light energy

Plants possess a rapidly (on the time scale of seconds) inducible NPQ mechanism, termed ΔpH-dependent quenching (qE), for harmless thermal dissipation of excess light energy absorbed in the light-harvesting antenna of PSII (Fig. 7a). The mechanism responsible for qE component is associated with the conversion of violaxanthin via antheraxanthin to zeaxanthin by violaxanthin de-epoxidase and the protonation of the PSII subunit PsbS, which functions as a sensor of lumen pH in plants (Li et al. 2000; Niyogi et al. 2005). Both reactions are enhanced by low lumen pH, which is accompanied by ΔpH generation through electron transport at high light (Niyogi 1999). Thus, qE component of NPQ can be considered as feedback regulation of the light-dependent reactions of photosynthesis.

Thermal dissipation might protect PSII from photoinhibition by decreasing the rate of PSII photodamage under strong light (Havaux and Niyogi 1999; Li et al. 2002). However, a recent study on Arabidopsis mutants defective in NPQ revealed that defects in thermal dissipation inhibited PSII repair without notable effects on PSII photodamage; this inhibition was attributed to suppression of de novo protein synthesis, especially that of D1 (Takahashi et al. 2009). ROS accelerated photoinhibition by inhibiting PSII repair rather than by being directly involved in photodamage (Nishiyama et al. 2006). Thus, it appears that thermal dissipation plays a role in preventing ROS generation and avoiding ROS-mediated inhibition of de novo D1 synthesis. There is still a possibility that the ROS could damage PSII depending on the light conditions, types of ROS (e.g., O_2^-, H_2O_2 and OH·) and the ROS concentrations (Blot et al. 2011; Fan et al. 2016), since it has been also reported that ROS can photodamage PSII directly (Fan et al. 2016; Hideg et al. 2011; Kornyeyev et al. 2010).

Cyclic electron transport around PSI

Cyclic electron transport around PSI enhances generation of ΔpH across the thylakoid membrane by increasing electron transfer from PSI to the plastoquinone pool, and then back to PSI through the proton-pumping Cyt b_6/f complex (Fig. 7b). Cyclic electron transport around PSI is proposed to be essential for balancing the ATP/NADPH production ratio by increasing ΔpH to increase ATP synthesis (Yamori and Shikanai 2016). In addition, the additional generation of ΔpH induces qE to dissipate excess absorbed light energy (Müller et al. 2001; Niyogi 1999). The electron flow through the Cyt b_6/f complex slows as ΔpH increases. Thus, ΔpH plays a regulatory roles via the acidification of the thylakoid lumen by the down-regulation of electron transport through the Cyt b_6/f complex (Golding et al. 2004; Kramer et al. 2004; Suorsa et al. 2012; Tikkanen et al. 2014). Therefore, cyclic electron transport around PSI protects both photosystems from damage caused by stromal over-reduction (Miyake 2010; Takahashi and Badger 2011; Yamori and Shikanai 2016). It is worth noting that cyclic electron transport around PSII, which requires only PSII photochemical reactions, has been proposed to operate efficiently under excess light conditions (Miyake and Okamura 2003; Prasil et al. 1996), although its physiological roles and molecular mechanisms are still not clear.

In angiosperms, two alternative pathways of cyclic electron transport around PSI have been identified (for a review, see Yamori and Shikanai 2016). The major pathway in Arabidopsis depends on two proteins, PROTON GRADIENT REGULATION 5 (PGR5) (Munekage et al. 2002, 2004) and PGR5-Like PHOTOSYNTHETIC PHENOTYPE 1 (PGRL1) (DalCorso et al. 2008; Hertle et al. 2013), whereas the minor pathway is mediated by the chloroplast NADH dehydrogenase-like (NDH) complex (Burrows et al. 1998; Horváth et al. 2000; Kofer et al. 1998; Shikanai et al. 1998), which forms a supercomplex with PSI (Peng et al. 2011). Both the PGR5/PGRL1-dependent pathway (DalCorso et al. 2008; Hertle et al. 2013; Munekage et al. 2002, 2004) and the NDH-dependent pathway (Yamamoto et al. 2011; Yamamoto and Shikanai 2013) are involved in ferredoxin-dependent cyclic electron transport around PSI. In C_3 plants, approximately $\leq$10–15 % of total electron transport is derived from cyclic electron transport around PSI in the steady state (e.g., Fan et al. 2007; Kramer et al. 2004; Kuvykin et al. 2011; Laisk et al. 2005, 2007; Miyake et al. 2005). However, when demand for ATP is higher than that for NADPH (e.g., during photosynthetic induction, at high or low temperature, at low CO_2 concentration, or under drought), cyclic electron transport around PSI is likely to be activated (for a recent review, see Yamori and Shikanai 2016). Complete inhibition of both cyclic electron transports around PSI in the Arabidopsis *crr2 pgr5* double mutant severely impairs photosynthesis and growth (Munekage et al. 2004), indicating that cyclic electron transport around PSI is essential for photosynthesis in C_3 species.

Plastoquinol terminal oxidase (PTOX)

Plastoquinol terminal oxidase (PTOX) serves as an alternative electron sink, which oxidizes plastoquinol (PQH_2) and reduces O_2–H_2O when the plastoquinone pool is over-reduced (McDonald et al. 2011; Nawrocki et al. 2015; Peltier and Cournac 2002). In principle, PTOX could contribute to ATP production, and it plays a role in the control of the redox poise in chloroplasts (Fig. 7c). It has been proposed that PTOX is capable of modulating the balance between linear electron transport and cyclic electron transport around PSI during the dark-to-light transition (Trouillard et al. 2012). The alpine plant species *Ranunculus glacialis* has high levels of PTOX, which may act in effective alternative electron transport (Streb et al. 2005). However, because PTOX is expressed at very low levels in most C_3 plants (e.g., Arabidopsis or tomato), it is likely to act as a safety valve to keep the plastoquinone pool oxidized and to prevent photo-oxidative damage under stress conditions (Josse et al. 2000; McDonald et al. 2011).

It is likely that PTOX is involved in chloroplast development (McDonald et al. 2011). During carotenoid synthesis, desaturation requires plastoquinone and is driven by a redox chain in which PTOX is likely to re-oxidize the reduced plastoquinone (Carol and Kuntz 2001; Kuntz 2004). The lack of PTOX causes the variegated leaf phenotype of the Arabidopsis *immutans* mutant and the tomato *ghost* mutant, in which the bleached spots originate at early stage during chloroplast biogenesis as a result of shortage in carotenoid synthesis (Carol and Kuntz 2001). Therefore, PTOX appears to play a role in carotenoid synthesis. It is likely that the relative importance of PTOX to electron transport could vary depending on the developmental and physiological context.

ROS scavenging through the water–water cycle

The water–water cycle (Asada 1999, 2006), which includes the Mehler reaction of O_2 reduction by PSI (Mehler 1951), occurs by the photoreduction of O_2–H_2O at the reducing side of PSI via electrons generated from H_2O in PSII ($H_2O \rightarrow PSII \rightarrow PSI \rightarrow O_2 \rightarrow H_2O$) (Fig. 7d). The superoxide (O_2^-) formed in this reaction is scavenged by superoxide dismutase (SOD) and ascorbate peroxidase (APX) with consumption of NADPH (Asada 1999, 2006). The consumption of NADPH by the water–water cycle allows linear electron transport to continue, thereby producing ATP. Thus, the water–water cycle is eventually coupled to the generation of ΔpH, which drives ATP synthesis without NADPH accumulation. It should be noted that ROS production under excess light is accelerated not only at PSI but also at PSII, although each photosystem produces different ROS types; superoxide (O_2^-) and hydrogen peroxide (H_2O_2) in PSI and singlet-state oxygen ($^1O_2$) in PSII (for a review, see Asada 2006). To avoid such oxidative stress, chloroplasts detoxify ROS effectively using multiple enzymes, including SOD, APX and peroxiredoxin (Prx).

In the leaves of most C3 species, the water–water cycle contributes <5 % of linear electron transport even when CO_2 assimilation is inhibited (Clarke and Johnson 2001; Ruuska et al. 2000), but in rice leaves this cycle appears to operate at a substantial level during photosynthetic induction (Makino et al. 2002). Thus, the water–water cycle likely plays a photoprotective role by ROS detoxification and dissipation of excess energy, and could also balance the levels of ATP and reductants (for reviews, see Asada 1999; Miyake 2010; Ort and Baker 2002).

It should be noted that, to minimize the effects of oxidative stress, plants have also evolved a non-enzymatic antioxidant system, such as low-molecular weight antioxidants of plant cells (e.g., glutathione, ascorbate, tocopherol and carotenoids) (for a review, see Apel and Hirt 2004; DellaPenna and Pogson 2006; Foyer et al. 2006). Mutants with decreased contents of ascorbic acid are hypersensitive to stress (Conklin et al. 1996). Moreover, overexpression of β-carotene hydroxylase in Arabidopsis leads to increased amounts of xanthophyll in chloroplasts, resulting in enhanced tolerance to oxidative stress (Davison et al. 2002). Studies using various double knockout mutants in Arabidopsis showed compensatory effects of ROS scavengers, including tocopherol, ascorbate and glutathione (Kanwischer et al. 2005). The enhancement of chloroplast antioxidant defenses has proved to be one of the most effective ways of protecting plant cells from abiotic stress (Chang et al. 2009; Ishikawa and Shigeoka 2008).

Metabolic interactions between chloroplasts and mitochondria: the malate–oxaloacetate (OAA) shuttle

NADPH generated by photosynthetic electron transport under high light can be re-oxidized by the mitochondrial respiratory chain, in which NADPH is consumed by the reduction of OAA to malate and the malate is exported from chloroplasts to mitochondria (Fig. 7e). This pathway is called 'malate–OAA shuttle' (Noguchi and Yoshida 2008; Scheibe 2004).

Although metabolic interactions between chloroplasts and mitochondria have multiple physiological consequences, the contribution of the mitochondria as an electron sink for photosynthesis in vivo is still unclear (for a review, see Noctor et al. 2004). The malate–OAA shuttle appears to have low capacity to regulate the ATP/NADPH ratio (Scheibe et al. 2005). However, in transgenic potato with reduced levels of malate dehydrogenase (MDH), the malate–OAA shuttle can contribute up to 10 % of total electron flow from PSII (Laisk et al. 2007). Thus, mitochondrial respiration could neutralize excess photosynthetic reducing power and prevent oxidative damage of thylakoid membranes and other cellular components (Noguchi and Yoshida 2008; Raghavendra and Padmasree 2003).

The photorespiration pathway

Since any efficient sink for electrons produced by water splitting in PSII may lower the risk of photoinhibition, it is relevant to include reactions of CO_2 assimilation itself and photorespiration (Fig. 7f). In the Calvin–Benson cycle, Rubisco can fix both CO_2 in photosynthesis and O_2 in photorespiration (Bauwe et al. 2010). Photosynthetic carbon fixation produces two 3-phosphoglycerate (PGA) molecules for every carbon fixed, whereas photorespiration produces one PGA and one 2-phosphoglycolate, which is recycled to PGA with the loss of CO_2 and ammonia. Thus, the photorespiratory pathway can be considered to consist of the photorespiratory carbon and nitrogen cycles. Photosynthesis results in net fixation of CO_2, whereas the photorespiratory pathway requires ATP and releases previously fixed CO_2. Photorespiration rate increases with a decrease in the CO_2/O_2 ratio in the chloroplast, and also under drought and high temperature (Ogren 1984; Sage et al. 2012). At current atmospheric CO_2 concentrations and 30 °C, the rate of photorespiratory CO_2 release from the mitochondria is approximately 25 % of the rate of net CO_2 assimilation (Sage et al. 2012).

Although photorespiration is generally seen as a wasteful pathway, photorespiration is thought to act as a mechanism by which excess light energy can be used, reducing photodamage in the chloroplast (André 2011). The impairment of the photorespiratory pathway diminishes CO_2 assimilation (because of the shortage of metabolites in the Calvin–Benson cycle and accumulation of intermediates of the photorespiratory pathway that can inhibit the Calvin–Benson cycle) and accelerates photoinhibition (Kozaki and Takeba 1996; Osmond 1981). In Arabidopsis mutants with impairments of ferredoxin-dependent glutamate synthase, serine hydroxymethyltransferase, glutamate/malate transporter, and glycerate kinase, photoinhibition caused by the impairment of the photorespiratory pathway is due to inhibition of the repair of photodamaged PSII, not acceleration of PSII photodamage (Takahashi et al. 2007). Therefore, the photorespiratory pathway could play a role in maintaining PSII repair by maintaining energy utilization in the Calvin–Benson cycle, which is important for decreasing ROS generation under stress.

Recent findings on the regulatory mechanisms of photosynthesis under fluctuating light

Analysis in several Arabidopsis mutants indicates that PGR5/PGRL1-dependent cyclic electron transport around PSI is crucial for photosynthesis regulation under fluctuating light (for a review, see Yamori and Shikanai 2016), especially at early developmental stages (Suorsa et al. 2012). In wild type, rapid induction of NPQ upon increase in light intensity prevents over-reduction of the plastoquinone pool. The *pgr5* mutant and the NPQ mutants *npq1* and *npq4* induce little NPQ; fluctuating light hardly gives damage to the *npq1* and *npq4* mutants (Tikkanen et al. 2010), but it is lethal for the *pgr5* mutant (Kono et al. 2014; Suorsa et al. 2012; Tikkanen et al. 2010). Unlike the *npq4* mutant (Grieco et al. 2012; Tikkanen et al. 2015), the *pgr5* mutant cannot oxidize P700 under high light, and this defect leads to PSI photodamage (Munekage et al. 2002). Thus, the absence of NPQ seems only to play an indirect role in response to fluctuating light. Similar to Arabidopsis *pgr5* mutants, *PGR5*-knockdown rice (Yamori et al. 2016a) suffers from fluctuating light, with PSI as the primary target of photodamage and a stunted phenotype. The cumulative strong reduction of the entire electron transport system under fluctuating light for a couple of hours would cause a strong reducing burst at the acceptor side of PSI, leading to photodamage at PSI (Kono et al. 2014; Yamori et al. 2016a). Therefore, in higher plants the PGR5/PGRL1-dependent pathway is essential for effective responses to considerable fluctuations of light intensity and for avoiding photodamage (for a review see, Yamori and Shikanai 2016).

In rice, the impairment of NDH-dependent cyclic electron transport around PSI reduces photosynthetic rate under fluctuating light, leading to PSI photoinhibition, and consequently reduces biomass (Yamori et al. 2016a). During low-light phases, the NDH-dependent pathway maintains the electron transport chain on the acceptor side of PSI oxidized, which seems to be essential to prevent PSI over-reduction during subsequent high-light phases. This finding is supported by the important role of NDH-dependent PSI cyclic electron transport in regulation of the chloroplast redox state under constant low light, when light reactions limit photosynthesis (Yamori et al. 2015). In Arabidopsis, even the complete absence of the NDH complex does not reduce growth and photosynthesis under fluctuating light (Kono et al. 2014; Suorsa et al. 2012), indicating an interspecific difference in the physiological role of NDH-dependent cyclic electron transport around PSI under fluctuating light. This difference may depend on the activity of other alternative electron transport pathways, including the water–water cycle (Yamori and Shikanai 2016).

During acclimation to growth light environments, many plants change biochemical composition and morphology (e.g., Smith 1982; Terashima et al. 2005). Acclimation to low light enhances nitrogen allocation to components involved in light acquisition (e.g., chlorophylls and light-harvesting complexes), whereas acclimation to high light enhances components involved in light energy utilization (e.g., Rubisco and other Calvin–Benson cycle enzymes) and photoprotective potential. Photosynthetic acclimation to fluctuating light would require specific mechanisms, because plants acclimated to low light cannot cope with high light, and plants acclimated to high light cannot use low light efficiently. In rice, both PGR5/PGRL1-dependent and NDH-dependent cyclic electron transport around PSI sustain photosynthesis and plant growth under fluctuating light (Yamori et al. 2016a). The highly responsive regulatory system controlled by cyclic electron transport around PSI could optimize photosynthesis and plant growth under naturally fluctuating light (Yamori and Shikanai 2016).

Future perspectives

Despite extensive research on improving photosynthesis to increase crop yields (Yamori 2013; Yamori et al. 2016b), the photosynthetic responses to naturally fluctuating environments remains unclear. To optimize energy gain at low light and to protect the photosynthetic machinery at high light, plants have various photosynthetic regulation mechanisms that are either constitutively active or are activated when needed (Fig. 7; Demmig-Adams and Adams 1992; Niyogi 2000). It has not been clarified what would be the strategy to cope with fluctuations in each environmental factor (e.g., humidity, temperature, CO_2). Thus, it would be needed to examine a role of each photoprotective strategy in avoidance of photoinhibition under various fluctuating environmental factors. Photoprotection is an essential adaptation to prevent severe photoinhibition and reduction of photosynthesis and thus plant growth. Therefore, understanding the physiological and molecular basis of photoprotection under fluctuating environments would help to develop selection markers for breeding aimed at enhancing stress tolerance in crops and ensuring food security. Recent advances in nuclear or chloroplast genome transformation facilitate manipulation of photosynthesis. Analysis of mutants or transformants could considerably improve our understanding of photosynthetic regulation under fluctuating conditions. Additionally, understanding of the responses of photosynthesis to fluctuating environments could lead to improvements of model predictions of dynamic photosynthesis under fluctuating environments in nature.

Acknowledgments This work was supported by the Japan Science and Technology Agency, PRESTO (to W.Y.).

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