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

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

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Running title: light spectral distribution for evaluating leaf photosynthesis

Abstract

Relative spectral distributions of light during growth and for measurement do not only directly affect the net photosynthetic rate (P_n), but also affect it indirectly through interaction with the spectral distribution. This letter explains a plausible mechanism of the statistical interaction, some situations in which the interaction should be considered, and recommendations for selecting appropriate spectral distributions of measuring light to evaluate photosynthesis. A leaf adjusts the excitation energy distribution balance between photosystems in response to the relative spectral distribution of growth light. This adjustment modifies the response of P_n to the relative spectral distribution of measuring light. Therefore, evaluating the P_n of leaves of plants grown under different relative spectral distributions of growth light with a single spectral distribution of measuring light causes P_n overestimation or underestimation. The obtained results must be discussed in relation to the spectral distribution of measuring light to avoid producing biased evaluations. Depending on the study purpose, P_n should be evaluated under appropriate measuring light. For instance, in retrospective studies aimed at elucidating the causes of differences in growth brought about by the growth conditions, P_n should be measured under light with the same spectral distributions as those under which the plants were grown.

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 (i.e. the spectral distribution normalized to the peak or mean value) 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. LI-6400, LI-COR Inc., Lincoln, NE, USA; GFS-3000, 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 (300 μmol m^{-2} s^{-1}) without and with supplemental far-red (FR) LED light (70 μmol m^{-2} s^{-1}) (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) at a photosynthetic PFD (PPFD) of 300 μmol m^{-2} s^{-1}. The mean P_n of W-grown-leaves (mean ± SE: 12.2 ± 0.5 μmol m^{-2} s^{-1}) was 36% greater than that of WFR-grown-leaves (8.9 ± 0.7 μmol m^{-2} s^{-1}) under BR-light (95% confident interval: +0.6 to +5.9, P = 0.027), while the mean value of W-grown-leaves (10.1 ± 0.5 μmol m^{-2} s^{-1}) were comparable to—or 3% smaller than—that of WFR-grown-leaves (10.4 ± 0.3 μmol m^{-2} s^{-1}) under the artificial sunlight (95% confident interval: −1.9 to +1.3, P = 0.65) (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 statistical 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 chl *a* can absorb longer wavelengths of light than chl *b* (e.g. Gates et al. 1965), and PSI contains more chl *a* than does PSII (e.g. Laisk et al. 2014). 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 both photosystems—under a given relative spectral distribution of light. The idea of EED is adopted in the following equations for the electron transport rate (ETR) estimation originated from Genty et al. (1989),

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

where α_{leaf} (frequently assumed to be 0.84) and α_{PS} are absorptances of the leaf and the photosystems, β_{leaf} (frequently assumed to be 0.50) and β_{PS} are EEDs to PSII on the basis of the absorptions by the leaf and by the photosystems, and Y_{II} (also known as Φ_{PSII}, F_q'/F_m', or $\Delta F/F_m'$) is a photochemical quantum yield of PSII obtained from chl fluorescence measurement. Although β_{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 β_{PS} approximated from their relative spectral distributions and the spectrum of excitation balance (Fig. 1)—mainly judged by the proportions of PFD 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). For two relative spectral distributions of light, one that presumably lowers β_{PS} (i.e. FR-rich light) is categorized into PSI-light and the other (i.e. FR-poor light) into PSII-light.

Because the photosynthetic electron transport reactions occur in series, 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 an actual ETR smaller than the potential 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 exposure to light with an imbalanced EED 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 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. $\beta_{PS} \sim 0.5$; Fig. 2a), can overexcite PSII in PSI-light-grown leaves (i.e. $\beta_{PS} > 0.5$; Fig. 2c). The opposite also holds; light that is evenly absorbed by PSII and PSI in PSI-light-grown leaves (i.e. $\beta_{PS} \sim 0.5$; Fig. 2d), can overexcite PSI in PSII-light-grown leaves (i.e. $\beta_{PS} < 0.5$; Fig. 2b). 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 response of ETR, and therefore that of P_n, to the relative spectral 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 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 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 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 O_2 evolution (in *Arabidopsis thaliana*; Walters and Horton, 1995), the photosynthetic quantum yield of 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 results will inevitably be biased depending on the selection 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 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. On the other hand, under high PPFDs and/or low CO_2 concentrations, where the ribulose-1,5-bisphosphate carboxylation rate in the Calvin cycle is a limiting factor for photosynthesis (von Caemmerer and Farquhar, 1981), the interaction is expected to be negligible because both PSII and PSI are light saturated. Contrary to this expectation, however, the interaction was detected in our previous research even in such a condition (PPFD of 1200 μmol m^{-2} s^{-1}, intercellular CO_2 partial pressure of 20 Pa). We cannot fully explain the origin of this interaction, but one possible cause of this interaction is photoinactivation of photosystems induced by the imbalanced excitation. That is, PSI of PSII-light-grown leaves under PSI-light (Fig. 2b) and/or PSII of PSI-light-grown leaves under PSII-light (Fig. 2c) might be inactivated, resulting in lower P_n. Therefore, the interaction should be considered carefully when measuring P_n irrespective of the light- and CO_2-conditions.

The mechanisms of how EED properties adapt to relative spectral distributions of growth light have not yet been fully elucidated. Considering that the photosystem stoichiometry is sensitive to the relative spectral distribution 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 with different relative spectral distributions. Mechanisms other than the adjustment of the photosystem stoichiometry might be involved in the EED properties, as discussed in Murakami et al. (2016). Particular attention should be paid to the effects of the interaction on P_n, at least when the evaluated leaves are expected to represent different EED properties, as described below.

Many studies published over the last decade have investigated the effects of the relative spectral distribution 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). Most light sources used for providing growth light, such as fluorescent lamps, metal halide lamps, high-pressure sodium lamps, and blue, red, and white LEDs, emit light containing little PFD in the FR waveband (i.e. PSII-light; Fig. 4). This is primarily because FR light is hardly ‘photosynthetically active’ and causes 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 may be 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 photosynthetic characteristics of individual leaves of plants grown in closed canopy. While leaves in the upper layers are acclimated to sunlight, those in the lower layers are acclimated to sunlight 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 PFD in the FR waveband (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 relative spectral distributions of measuring light for evaluating photosynthetic rates

Ideally, photosynthetic rates and related indices should be evaluated under in situ conditions. In prospective studies focusing on plant growth after measurements, the evaluations should be made under the spectral distribution of light to which the plant will be subjected. For instance, when evaluating transplants grown under artificial lighting (e.g. Kozai, 2007), the measurements should be made under sunlight because the plants will be transferred to a greenhouse or an open field and cultivated under sunlight. However, the measurements under actual sunlight may be less reliable because of the short-term fluctuations and diurnal changes in the spectral distributions. In this case, therefore, the use of artificial light sources, which provide light with relative spectral distributions approximating to that of sunlight (e.g. Fujiwara et al., 2013), may be necessary to make comparable, reproducible and reliable in situ evaluations. In retrospective studies that aim to explain differences in growth brought about by the different growth conditions, the measurements should be made under the spectral distributions 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 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 physiological 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 readers know 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 statistical interaction should always be considered to make circumspect conclusions.

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Captions

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

Fig. 2 Conceptual diagrams of effects of excitation energy distribution between photosystems (PSII and PSI) on photosynthetic electron transport rate (ETR). Electron transport is driven by photochemical reactions at reaction centers (gears) consuming the distributed excitation energy. Figure shows electron flow (white 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 (e.g. photosystem stoichiometry indicated as the size of inverted triangles) 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 the photosystems of leaves grown under PSII-light (PSII-leaves) and PSI-light (PSI-leaves) in response to the PSII/PSI-biased 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).

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Fig. 1

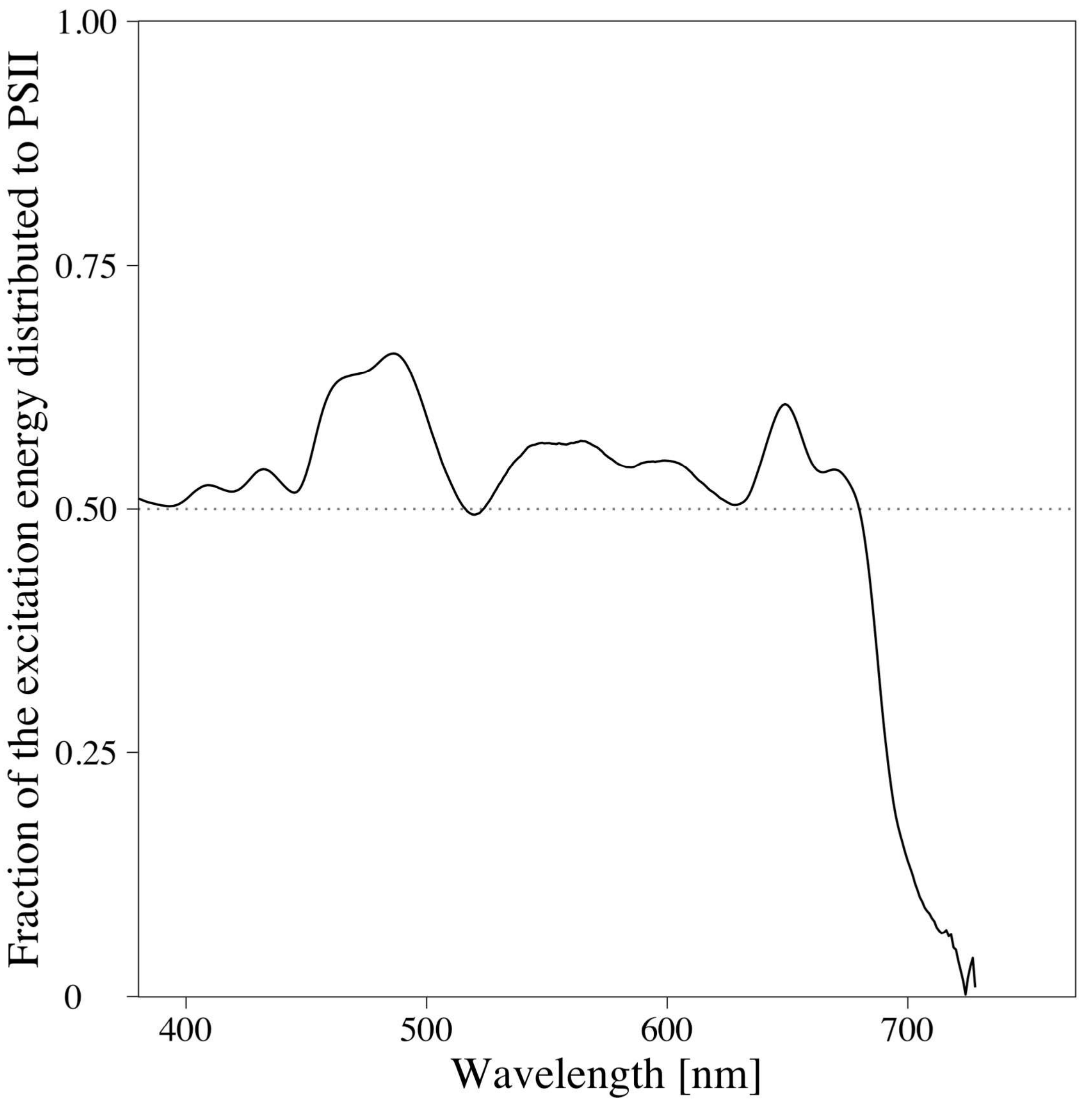
1.00
0.75
0.50
0.25
0
Fraction of the excitation energy distributed to PSII
400
500
600
700
Wavelength [nm]

Fig. 2

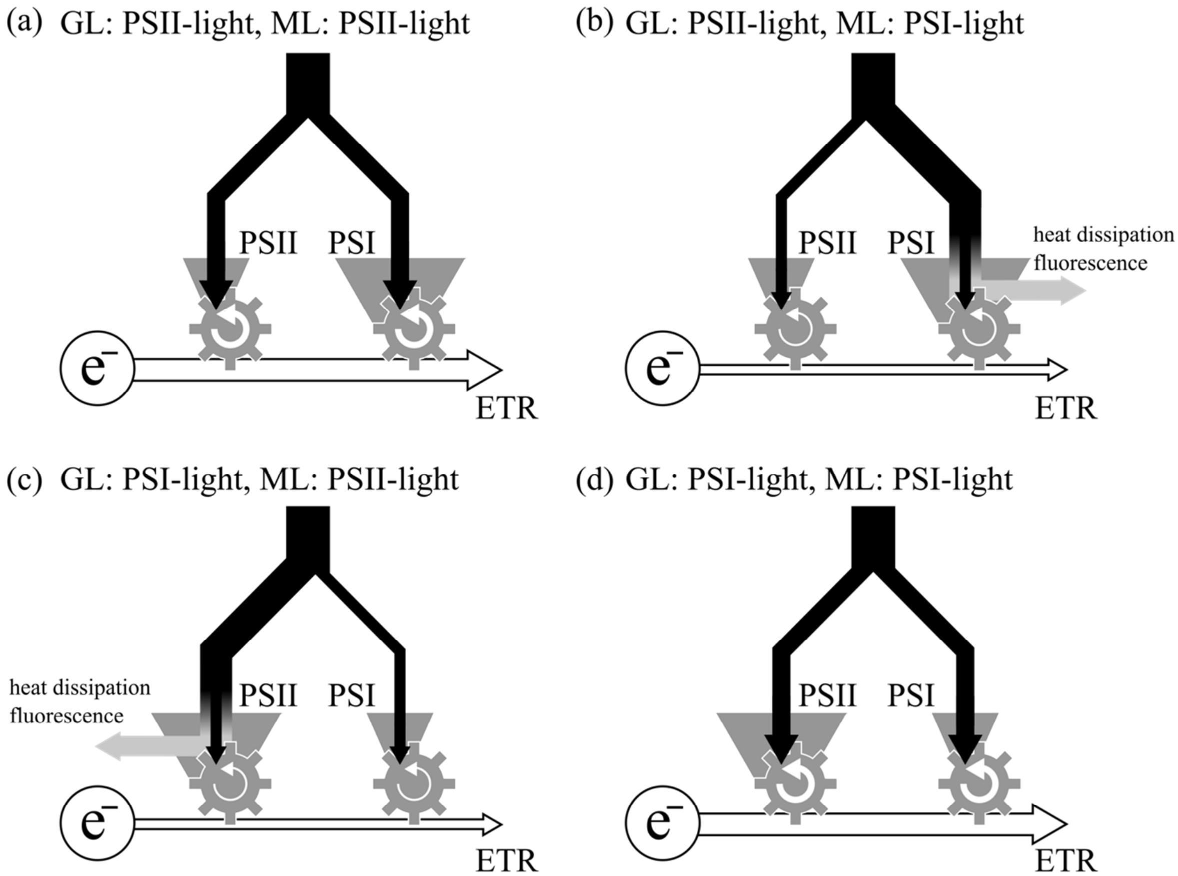
(a) GL: PSII-light, ML: PSII-light
PSII
PSI
e⁻
ETR
(b) GL: PSII-light, ML: PSI-light
PSII
PSI
heat dissipation
fluorescence
e⁻
ETR
(c) GL: PSI-light, ML: PSII-light
heat dissipation
fluorescence
PSII
PSI
e⁻
ETR
(d) GL: PSI-light, ML: PSI-light
PSII
PSI
e⁻
ETR

Fig. 3

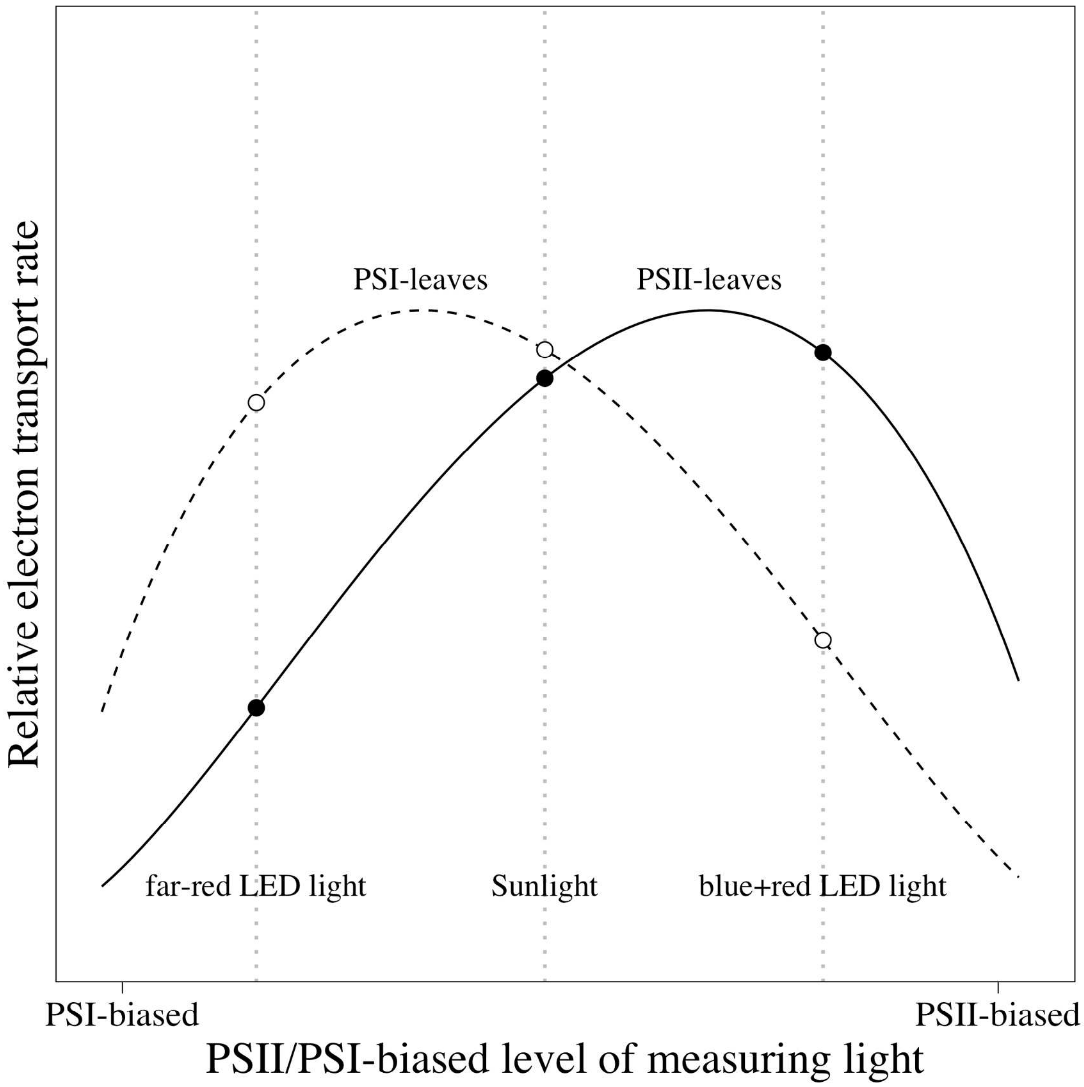
PSI-leaves
PSII-leaves
Relative electron transport rate
far-red LED light
Sunlight
blue+red LED light
PSI-biased
PSII-biased
PSII/PSI-biased level of measuring light

Fig. 4 (color)

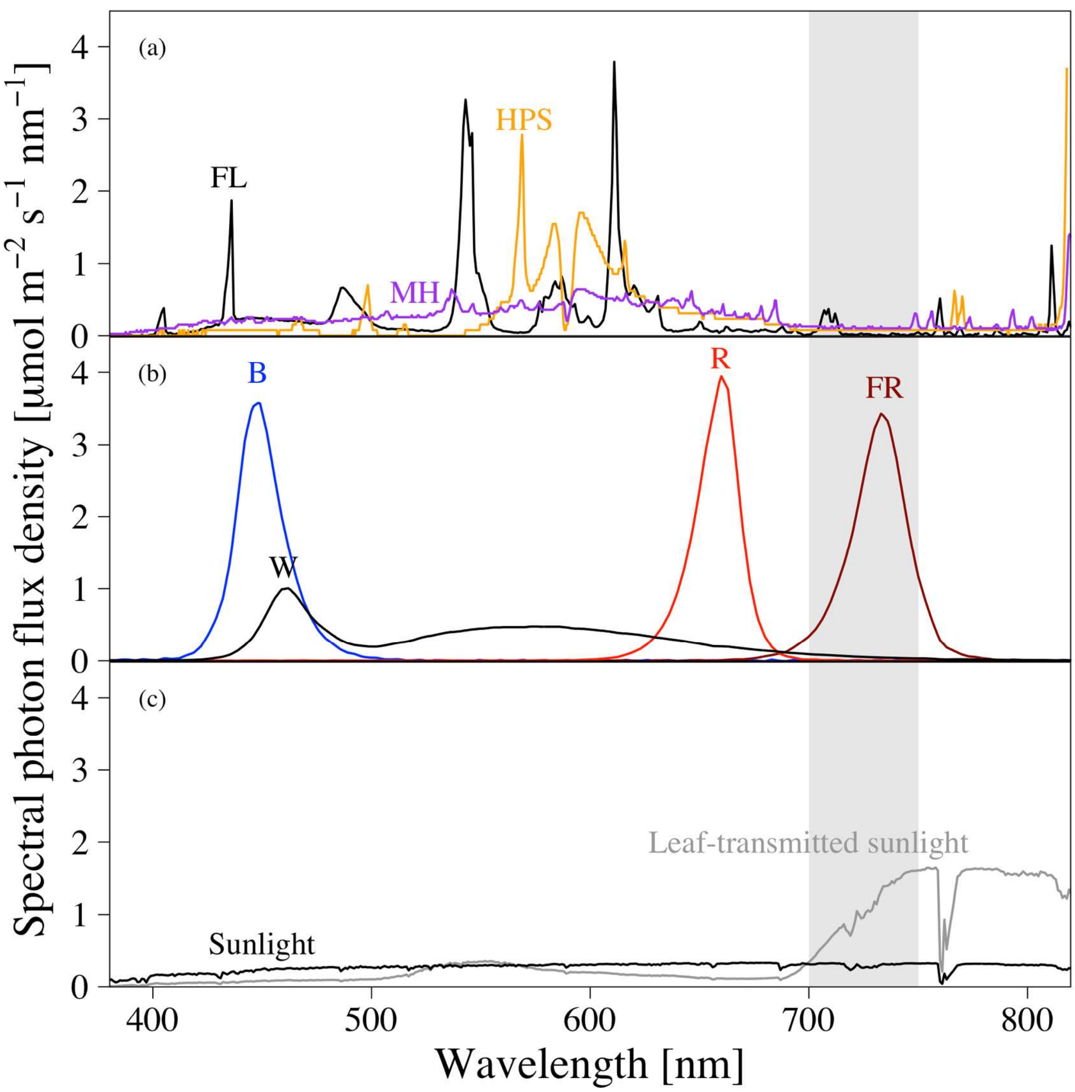
(a)
FL
HPS
MH
(b)
B
W
R
FR
(c)
Leaf-transmitted sunlight
Sunlight
Spectral photon flux density [μmol m^-2 s^-1 nm^-1]
Wavelength [nm]
400
500
600
700
800
0
1
2
3
4

Fig. 4 (greyscale)