Evaluating effects of light quality: A basis for selecting the spectral photon flux density distribution of light for measuring photosynthetic rates of leaves

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Abstract

The spectral photon flux density distributions (SPDs) of light during growth and for measurements do not only directly affect the net photosynthetic rate (P_n), but also interacts on it. 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. The P_n should be measured under *in situ* conditions, depending on the purpose of the study. For studies focusing on plant growth after measurements, P_n should be measured under the SPD of light that the plant will be subjected to. In retrospective studies aiming to elucidate the causes of differences among experimental groups, measurements should be made under the SPDs of the lights the plants were grown under. In descriptive studies, P_n should be evaluated under several SPDs of measuring light to understand the general photosynthetic characteristics of the leaves. The P_n under a single-pattern SPD of measuring light is only one aspect of the photosynthetic characteristics of a leaf. The obtained results must be discussed in relation to the SPD 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, SPD: relative spectral PFD distribution

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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 studies, the effectiveness of treatments is sometimes discussed based on the measured photosynthetic rates and calculated indices. Therefore, accurate measurements of photosynthetic rates are essential.

A number of studies have reported that the relative spectral photon-flux-density (PFD) distribution (SPD) 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 SPD of measuring light irrespective of leaf 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. LI6400 and LI6400XT, LI-COR Inc., Lincoln, NE; GFS-3000, Heinz Walz GmbH, Effeltrich, Germany). The use of artificial light sources enables precise control of the photosynthetic PFD (PPFD) and SPD incident on the leaf, and therefore, ensures reproducibility and reliability among experiments.

Walters (2005) noted that photosynthetic rates measured with a SPD 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 experimentally demonstrated this problem in P_n measurements in our recent study (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 SPD resembling 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 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 SPD of growth light on P_n depends on the SPD of measuring light. In other words, the interaction between the SPDs 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 an appropriate SPD for P_n measurements. Several mechanisms other than the excitation balance, such as stomatal responses (Shimazaki et al., 2007), photoinhibition (Zavafer et al., 2015), and vertical PFD profile within a leaf (Terashima et al., 2009) affect photosynthesis via the SPD of measuring light. Although these subjects are not discussed in this article, several cited articles are available for these topics.

Plausible origin of the interaction

Fundamental knowledge about photosynthetic electron transport 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 light absorption distributions due to their different compositions of binding pigments, mainly chl *a* and chl *b*. Within the chlorophyll (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 (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) under a given SPD of light. Light with a given SPD is sometimes categorized as either PSII- or PSI-light according to whether the excitation energy is preferentially distributed to PSII or PSI (e.g. Chow et al., 1990; Melis, 1991; Pfannschmidt et al., 2001, 2009; Fan et al., 2007; Dietzel et al., 2008, 2011; Hogewoning et al., 2012).

Because the photosynthetic electron transport reactions occur in series, the electron transport rate (ETR) through the thylakoid membrane 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 photochemical reaction rates at PSI than at PSII. This shortage in the EED to PSI limits the ETR, thereby leading to lower photochemical quantum yield of PSII and balaced ETR between PSII and PSI (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 and fluorescence. Consequently, the entire photosynthetic quantum yield—ETR per absorbed photons by the leaf—becomes smaller. Therefore, balancing the EED between PSII and PSI is essential for plants to retain a high photosynthetic quantum yield. Imbalanced excitation between the photosystems is 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 SPD of light is also affected by the composition of the thylakoid components, especially the stoichiometry between PSII and PSI. The stoichiometry appears to adjust to the SPD of the growth light. Under PSII-light, the relative amount of the reaction center complex of PSII to that of PSI in leaves decreases; conversely, under PSI-light, the relative amount increases to achieve a balance (e.g. Melis, 1991; Pfannschmidt et al., 1999). These adjustments in the EED properties might help the leaves to maintain a high photosynthetic quantum yield under different growth lights (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 SPD of the growth light. 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, the SPD of light that is evenly absorbed by PSII and PSI in PSII-light-grown leaves (Fig. 2A), can overexcite PSII in PSI-light-grown leaves (Fig. 2C). Therefore, the terms 'PSII-light' and 'PSI-light' are used only in a relative context. 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 (LHCII) 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 SPD of growth light affects the EED properties of a leaf. This modifies the ETR responses, and therefore the P_n, to the SPD of measuring light. Thus, the SPDs of growth light and measuring light not only directly affect the P_n, but also indirectly affect it through their interaction. This expected interaction has been reported in several studies (Chow et al., 1990; Walters and Horton, 1995; Hogewoning et al., 2012; Murakami et al., 2016). In their pioneering study, 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 O_2 evolution—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; when measured under PSI-light, the yield was higher in the PSI-light-grown leaves. Similar trends in the photosynthetic quantum yield of O_2 evolution (in *Arabidopsis thaliana*; Walters and Horton, 1995), in the photosynthetic quantum yield of CO_2 uptake (in *Cucumis sativus*; Hogewoning et al., 2012), and in P_n (in *C. sativus*, see also Introduction; Murakami et al., 2016) were observed.

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 leaf under measuring light with a PSII/PSI-biased level similar to that of the growth light (Fig. 3). When leaves grown under different SPDs of light are compared and evaluated under a specific SPD of measuring light, the results will inevitably be biased depending on the SPD of the measuring light.

Some situations in which the interaction should be concerned

The interaction may have a considerable impact on P_n, especially when it is measured under low PPFDs and/or high CO_2 concentrations, where the ETR is a limiting factor for photosynthetic CO_2 fixation (von Caemmerer and Farquhar, 1981). Under such conditions, any bias in the ETR is directly reflected in P_n. Therefore, the interaction should be considered carefully when measuring P_n under such conditions.

The mechanisms of how EED properties adapt to SPD have not yet been fully elucidated (see Murakami et al., 2016). Considering the sensitive adjustments of photosystem stoichiometry in response to the SPD of growth light (e.g. Walters and Horton, 1995), the interaction should always be taken into account whenever the P_n and related

indices are compared among leaves grown under different SPDs of light. Particular attention should be paid to the effects of the interaction on P_n, at least when the measured leaves are expected to represent different EED properties.

Several studies published over the last decade have investigated the effects of the SPD of the growth light on plant growth and photosynthesis (e.g. Matsuda et al., 2004, 2007, 2008; Hogewoning et al., 2010a, 2010b, 2012; Shibuya et al., 2015; Trouwborst et al., 2016). Growth light provided by most artificial light sources contains little FR light. In general, fluorescent lamps, metal halide lamps, high-pressure sodium lamps, and blue, red, and white LEDs used for assimilation lighting all emit typical PSII-light (Fig. 4). This is because FR light is hardly 'photosynthetically active' and promotes excessive stem elongation. However, several recent papers have suggested the significance of supplemental FR light on plant growth and development (for a review, see Demotes-Mainard et al., 2016). Since FR light overexcites PSI, leaves grown under PSII-light with supplemental FR light are more similar to PSI-leaves in terms of their EED properties, compared with leaves of plants grown without supplemental FR light. Therefore, comparing the P_n of leaves of plants grown with and without supplemental FR light using BR-light as the measuring light might lead to a biased evaluation because of the interaction, as demonstrated in our recent report (Murakami et al., 2016).

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

Selecting appropriate SPDs of measuring light for evaluating photosynthetic rates

Ideally, photosynthetic rates and related indices should be measured under *in situ* conditions. In prospective studies focusing on plant growth after measurements, the measurements should be made under the SPD of light that the plant will be subjected to. For instance, when evaluating plants grown under artificial lighting that will be transplanted (e.g. Kozai, 2007), the measurements should be made under sunlight because the plants will be transferred to a greenhouse and cultivated under sunlight. However, the measurements under sunlight may be less reliable because of fluctations in the incident PPFD. In such cases, SPD-controllable light sources might be helpful (e.g. Yano and Fujiwara, 2012; Fujiwara et al., 2013) to make *in situ* evaluations under PPFD-stable conditions and to ensure reproducibility and reliability of the results. In retrospective studies that aim to explain differences among experimental groups, the measurements should be made under the SPDs of light that the plants received during the treatments. For instance, when differences in dry weight between plants grown under white LEDs and those grown under 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 white LEDs and using the fluorescent lamps for those grown under fluorescent lamps. In both prospective and retrospective studies, these simple *in situ* measurements will eliminate the problems caused by the interaction between the growth and the measuring light.

On the other hand, in descriptive studies that hardly make assumption about the *in situ* conditions, P_n measurements should be made under several SPDs of light including PSII- and PSI-light. It is better for researchers to report on the 'general' 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-pattern of SPD of measuring light because there is no other option, the light source must be described in the materials and methods section so that the reader knows the SPD.

Concluding remarks

The P_n under a single-pattern SPD 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 SPD of the measuring light. Photosynthesis should be evaluated under *in situ* conditions or multi-pattern SPDs of measuring light so that the evaluation is not biased by the interaction between the SPDs of the growth and measureing lights. Imitating the various SPDs 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 multi-pattern SPDs 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.

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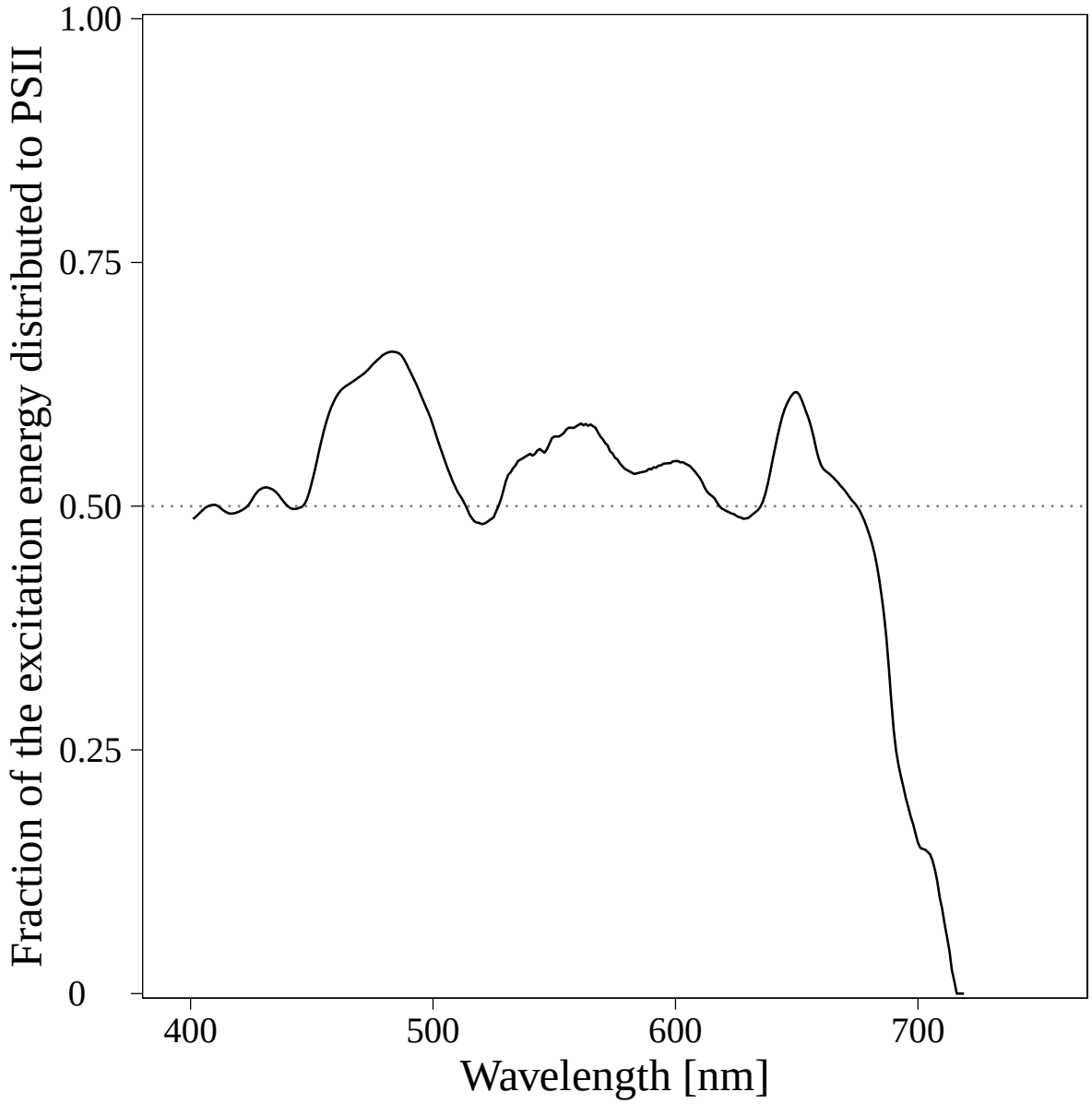

Fig. 1 Typical excitation balance between photosystems in response to wavelength of measuring light. Spectrum was calculated from absorbance spectra of PSII and PSI complexes in solvent (Hogewoning et al. 2012).

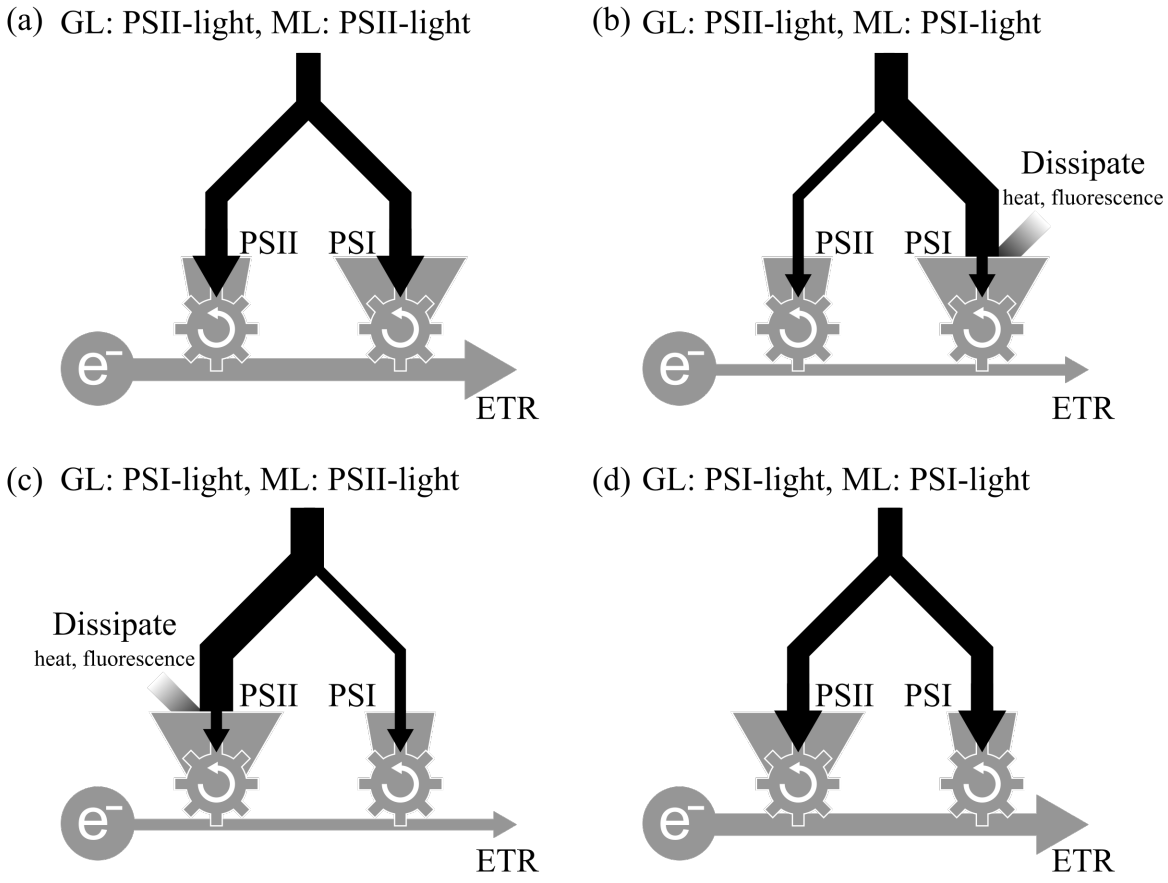

Fig. 2 Conceptual diagrams of effects of excitation energy distribution between photosystems (PSII and PSI) on photosynthetic electron transport rate (ETR). Figure shows electron flow (grey lines) and energy flow (black lines) in leaves grown under PSII-light (a, b) and PSI-light (c, d) and measured using PSII-light (a, c) and PSI-light (b, d). Excitation energy distribution properties of leaves are adjusted depending on growth light. GL: growth light, ML: measuring light.

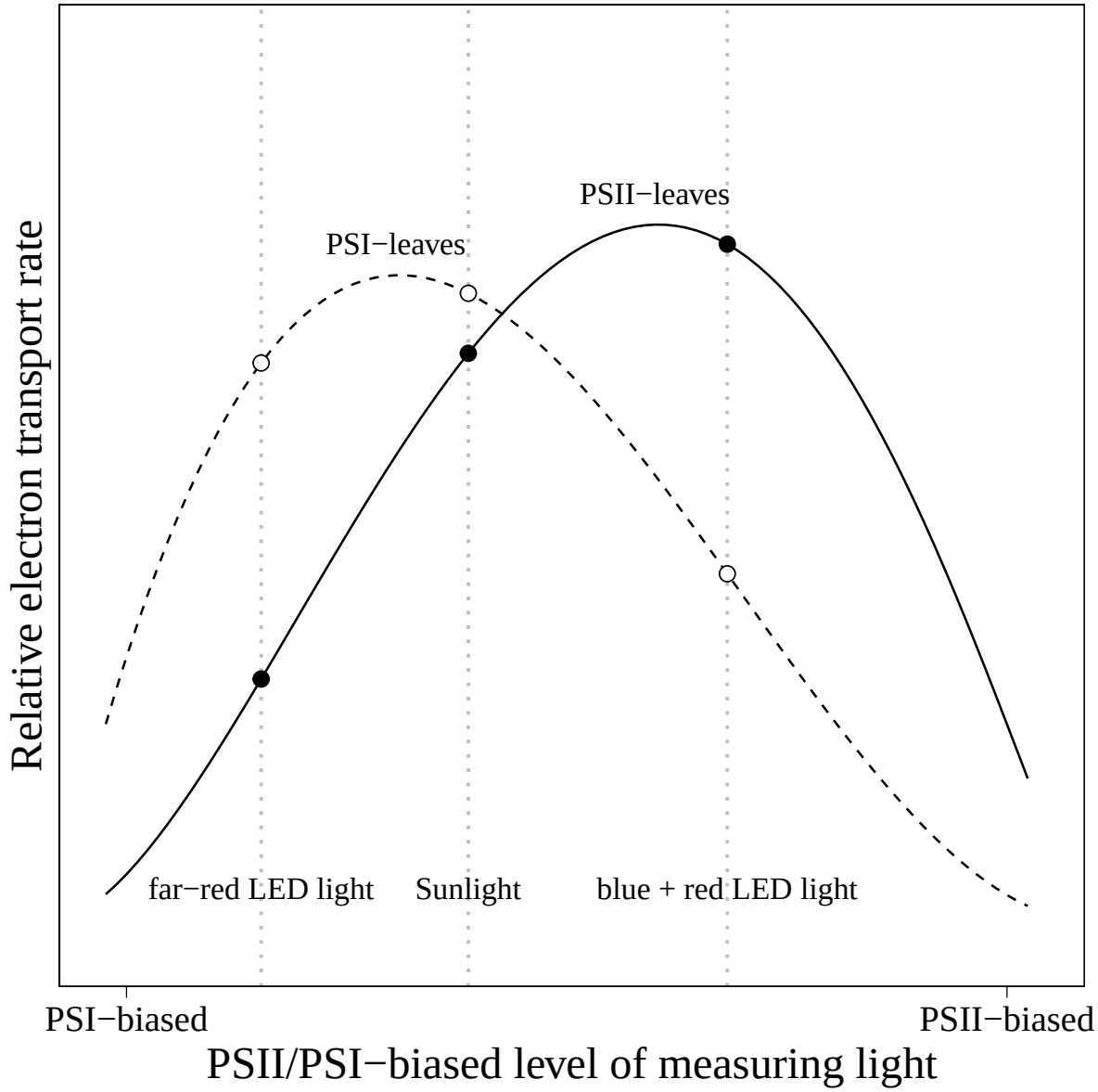

Fig. 3 Conceptual diagram of photosynthetic electron transport rates per absorbed photons by leaves grown under PSII-light (PSII-leaves) and PSI-light (PSI-leaves) in response to the PSII/PSI-bised level of measuring light.

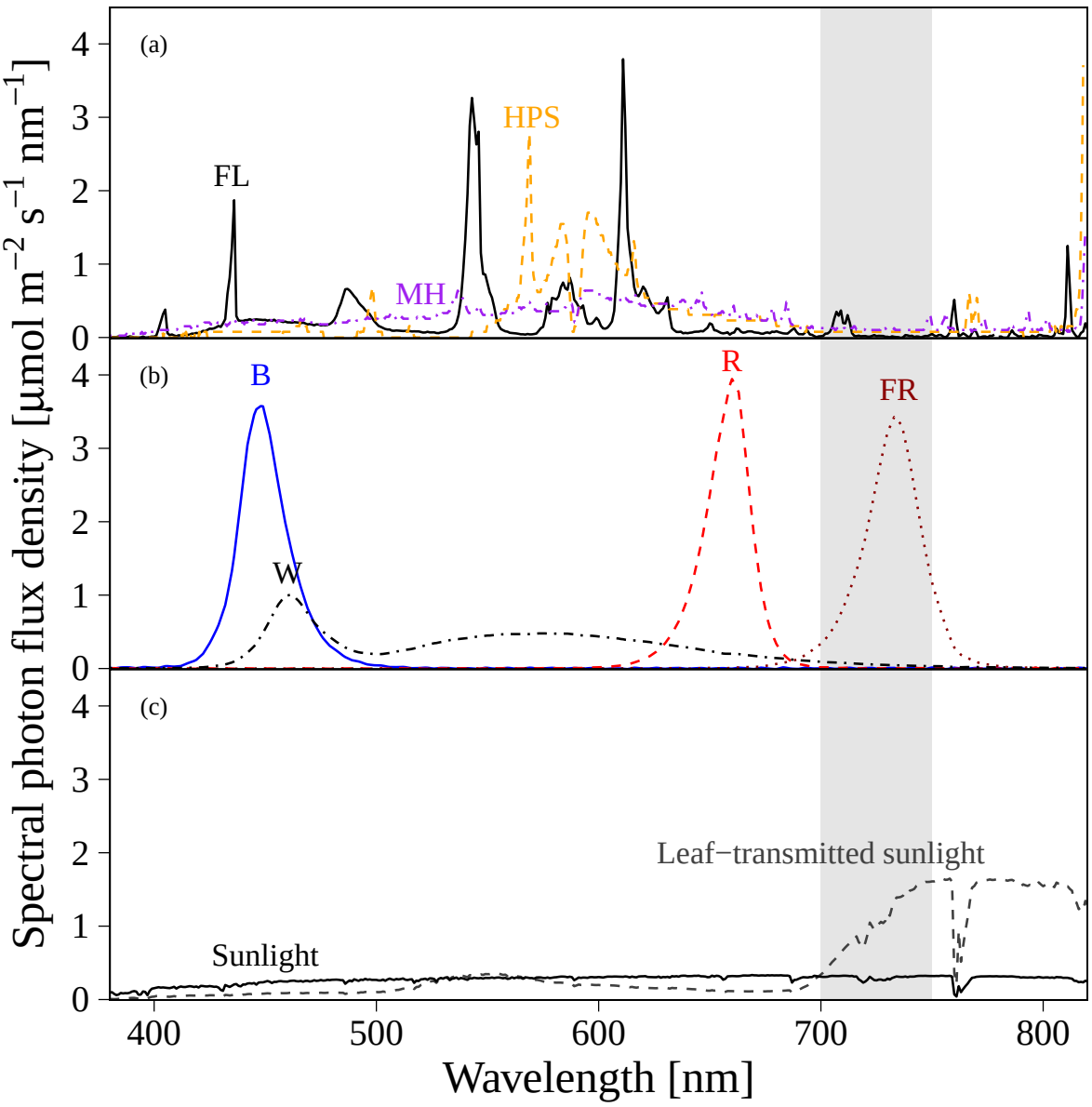

Fig. 4 Spectral photon flux density distributions of light provided by (a) fluorescent lamp (FL; FPL55EX-N[1]); metal halide lamp (MH; M220FCELS-W/BUD[1]); high-pressure sodium lamp (HPS; NH220FLS[1]), (b) blue (B; HBL3-3S55-LE[2]), red (R; SRK3-3A80-LE[2]), far-red (FR; L735-36AU[3]), and white (W; NSPW310DS[4]) light-emitting diodes, and (c) incident and leaf-transmitted sunlight. Distributions at a photon flux density of 100 µmol m^{-2} s^{-1} within 400–750 nm are shown. Grey shading indicates far-red waveband (700–750 nm). Distribution of sunlight is from International Electrotechnical Commission Standard 60904–3 (IEC Standard, 2007). Distribution of leaf-transmitted sunlight was calculated from that of incident sunlight and transmittance spectrum of cucumber leaf (Murakami et al. 2016).[1]IWASAKI ELECTRIC CO., LTD, Tokyo, Japan; [2]Tricon Co., Shimane, Japan; [3]Epitex Inc., Kyoto, Japan; [4]Nichia Chemical Industries Ltd., Tokushima, Japan.

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