

# A basis for selecting light spectral distribution for evaluating leaf photosynthetic rates of plants grown under different light spectral distributions

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## Abstract

Relative spectral distributions of light during growth and for measurements do not only directly affect the net photosynthetic rate ( $P_n$ ), but also indirectly affect it through the interaction between the distributions of the growth and the measuring light. This paper summarizes a plausible mechanism of the interaction, some situations in which the interaction should be considered, and recommendations for selecting appropriate measuring light to evaluate photosynthesis. In agricultural and horticultural studies, the  $P_n$  should be measured under *in situ* conditions, depending on the purpose of the study. For prospective studies focusing on the evaluation of plant growth after measurements,  $P_n$  should be measured under the spectral distribution of light to which the plant will be subjected. In retrospective studies aiming to elucidate the causes of differences in growth brought about by the different growth conditions, measurements should be made under the spectral distributions of the lights under which the plants were grown. The  $P_n$  under a single spectral distribution of measuring light is only one aspect of the photosynthetic characteristics of a leaf. The obtained results must be discussed in relation to the spectral distribution of measuring light so as not to make biased evaluations.

## Abbreviations

BR-light: blue and red LED light, Chl: chlorophyll, ETR: electron transport rate, FR: far-red, LED: light-emitting diode,  $P_n$ : net photosynthetic rate, PFD: photon flux density, PPFD: photosynthetic photon flux density, PSI: photosystem I, PSII: photosystem II,

## Keywords

Excitation energy distribution, Light quality, Photosystems, PSII, PSI

## Introduction

The photosynthetic rate is one of the most important and fundamental aspects for plant growth. In many studies this rate is measured, evaluated, and compared among the leaves of plants cultivated under different conditions. The measured rates are also used to calculate other photosynthesis-related indices, such as photosynthetic light-, water-, and nitrogen-use efficiencies. In agricultural and horticultural researches, the effectiveness of treatments is sometimes discussed based on the measured photosynthetic rates and calculated indices.

A number of researches have reported that the relative spectral photon flux density (PFD) distribution of light used for measurement (i.e. measuring light or actinic light) affects leaf net photosynthetic rates ( $P_n$ ) (e.g. McCree, 1972; Inada, 1976). To eliminate this direct effect from the comparison,  $P_n$  is usually measured under a common spectral distribution of measuring light irrespective of growth conditions in agricultural and horticultural studies. One of the most widely-used measuring lights is a mixture of blue and red light (BR-light) provided by light-emitting diodes

(LEDs) installed in commercial photosynthesis analysis systems (e.g. LI6400XT, LI-COR Inc., Lincoln, NE; GFS-3000, US, Heinz Walz GmbH, Effeltrich, Germany). The use of artificial light sources enables precise control of the spectral distribution of measuring light on the leaf, and therefore, ensures reproducibility and reliability among experiments.

Walters (2005) noted that photosynthetic rates measured with a relative spectral distribution of light different from that of the growth light do not necessarily reflect the functioning of photosynthesis under the actual growth conditions. Indeed, we have demonstrated this problem in  $P_n$  measurements in our recent experiment (Murakami et al., 2016). In that experiment, cucumber seedlings were grown under white LED without and with supplemental far-red (FR) LED light (W and WFR, respectively), and the  $P_n$  of the leaves was subsequently compared under BR-light and under light with a relative spectral distribution approximating to that of sunlight ('artificial' sunlight). The  $P_n$  of W-grown-leaves was greater than that of WFR-grown-leaves under BR-light, while the rates were comparable under the artificial sunlight (Murakami et al., 2016). Based on the results obtained from measurement under BR-light, the prospective leaf photosynthetic rate (i.e. leaf photosynthetic rates after the measurements) of WFR-grown-plants may be evaluated to be smaller than that of W-grown-plants, despite the comparable rates under sunlight.

The effect of the relative spectral distribution of growth light on  $P_n$  depends on the distribution of measuring light. In other words, the interaction between the relative spectral distributions of growth light and measuring light affect the  $P_n$  of a leaf. In this short article, we describe a plausible mechanism for this interaction, based on the excitation energy distribution balance between the photosystems. We then suggest situations in which the interaction should be particularly considered. We also discuss good practice for selecting measuring light with appropriate relative spectral distributions for  $P_n$  evaluations. Several mechanisms other than the excitation balance, such as stomatal responses (Shimazaki et al., 2007), photoinactivation (Zavafer et al., 2015), and vertical PFD profile within a leaf (Terashima et al., 2009) affect photosynthesis via the relative spectral distribution of measuring light. Although these subjects are not discussed in this article, the cited articles are available for these topics.

## Plausible origin of the interaction

We first summarize the physiological basis of photosynthetic electron transport, which is required to understand the mechanism of the interaction. Light energy absorbed by a leaf drives photosynthetic electron transport,  $O_2$  evolution, and  $CO_2$  uptake. In higher plants, the photosynthetic electron transport chain is anchored by photochemical reactions that occur at the two photosystems; PSII and PSI. The excitation energy derived from absorbed photons and transferred to the reaction centers of the photosystems is consumed by photochemical reactions. The serial photochemical reactions at PSII and PSI enable electron transfer from water to  $NADP^+$ , via the so-called Z scheme.

The two photosystems—PSII and PSI—represent different spectral distributions of light absorption due to their different compositions of binding pigments, mainly chlorophyll (chl) *a* and chl *b*. Within the chl absorption band (approximately 350–750 nm), longer wavelengths of light ( $> 680$ – $690$  nm) are estimated to be preferentially absorbed by PSI, and PSI is drastically overexcited compared with PSII (Fig. 1; Evans and Anderson, 1987; Hogewoning et al., 2012; Wientjes et al., 2013; Laisk et al., 2014). This is because only chl *a* can absorb longer wavelengths of light, and PSI contains more chl *a* than does PSII. In contrast, monochromatic light at shorter wavelengths ( $< 680$ – $690$  nm) is estimated to be preferentially absorbed by PSII, or evenly absorbed by both photosystems (Fig. 1; Evans and Anderson, 1987; Hogewoning et al., 2012; Wientjes et al., 2013; Laisk et al., 2014). These wavelength dependencies of the excitation balance between PSII and PSI determine the excitation energy distribution (EED)—the fraction of the excitation energy distributed to PSII (or PSI) to that absorbed by the leaf or by the photosystems—under a given relative spectral distribution of light. The idea of EED is adopted in the following equations for ETR estimation originated from Genty et al. (1989),

$$ETR = PFD \times \alpha_{\text{leaf}} \times \beta_{\text{leaf}} \times Y_{\text{II}},$$

$$ETR = PFD \times \alpha_{\text{PS}} \times \beta_{\text{PS}} \times Y_{\text{II}},$$

where  $\alpha_{\text{leaf}}$  (frequently assumed to be 0.84) and  $\alpha_{\text{PS}}$  are absorptances of the leaf and the photosystems,  $\beta_{\text{leaf}}$  (frequently assumed to be 0.50) and  $\beta_{\text{PS}}$  are EEDs to PSII on the bases of the absorptions by the leaf and by the photosystems, and  $Y_{\text{II}}$  (also known as  $\Phi_{\text{PSII}}$ ,  $F_q'/F_m'$ , or  $\Delta F/F_m'$ ) is a photochemical quantum yield of PSII obtained from

chl fluorescence measurement. Although  $\beta_{\text{leaf}}$  is frequently assumed to be 0.50, it is not always valid as mentioned above. Lights with different spectral distributions are sometimes categorized into PSII- and PSI-light based on the  $\beta_{\text{PS}}$  approximated from their relative spectral distributions and the spectrum of excitation balance (i.e. Fig. 1)—mainly judged by the proportions of PFDs in the FR waveband (e.g. Chow et al., 1990; Melis, 1991; Pfannschmidt et al., 2001, 2009; Dietzel et al., 2008, 2011; Hogewoning et al., 2012).

Because the photosynthetic electron transport reactions occur in series, the electron transport rate (ETR) is limited by the slowest step (Fig. 2). When there is excess excitation energy at PSII (i.e. under PSII-light), the smaller amount of excitation energy distributed to PSI results in lower potential ETR at PSI than that at PSII. In this case, the smaller potential ETR at PSI limits the bulk ETR and PSII represents a smaller ETR than the potential that by decreasing the photochemical quantum yield (Fig. 2C). When PSI absorbs excess excitation energy (i.e. under PSI-light), the excitation energy distributed to PSII limits the ETR and lowers the yield of PSI (Fig. 2B). In both cases, the excess energy is dissipated mainly as heat, thereby leading to a lower photosynthetic quantum yield—ETR per absorbed photons by the photosystems—than that under light with suitable EED for the leaf. Therefore, balancing the EED between PSII and PSI is essential for plants to retain a high photosynthetic quantum yield. Prolonged imbalances in the EED are supposed to damage leaves by generating reactive oxygen species, which cause oxidative damage to chloroplast components (for reviews, see Asada, 1999, 2006).

Apparently, the EED at a given relative spectral distribution of light is affected by the composition of the thylakoid components, especially the stoichiometry between PSII and PSI. The stoichiometry appears to adjust to the relative spectral distribution of the growth light. When growth light was changed from PSII-light to PSI-light, the relative amount of the reaction center complex of PSII to that of PSI in leaves increases; conversely, when changed from PSI-light to PSII-light, the relative amount decreases (e.g. Melis, 1991; Pfannschmidt et al., 1999). These adjustments in the EED properties help the leaves to maintain a high photosynthetic quantum yield under growth conditions (Chow et al., 1990). As a result of these adjustments in the EED properties of a leaf, the spectrum of excitation balance (Fig. 1) differs depending on the relative spectral distribution of the growth light. Note that the categories of light, that is, ‘PSII-light’ and ‘PSI-light’, are defined for a given leaf on a relative scale, not an absolute scale. For instance, a relative spectral distribution of light that is evenly absorbed by PSII and PSI in PSII-light-grown leaves (i.e.  $\beta_{\text{PS}} = 0.5$ ; Fig. 2A), can overexcite PSII in PSI-light-grown leaves (i.e.  $\beta_{\text{PS}} > 0.5$ ; Fig. 2C). In the short term within an hour, an imbalance in the EED is, at least partly, relieved by the reversible allocation of the light-harvesting antenna complexes of PSII between PSII and PSI (state transition; for a review, see Goldschmidt-Clermont and Bassi, 2015). Although a slight imbalance in the EED might be compensated for by state transitions, the long-term adjustments in the EED properties are thought to occur when state transitions are insufficient to counterbalance the uneven EED (Dietzel et al., 2008).

The relative spectral distribution of growth light affects the EED properties of a leaf. This modifies the responses of ETR, and therefore that of  $P_n$ , to the relative spectral PFD distribution of measuring light. Thus, the relative spectral distributions of growth light and measuring light do not only directly affect the  $P_n$ , but also indirectly affect it through the interaction between the distributions of the growth and the measuring lights. This expected interaction has been reported in several researches (Chow et al., 1990; Walters and Horton, 1995; Hogewoning et al., 2012; Murakami et al., 2016). In their pioneering research, Chow et al. (1990) grew *Pisum sativum* plants under light provided by cool-white fluorescent lamps with yellow Plexiglas (PSII-light) and incandescent bulbs with red Plexiglas (PSI-light) and measured the photosynthetic quantum yield of  $\text{O}_2$  evolution— $\text{O}_2$  evolution rate per absorbed photons by the leaf—under the PSII- and PSI-lights reciprocally. When measured under PSII-light, the yield was higher in the PSII-light-grown leaves than in the PSI-light-grown leaves; when measured under PSI-light, in contrast, the yield was higher in the PSI-light-grown leaves. Similar trends were observed for the photosynthetic quantum yield of  $\text{O}_2$  evolution (in *Arabidopsis thaliana*; Walters and Horton, 1995), the photosynthetic quantum yield of  $\text{CO}_2$  uptake (in *Cucumis sativus*; Hogewoning et al., 2012), and  $P_n$  (in *C. sativus*, see also Introduction; Murakami et al., 2016).

These reports suggested that the EED properties of a leaf might be tuned to the PSII/PSI-biased level of growth light. It is expected that a leaf will perform a higher ETR per absorbed photons by the photosystems under measuring light with a PSII/PSI-biased level similar to that of the growth light (Fig. 3). When leaves grown under different spectral distributions of light are compared and evaluated under measuring light with a specific distribution, therefore, the

136 results will inevitably be biased depending on the selecting of the measuring light.

## 137 **Some situations in which the interaction should be concerned**

138 The interaction may have a considerable impact on  $P_n$ , especially when measured under low PPFDs and/or high CO<sub>2</sub>  
139 concentrations, where the ETR is a limiting factor for photosynthetic CO<sub>2</sub> fixation (von Caemmerer and Farquhar,  
140 1981). Under such conditions, any bias in the ETR is directly reflected in  $P_n$ . Therefore, the interaction should be  
141 considered carefully when measuring  $P_n$  under such conditions.

142 The mechanisms of how EED properties adapt to relative spectral distributions of growth light have not yet been  
143 fully elucidated as discussed in Murakami et al. (2016). Considering that the photosystem stoichiometry is sensitive  
144 to the relative spectral distribution of growth light (e.g. Walters and Horton, 1995), the interaction should always  
145 be taken into account whenever the  $P_n$  and related indices are compared among leaves grown with different relative  
146 spectral distributions. Particular attention should be paid to the effects of the interaction on  $P_n$ , at least when the  
147 evaluated leaves are expected to represent different EED properties, as described below.

148 Many studies published over the last decade have investigated the effects of the relative spectral distribution of the  
149 growth light on plant growth and photosynthesis (e.g. Matsuda et al., 2004, 2007, 2008; Hogewoning et al., 2010a,  
150 2010b, 2012; Shibuya et al., 2015; Trouwborst et al., 2016). Most light sources used for promoting photosynthetic  
151 and growth rates, such as fluorescent lamps, metal halide lamps, high-pressure sodium lamps, and blue, red, and  
152 white LEDs, emit light containing little PFD in the FR waveband (i.e. PSII-light; Fig. 4). This is because FR light  
153 is hardly ‘photosynthetically active’ and causes excessive stem elongation. However, several recent papers have  
154 suggested the significance of supplemental FR light on plant growth and development (for a review, see Demotes-  
155 Mainard et al., 2016). Since FR light overexcites PSI, leaves grown under PSII-light with supplemental FR light  
156 may be more similar to PSI-leaves in terms of their EED properties, compared with leaves of plants grown without  
157 supplemental FR light. Therefore, comparing the  $P_n$  of leaves of plants grown with and without supplemental  
158 FR light using BR-light as the measuring light might lead to a biased evaluation because of the interaction, as  
159 demonstrated in our recent report (Murakami et al., 2016).

160 Such biases can also occur when evaluating the vertical profiles of photosynthetic characteristics of individual leaves  
161 of plants grown in closed canopy. While leaves in the upper layers are acclimated to sunlight, those in the lower  
162 layers are acclimated to sunlight that has penetrated through the upper leaves. Due to the higher transmittance in  
163 the FR waveband of a leaf, the transmitted light incident on lower leaves contains a relatively greater proportion of  
164 PFD in the FR waveband (Fig. 4) and is therefore PSI-light. Consequently, when measured using BR-light, the  $P_n$   
165 of upper leaves might be overestimated while that of lower leaves might be underestimated.

## 166 **Selecting appropriate relative spectral distributions of measuring light for** 167 **evaluating photosynthetic rates**

168 Ideally, photosynthetic rates and related indices should be evaluated under *in situ* conditions. In prospective studies  
169 focusing on plant growth after measurements, the evaluations should be made under the spectral distribution of  
170 light to which the plant will be subjected. For instance, when evaluating transplants grown under artificial lighting  
171 (e.g. Kozai, 2007), the measurements should be made under sunlight because the plants will be transferred to a  
172 greenhouse or an open field and cultivated under sunlight. However, the measurements under actual sunlight may  
173 be less reliable because of the short-term fluctuations and diurnal changes in the spectral distributions. In this case,  
174 therefore, the use of artificial light sources, which provide light with relative spectral distributions approximating to  
175 that of sunlight (e.g. Fujiwara et al., 2013), may be necessary to make comparable, reproducible and reliable *in situ*  
176 evaluations. In retrospective studies that aim to explain differences in growth brought about by the different growth  
177 conditions, the measurements should be made under the spectral distributions of light that the plants received during  
178 the treatments. For instance, when differences in dry weight between plants grown under white LEDs and those

grown under white fluorescent lamps are analyzed and  $P_n$  is used as an explanatory variable, the measurements should be made using the white LEDs for the plants grown under the LEDs and using the white fluorescent lamps for those grown under the fluorescent lamps. In both prospective and retrospective studies, these simple *in situ* evaluations will eliminate the problems caused by the interaction between the growth and the measuring lights.

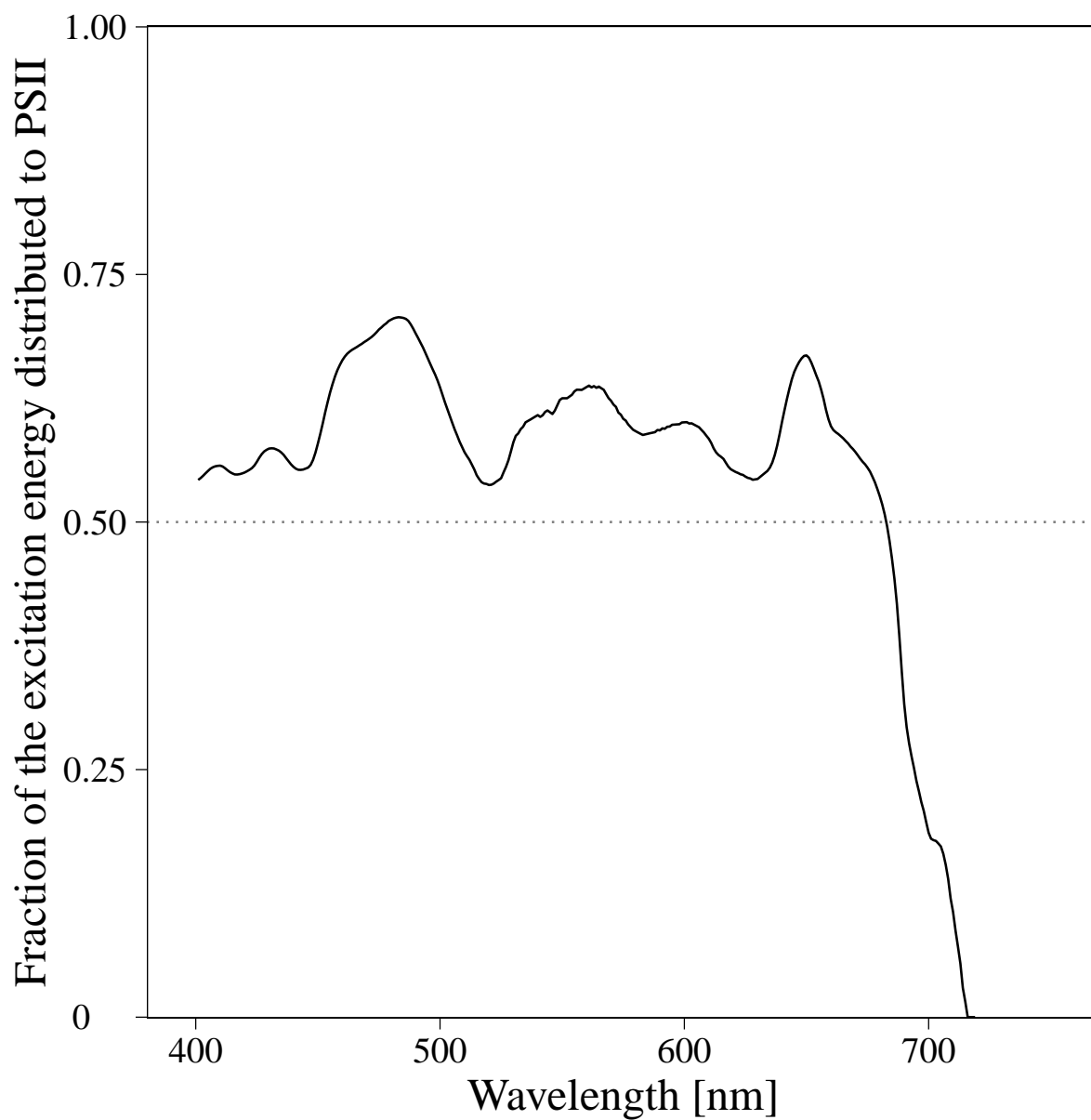
On the other hand, in descriptive studies that hardly make assumption about the *in situ* conditions (i.e. fundamental studies),  $P_n$  evaluations should be made under several relative spectral distributions of light including PSII- and PSI-light. It is better for researchers to report the ‘general’ photosynthetic characteristics of the leaves in these studies. Therefore, the interaction should be tested so as not to make biased evaluations. If there is any interaction, the results should be descriptively reported and should not be generalized. When the measurements are made only under a single spectral distribution of measuring light because there is no other option, detailed information on the light source (e.g. model number) must be described in the materials and methods section so that the reader knows the spectral distribution.

## Concluding remarks

The  $P_n$  under a relative spectral PFD distribution of measuring light is only one aspect of the photosynthetic characteristics of a leaf. Therefore, the obtained results must be discussed in relation to the relative spectral distributions of the growth and measuring lights. Photosynthesis should be evaluated under *in situ* light or several relative spectral distributions of light so that the evaluation is not biased by the interaction between the spectral distributions of the growth and measuring lights. Imitating the various spectral distributions of light incident on the leaf for *in situ* evaluation might be difficult or impossible for technical reasons. In addition, measuring the  $P_n$  under several spectral distributions is time-, resource-, and labor-consuming. Although these two approaches might not always be used to evaluate leaf  $P_n$ , the interaction should always be considered to make circumspect conclusions.

## Acknowledgements

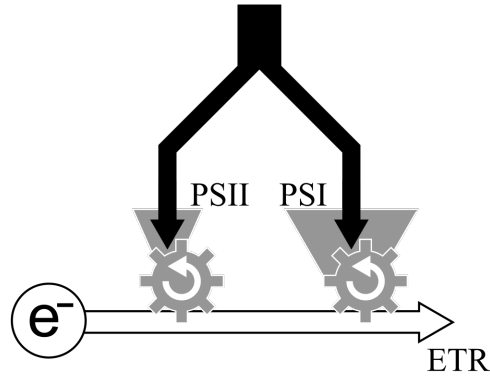
We thank Dr Sander W. Hogewoning (Plant Lighting B.V., the Netherlands) for providing data of absorbance spectra of photosystems. This work was supported by JSPS KAKENHI Grant Number 26-9372.



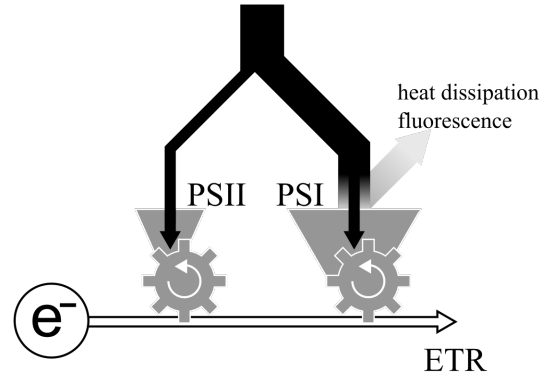
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204 Fig. 1 Typical excitation balance between photosystems in response to wavelength of measuring light. Spectrum  
 205 was calculated from absorbance spectra of PSII and PSI complexes in solvent (Hogewoning et al. 2012) with a  
 206 little modifications. The spectrum is adjusted so that the excitation energy distributed to PSII under red LED light  
 207 matches a quantified value (55%, unpublished data).

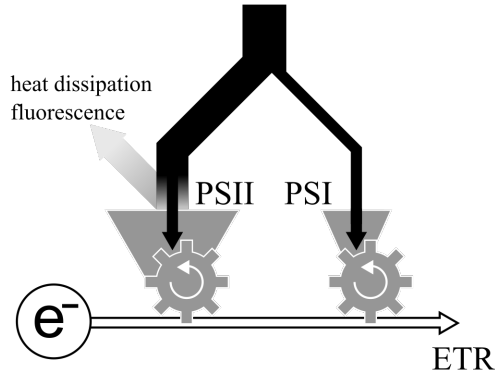
(a) GL: PSII-light, ML: PSII-light



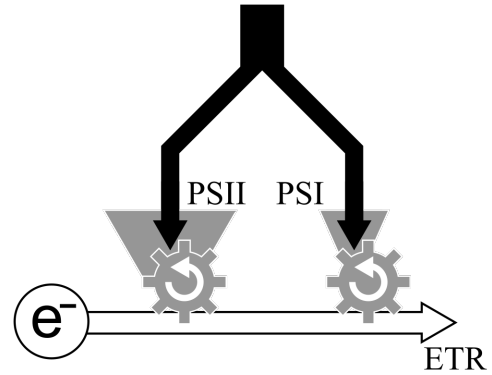
(b) GL: PSII-light, ML: PSI-light



(c) GL: PSI-light, ML: PSII-light

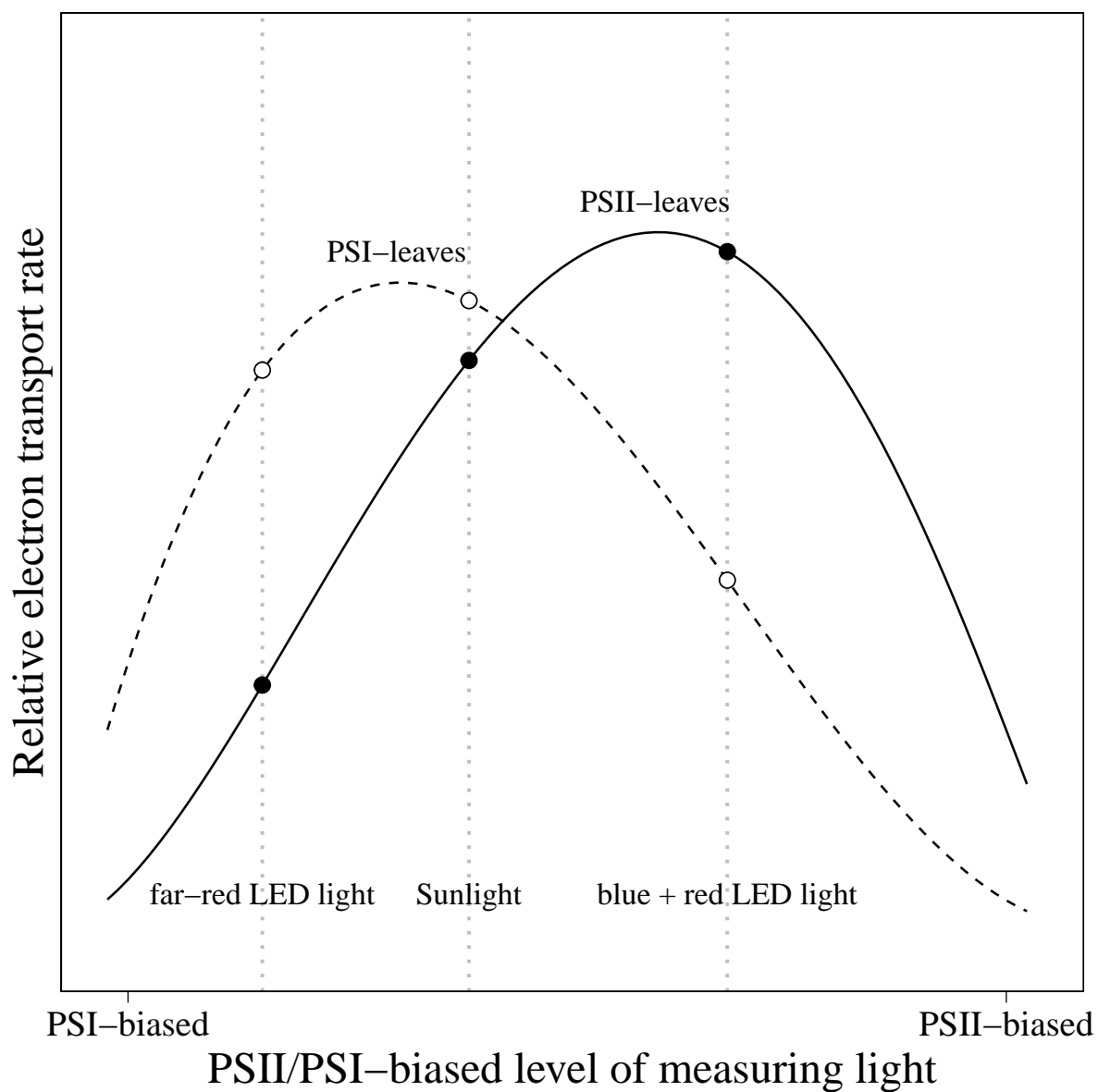


(d) GL: PSI-light, ML: PSI-light



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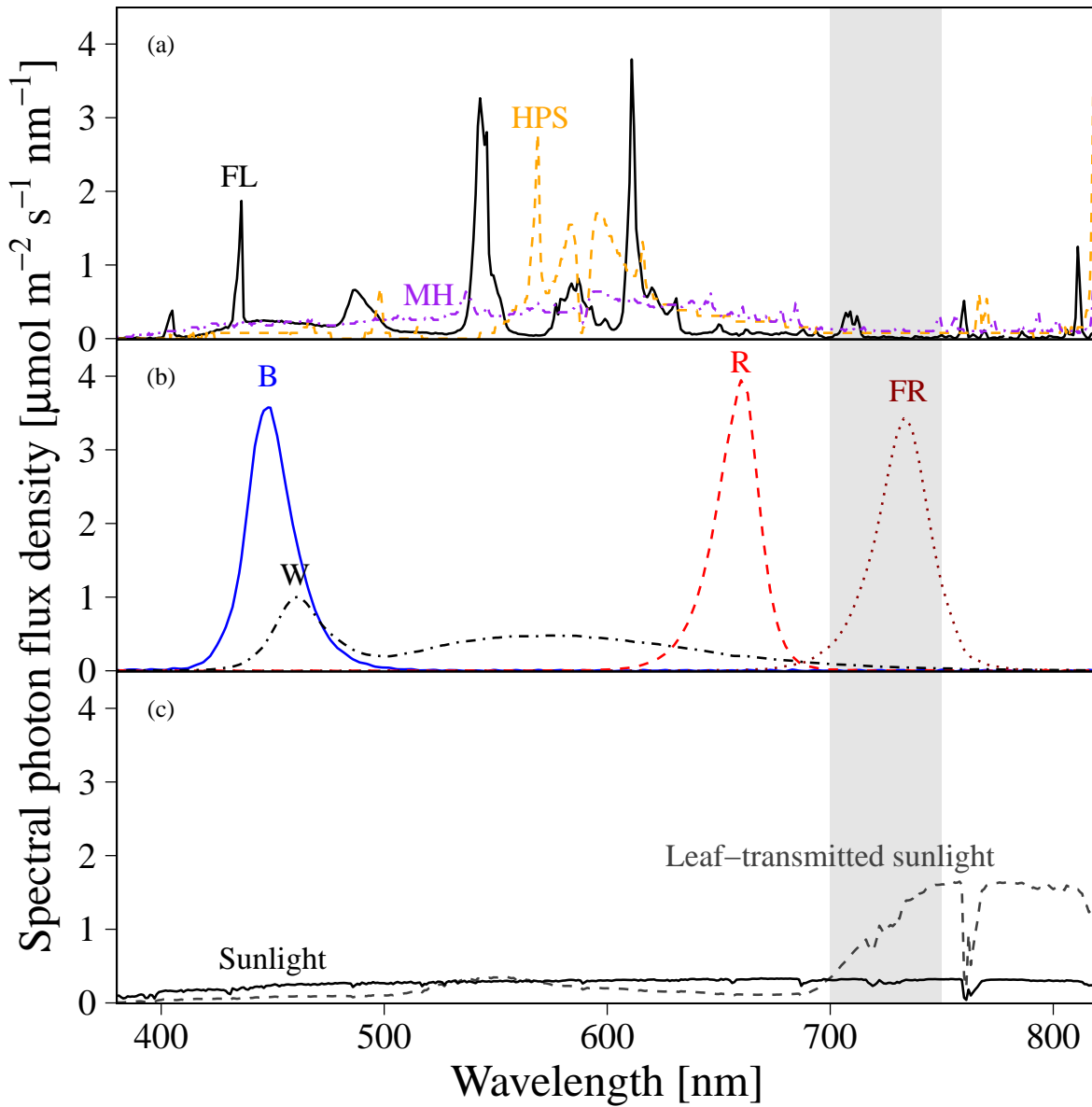
209 Fig. 2 Conceptual diagrams of effects of excitation energy distribution between photosystems (PSII and PSI) on  
 210 photosynthetic electron transport rate (ETR). Electron transport is driven by photochemical reactions at reaction  
 211 centers (gears) consuming the distributed excitation energy. Figure shows electron flow (white lines) and energy  
 212 flow (black lines) in leaves grown under PSII-light (a, b) and PSI-light (c, d) and measured using PSII-light (a, c)  
 213 and PSI-light (b, d). Excitation energy distribution properties of leaves are adjusted depending on growth light. GL:  
 214 growth light, ML: measuring light.



215

216 Fig. 3 Conceptual diagram of photosynthetic electron transport rates per absorbed photons by the photosystems of  
 217 leaves grown under PSII-light (PSII-leaves) and PSI-light (PSI-leaves) in response to the PSII/PSI-biased level of  
 218 measuring light.





219

220 Fig. 4 Spectral photon flux density distributions of light provided by (a) fluorescent lamp (FL; FPL55EX-N<sup>1</sup>); metal  
 221 halide lamp (MH; M220FCELS-W/BUD<sup>1</sup>); high-pressure sodium lamp (HPS; NH220FLS<sup>1</sup>), (b) blue (B; HBL3-  
 222 3S55-LE<sup>2</sup>), red (R; SRK3-3A80-LE<sup>2</sup>), far-red (FR; L735-36AU<sup>3</sup>), and white (W; NSPW310DS<sup>4</sup>) light-emitting  
 223 diodes, and (c) incident and leaf-transmitted sunlight. Distributions at a photon flux density of 100  $\mu\text{mol m}^{-2} \text{s}^{-1}$   
 224 within 400–750 nm are shown. Grey shading indicates far-red waveband (700–750 nm). Distribution of sunlight is  
 225 from International Electrotechnical Commission Standard 60904–3 (International Electrotechnical Commission).  
 226 Distribution of leaf-transmitted sunlight was calculated from that of incident sunlight and transmittance spectrum  
 227 of cucumber leaf (Murakami et al. 2016).<sup>1</sup>IWASAKI ELECTRIC CO., LTD, Tokyo, Japan; <sup>2</sup>Tricon Co., Shimane,  
 228 Japan; <sup>3</sup>Epitex Inc., Kyoto, Japan; <sup>4</sup>Nichia Chemical Industries Ltd., Tokushima, Japan.

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