

# A practical guide for selecting the spectral photon flux density distribution of light during the measurements of the leaf photosynthetic rate

Keach Murakami<sup>1\*</sup>, Ryo Matsuda<sup>1</sup>, Kazuhiro Fujiwara<sup>1</sup>

- Introduction
- How the interaction is generated?
- Where the interaction should be concerned?
- How the photosynthesis should be measured?
- Concluding remarks
- Supplemental Information S1
- References

Affiliations: <sup>1</sup>Graduate School of Agricultural and Life Sciences, The University of Tokyo

Address: <sup>1</sup>Yayoi, Bunkyo, Tokyo, 113–8657, Japan

e-mail: keach.murakami@gmail.com (mailto:keach.murakami@gmail.com)

---

## Abstract

---

**Abbreviations** BR-light: blue + 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

---

## Introduction

The photosynthetic rate is one of the most important and fundamental traits of the plant. The rates are measured, evaluated, and compared among the leaves cultivated under different conditions. The measured rates are also used for the calculation of the other photosynthetic parameters, such as light, water, and nitrogen use efficiencies. In agricultural and horticultural studies, the effectiveness of treatments is sometimes discussed based on the measured photosynthetic rate and calculated parameters. Therefore, the accurate measurements of the photosynthetic rate must be essential.

A number of studies have reported that the relative spectral photon-flux-density (PFD) distribution (SPD) of light used for the measurement (i.e. measuring light or actinic light) affected the net photosynthetic rates ( $P_n$ ) of leaves (e.g. McCree, 1972; Inada, 1976). To eliminate this direct effect from the comparison,  $P_n$  is usually measured under a single-level SPD of measuring light irrespective of the leaf growth conditions in these fields. The most widely-used measuring light might be mixture of blue + red LED light (BR-light) provided by light sources installed in commercial photosynthesis analyzing systems. The use of the artificial light sources might enable precise control of the photosynthetic PFD (PPFD) and SPD incident on the leaf thereby ensure the reproducibility and reliability of the experiments.

Walters (2005) pointed out that the measurements with a SPD of light different from growth light do not necessarily reflect the functioning of the photosynthesis under growth conditions. Our recent study, indeed, experimentally demonstrated this problem in the  $P_n$  measurements (Murakami et al., 2016). In that experiment, cucumber seedlings were grown under white light-emitting diode (LED) light without and with supplemental far-red (FR) LED light (W and WFR), and subsequently the  $P_n$  of the leaves were compared under BR-light and light with the SPD resembling that of sunlight. The  $P_n$  of W-leaves was greater than that of WFR-leaves under BR-light, while the rates were comparable under artificial sunlight (Murakami et al., 2016). Based on the results obtained from the measurement under BR-light, the prospective growth rate of WFR-plants may be evaluated to be smaller than that of W-plants despite the comparable rates under the sunlight.

The effect of the SPD of growth light on the  $P_n$  depended on the level of the SPD of measuring light. In other words, the SPDs of growth light and measuring light interacted on the  $P_n$  of a leaf. In this short article, we introduce a plausible cause of the interaction and several articles reporting the interaction. We then suggest the situations where the interaction should be cared. We also discuss the good practice for the selection of the SPD of measuring light used for  $P_n$  measurements. The SPD of light affects the photosynthesis through the other mechanisms, such as the stomatal response (Shimazaki et al., 2007), the photoinhibition (Zavafer et al., 2015), and the light-penetrating depth within a leaf (Terashima et al., 2009). Although these subjects are not referred in this article, the cited review articles on these topics are available.

## How the interaction is generated?

Fundamental knowledge about the photosynthetic electron transport is required to understand the mechanism of the interaction. Light energy absorbed by a leaf drives the electron transport and thereby the photosynthetic  $O_2$  evolution and  $CO_2$  uptake. In higher plants, the photosynthetic electron transport chain is anchored by photochemical reactions that occur at two types of photosystems, PSII and PSI. The reactions are powered by excitation energy derived from absorbed photons. The excitation energy transferred to the reaction centers of the photosystems is consumed by the photochemical reactions in units of moles. The serial photochemical reactions at PSII and PSI enables electron transfer against the redox potential (called the Z scheme). Because the photosynthetic electron transport reactions occur in series, the electron transport rate (ETR) through the thylakoid membranes should be limited by the slowest step (Fig. 1). When PSII absorbs excess excitation energy under PSII-biased light, the energy distribution to PSI limits the ETR and thus the photochemical quantum yield of PSII should be lowered (Fig. 1C). When PSI absorbs excess excitation energy, the energy distribution to PSII limits the ETR and the yield of PSI should be lowered (Fig. 1B). In both cases, the excess energy is dissipated as heat and fluorescence, and thus the entire photosynthetic quantum yield—ETR per absorbed photons by the leaf—becomes smaller. An imbalance excitation between the photosystems can harm leaves by generating reactive oxygen species, which cause oxidative damage to chloroplast components (for reviews, see Asada, 1999, 2006). Balancing the excitation energy distribution (EED) between PSII and PSI is essential for plants to keep the high photosynthetic quantum yield.

PSII and PSI represent different light absorption spectral distributions due to the difference in the 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 (Evans and Anderson, 1987; Hogewoning et al., 2012; Wientjes et al., 2013; Laisk et al., 2014). Such an imbalanced excitation is caused by the facts that only chl *a* can absorb the longer wavelengths of light and that PSI contains a greater amount of chl *a* than 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 (Evans and Anderson, 1987; Hogewoning et al., 2012; Wientjes et al., 2013; Laisk et al., 2014). These wavelength dependencies of the EED is a determinant of the EED under a given SPD of light. In several studies of the SPD acclimation of the photosynthetic apparatus, light with a given SPD is categorized as either PSII- or PSI-light according to whether the excitation energy is preferentially distributed to

PSII or PSI This categorization is defined in the relative scale, not in the absolute scale. For instance, a SPD of light, which is evenly absorbed by PSII and PSI in PSII-light-grown leaves (Fig. 1A), can overexcite PSII in PSI-light-grown leaves (Fig. 1C). Thus, the terms 'PSII-light' and 'PSI-light' are used only in a relative context.

Apparently, the EED at a given SPD of light is also affected by the composition of the thylakoid membrane, especially by the stoichiometry between PSII and PSI. The stoichiometry seems to be adjusted to the SPD of 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). The possible involvement of the change in the composition within the respective photosystems in the SPD acclimation was also suggested (Walters and Horton, 1995a; Murakami et al., 2016). The adjustments in the EED properties might help the leaves to keep the high photosynthetic quantum yield under growth light. 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 complex 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 covered up by the state transitions, the long-term adjustments in the EED properties are supposed 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, which modifies the responses of the ETR and thereafter the  $P_n$  to the SPD of measuring light. Thus, the SPDs of growth light and measuring light do not only directly affect the  $P_n$  but also indirectly affect it through their interaction. The expected interactions have been reported in several studies (Chow et al., 1990; Walters and Horton, 1995b; Hogewoning et al., 2012; Murakami et al., 2016). In their pioneering study on *Pisum sativum*, Chow et al. (1990) grew plants under light provided by cool-white fluorescent lamps with yellow Plexglas (FR-poor PSII-light) and incandescent bulbs with red Plexglas (FR-rich PSI-light), and subsequently measured the photosynthetic quantum yield of  $O_2$  evolution— $O_2$  evolution rate per absorbed photons by the leaf—under the PSII- and PSI-light. When measured under the PSII-light, the yield was higher in the PSII-light-grown leaves; when measured under the PSI-light, the yield was higher in the PSI-light-grown leaves. Similar trends were observed in *Arabidopsis thaliana* (Walters and Horton, 1995b) and *Cucumis sativus* (Hogewoning et al., 2012; Murakami et al., 2016). Hogewoning et al. (2012) observed the interaction in the photosynthetic quantum yield of  $CO_2$  uptake using artificial sunlight (PSII-light) and shadelight (PSI-light) as growth light and 19 monochromatic LED light as measuring light. They demonstrated that the interaction cannot occur only in the case growth light was used as measuring light but also in the case the other SPDs of light was used. Murakami et al. (2016) showed the interaction in the  $P_n$  using white LED light without or with FR LED light (PSII-light and PSI-light) as growth light and BR-light (PSII-light) and artificial sunlight (PSI-light) as measuring light. The potential problem in the use of BR-light for the  $P_n$  measurements was clearly demonstrated.

These reports might suggest that the EED property of a leaf is tuned to the PSII/PSI-biased level of growth light. It is expected that a leaf performs a higher ETR per absorbed photons by the photosystems under measuring light with the same PSII/PSI-biased level to that of growth light (Fig. 2). When leaves grown under different SPDs of light are compared and evaluated under a single-level SPD of light, the results should be inevitably biased depending on the SPD of measuring light.

## Where the interaction should be concerned?

This interaction may have considerable impact on the  $P_n$  especially in the measurements under the low PPFD and/or high  $CO_2$  concentration, where the extent of the ETR is a dominant factor for the photosynthetic rate (von Caemmerer and Farquhar, 1981). In such conditions, any bias in the ETR is directly reflected in the  $P_n$ . Therefore, the  $P_n$  under these conditions should be measured with particular attention on the interaction.

Note that such an interaction might have impacts on the other characteristics related to the photosynthetic electron transport, such as chl fluorescence parameters and the photoinhibition indicators. The overexcitation of PSII (or PSI) results in the lowered photochemical yield at PSII (or PSI) (e.g. Hogewoning et al., 2012; Laisk

et al., 2014), and the imbalance in the excitation should hasten the photoinhibition caused by the reactive oxygen species. Evaluation of these characteristics should also be measured with particular care on the interaction.

The mechanisms of the SPD acclimation of the EED property have not yet been fully elucidated (see Murakami et al., 2016). Considering the sensitively adjusted photosystem stoichiometry in response to the SPD of growth light (Walters and Horton, 1995b), the interaction should always be taken into account whenever the  $P_n$  and related parameters are evaluated. The impacts of the interaction on the  $P_n$  should be paid particular attention, at least when the measured leaves are expected to represent different EED properties.

For this decade, a number of studies have investigated the effects of the SPD of growth light on the plant growth and photosynthesis (e.g. Matsuda et al., 2004, 2007, 2008; Hogewoning et al., 2010a, 2010b; Shibuya et al., 2015; Trouwborst et al., 2016). Assimilation light provided by most of artificial light sources contain little FR. In general, fluorescent lamps, metal halide lamps, high-pressure sodium lamps, and blue, red, and white LEDs used for assimilation lighting emit typical PSII-light (Supplemental Information S1). This is because FR is not 'photosynthetically active' and FR-rich light promotes excessive stem elongation. On the other hand, several recent papers suggest the significance of supplemental FR on the plant growth and development (for a review, see Demotes-Mainard et al., 2016). Since FR overexcites PSI, leaves grown under PSII-light supplemented with FR LED can represent relatively PSI-leaves like EED property compared to those grown without supplemental FR. Therefore, comparing the  $P_n$  of leaves grown with and without supplemental FR using BR-light might result in typical biased evaluation caused by the interaction, as demonstrated in the previous report (Murakami et al., 2016).

Evaluating the vertical profiles of the photosynthetic characteristics of the plant stand cultivated in greenhouses may be vulnerable to the biases in the same manner. While the leaves in the upper layers were acclimated to sunlight, those in the lower layers were acclimated to the leaf transmitted light. Due to the higher transmittance in the FR waveband of a leaf, leaf transmitted light contains much FR, namely PSI-light (Supplemental Information S1). Therefore, when measured using BR-light, the  $P_n$  of upper leaves might be overestimated while that of lower leaves might be underestimated.

## How the photosynthesis should be measured?

Ideally, the photosynthetic rates and related parameters should be measured under the *in situ* conditions. In the prospective study focusing on the plant growth after the measurements, the measurements should be made under the SPD of light the plant will subject to. For instance, evaluation of the photosynthesis of the transplants grown under artificial lighting (e.g. Kozai, 2007) should be made under sunlight because they are subsequently transferred to a greenhouse and cultivated under sunlight. Note that the effect of the interaction seems to be less prominent than those of the other factors, such as the incident PPFD. The measurements under sunlight, which usually causes a fluctuation in the incident PPFD, should be avoided and thus the measurements should be made under the artificial light sources to ensure the reproducibility and reliability of the research. The use of artificial light sources will mitigate the uncertainty caused by the fluctuation in the incident PPFD at the expense of the possible biases caused by the interaction. This is because the SPDs of light from the artificial light sources are generally by far different from that of *in situ* light. To solve this dilemma between the *in situ* evaluation and the PPFD stability, SPD-controllable light sources might be helpful (e.g. Yano and Fujiwara, 2012; Fujiwara et al., 2013). In the retrospective study aiming to elucidate the causes of the differences between the experimental groups, the measurements should be made under the SPDs of light the plants received during the treatments. For instance, when the difference in the resultant dry weight between the plants grown under white LEDs and fluorescent lamps are analyzed and the  $P_n$  is used for the explanatory variable, the measurements should be made using the white LEDs for the plants grown under the white LEDs and using the fluorescent lamps for those grown under the fluorescent lamps. In both the prospective and retrospective studies, these simple *in situ* measurements will eliminate the problems caused by the interaction.

If the SPD of light the leaves will subject to is not predetermined, then the measurements should be made under several levels of SPDs of light including PSII- and PSI-light. Researchers had better report the 'general' characteristics of the leaves in these descriptive studies. Therefore, the interaction should be tested so as not to make biased evaluation. If any the interaction, the results should be descriptively reported and should not be generalized. When the measurements were made only under a single-level of SPD of measuring light because of unavoidable circumstances, the light source must be declared in the materials and methods section so that readers can follow the SPD.

## Concluding remarks

The  $P_n$  under a single-level SPD of measuring light is only an aspect of the photosynthetic characteristics of the leaf. Therefore, the obtained result must be discussed in connection with the SPD of measuring light. Evaluation of the photosynthesis should be made under the *in situ* conditions or multi-levels of SPDs of measuring light so that the evaluation is not biased by the interaction. Imitating the various SPDs of light incident on the leaf for *in situ* evaluation might be difficult or impossible from the technical reasons. In addition, measuring the  $P_n$  under multi-levels of SPDs costs much more time, resource, and labor. Thus, these two approaches might not always be applied for evaluation of the leaf  $P_n$ . Further research is required to make the quantitative analysis of the leaf  $P_n$  in response to the SPD of measuring light.

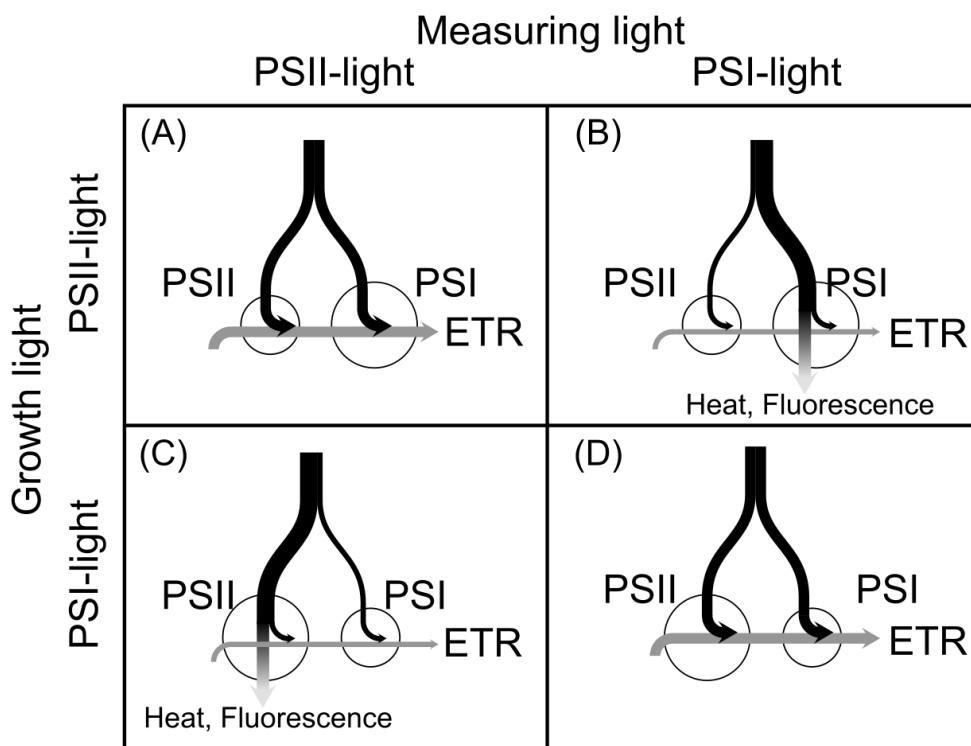


Fig. 1 The conceptual diagrams of the effects of the excitation energy distribution between the photosystems (PSII and PSI) on the photosynthetic electron transport rate (ETR). Electron flow (grey lines) and energy flow (black lines) of leaves grown under PSII-light (A, B) and PSI-light (C, D) measured using PSII-light (A, C) and PSI-light (B, D) were shown.

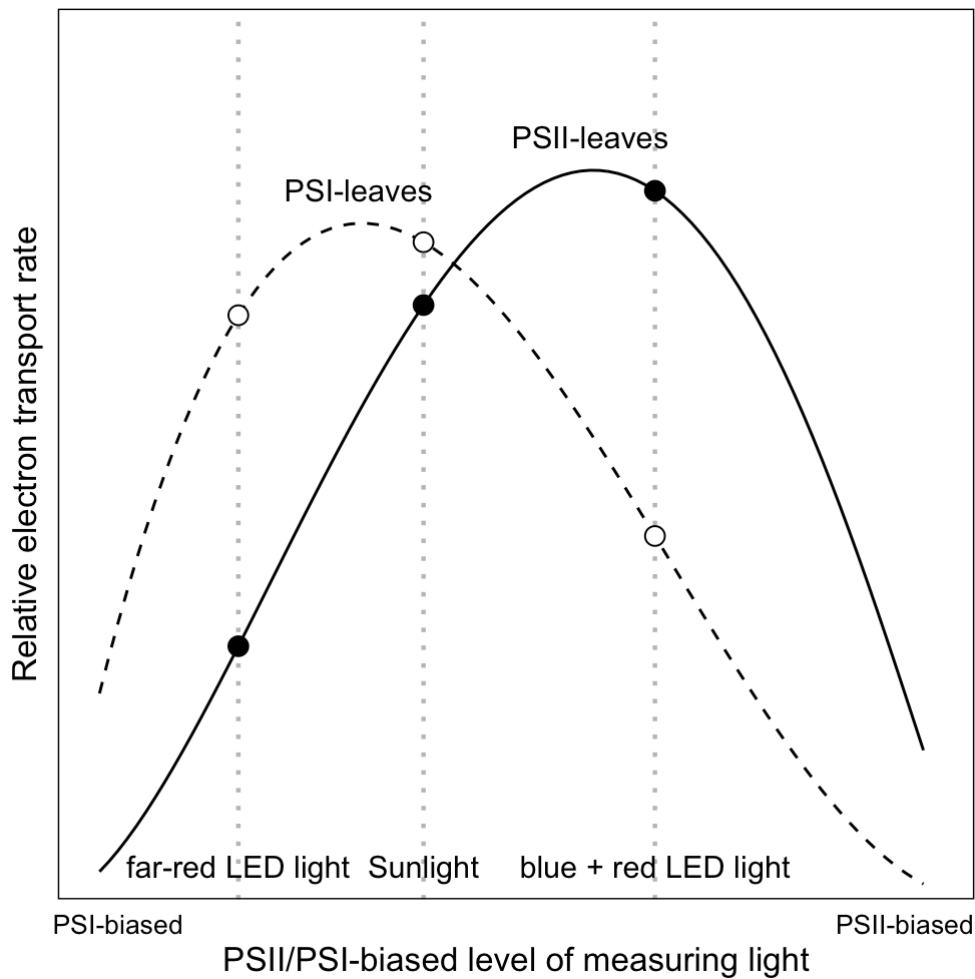


Fig. 2 The conceptual diagram of the photosynthetic electron transport rates per absorbed photons by the photosystems grown under PSII-light (PSII-leaves) and PSI-light (PSI-leaves) in response to the PSII/PSI-biased level of measuring light.

## Supplemental Information S1

Information of the spectral distributions of artificial assimilation light and sunlight.

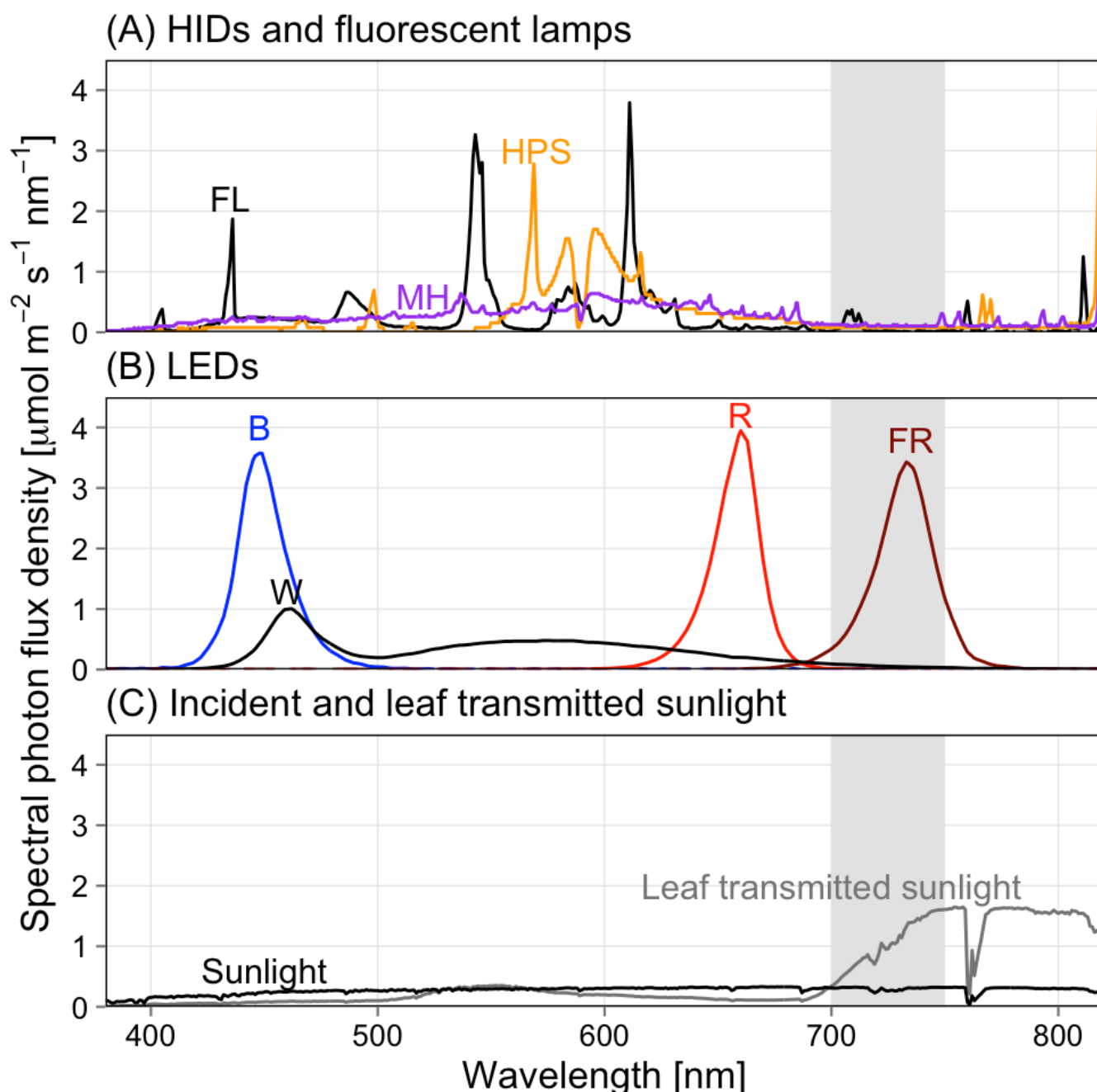


Fig. S1 The spectral photon flux density distributions of light provided by (A) high-intensity discharge lamps (HIDs) and fluorescent lamps, (B) light-emitting diodes (LEDs), and (C) incident and leaf transmitted sunlight (see also Table S1). The distributions at a photon flux density of  $100 \mu\text{mol m}^{-2} \text{s}^{-1}$  within 400–750 nm are shown. The distribution of sunlight was adopted from JIS C 8904-3. The distribution of the leaf transmitted sunlight was calculated from that of sunlight and the transmittance spectrum of a cucumber leaf (Murakami et al. 2016). The far-red waveband (700–750 nm) is filled in grey.

Table S1. Description of the light sources and the instruments used for the measurements of the spectral photon flux density distributions.

Light source (abbreviation)	Model code	Measuring instrument
Fluorescent lamp (FL)	FPL55EX-N <sup>*1</sup>	HR2000 (Ocean Optics Inc.)
Metal halide lamp (MH)	M220FCELS-W/BUD <sup>*1</sup>	HR2000 (Ocean Optics Inc.)
High-pressure sodium lamp (HPS)	NH220FLS <sup>*1</sup>	HR2000 (Ocean Optics Inc.)
Blue LED (B)	HBL3-3S55-LE <sup>*2</sup>	MS-720 (EKO Instruments Co. Ltd.)

Red LED (R)	SRK3-3A80-LE <sup>*2</sup>	MS-720 (EKO Instruments Co. Ltd.)
Far-red LED (FR)	L735-36AU <sup>*3</sup>	MS-720 (EKO Instruments Co. Ltd.)
White LED (W)	NSPW310DS <sup>*4</sup>	MS-720 (EKO Instruments Co. Ltd.)

<sup>\*1</sup>IWASAKI ELECTRIC CO., LTD., Tokyo, Japan; <sup>\*2</sup>Tricon Co., Shimane, Japan; <sup>\*3</sup>Epitex Inc., Kyoto, Japan; <sup>\*4</sup>Nichia Chemical Industries Ltd., Tokushima, Japan.

## Supplementary Reference

JIS C 8904-3. 2011. Photovoltaic devices-Part 3: Measurement principles for photovoltaic(PV) solar devices with reference spectral irradiance data (<http://www.jisc.go.jp/app/pager?id=2769864>).

## References

- Asada, K. (2006). Production and scavenging of reactive oxygen species in chloroplasts and their functions. *Plant Physiology* **141**: 391–396.
- Asada, K. (1999). THE WATER-WATER CYCLE IN CHLOROPLASTS: Scavenging of active oxygens and dissipation of excess photons. *Annual Review of Plant Biology* **50**: 601–639.
- Chow, W.S., Melis, A., Anderson, J.M. (1990). Adjustments of photosystem stoichiometry in chloroplasts improve the quantum efficiency of photosynthesis. *Proceedings of the National Academy of Sciences* **87**: 7502–7506.
- Demotes-Mainard, S., Péron, T., Corot, A., Bertheloot, J., Le Gourrierc, J., Pelleschi-Travier, S., Crespel, L., Morel, P., Huché-Thélier, L., Boumaza, R., Vian, A., Guérin, V., Leduc, N., Sakr, S. (2016). Plant responses to red and far-red lights, applications in horticulture. *Environmental and Experimental Botany* **121**: 4–21.
- Dietzel, L., Bräutigam, K., Pfannschmidt, T. (2008). Photosynthetic acclimation: State transitions and adjustment of photosystem stoichiometry—functional relationships between short-term and long-term light quality acclimation in plants. *Febs Journal* **275**: 1080–1088.
- Evans, J.R., Anderson, J.M. (1987). Absolute absorption and relative fluorescence excitation spectra of the five major chlorophyll-protein complexes from spinach thylakoid membranes. *Biochimica et Biophysica Acta (BBA)-Bioenergetics* **892**: 75–82.
- Fujiwara, K., Eijima, K., Yano, A. (2013). Second-generation LED-artificial sunlight source system available for light effects research in biological and agricultural sciences. In *Proceedings of the 7th lux pacifica (The Illuminating Engineering Institute of Japan (IEIJ): Bangkok)*, pp. 140–145.
- Goldschmidt-Clermont, M., Bassi, R. (2015). Sharing light between two photosystems: Mechanism of state transitions. *Current Opinion in Plant Biology* **25**: 71–78.
- Hogewoning, S.W., Douwstra, P., Trouwborst, G., van Ieperen, W., Harbinson, J. (2010a). An artificial solar spectrum substantially alters plant development compared with usual climate room irradiance spectra. *Journal of Experimental Botany* **61**: 1267–1276.
- Hogewoning, S.W., Trouwborst, G., Maljaars, H., Poorter, H., van Ieperen, W., Harbinson, J. (2010b). Blue light dose—responses of leaf photosynthesis, morphology, and chemical composition of *cucumis sativus* grown under different combinations of red and blue light. *Journal of Experimental Botany* **61**: 3107–3117.
- Hogewoning, S.W., Wientjes, E., Douwstra, P., Trouwborst, G., van Ieperen, W., Croce, R., Harbinson, J. (2012). Photosynthetic quantum yield dynamics: From photosystems to leaves. *The Plant Cell* **24**: 1921–1935.
- Inada, K. (1976). Action spectra for photosynthesis in higher plants. *Plant and Cell Physiology* **17**: 355–365.



- Kozai, T. (2007). Propagation, grafting and transplant production in closed systems with artificial lighting for commercialization in Japan. *Propagation of Ornamental Plants* **7**: 145–149.
- Laisk, A., Oja, V., Eichelmann, H., Dall'Osto, L. (2014). Action spectra of photosystems II and I and quantum yield of photosynthesis in leaves in State 1. *Biochimica et Biophysica Acta (BBA)-Bioenergetics* **1837**: 315–325.
- Matsuda, R., Ohashi-Kaneko, K., Fujiwara, K., Goto, E., Kurata, K. (2004). Photosynthetic characteristics of rice leaves grown under red light with or without supplemental blue light. *Plant and Cell Physiology* **45**: 1870–1874.
- Matsuda, R., Ohashi-KANEKO, K., Fujiwara, K., Kurata, K. (2007). Analysis of the relationship between blue-light photon flux density and the photosynthetic properties of spinach (*spinacia oleracea* L.) leaves with regard to the acclimation of photosynthesis to growth irradiance. *Soil Science and Plant Nutrition* **53**: 459–465.
- Matsuda, R., Ohashi-Kaneko, K., Fujiwara, K., Kurata, K. (2008). Effects of blue light deficiency on acclimation of light energy partitioning in PSII and CO<sub>2</sub> assimilation capacity to high irradiance in spinach leaves. *Plant and Cell Physiology* **49**: 664–670.
- McCree, K. (1972). The action spectrum, absorptance and quantum yield of photosynthesis in crop plants. *Agricultural Meteorology* **9**: 191–216.
- Melis, A. (1991). Dynamics of photosynthetic membrane composition and function. *Biochimica et Biophysica Acta (BBA)-Bioenergetics* **1058**: 87–106.
- Murakami, K., Matsuda, R., Fujiwara, K. (2016). Interaction between the spectral photon flux density distributions of light during growth and for measurements in net photosynthetic rates of cucumber leaves. *Physiologia Plantarum*: n/a–n/a.
- Pfannschmidt, T., Nilsson, A., Allen, J.F. (1999). Photosynthetic control of chloroplast gene expression. *Nature* **397**: 625–628.
- Shibuya, T., Endo, R., Yuba, T., Kitaya, Y. (2015). The photosynthetic parameters of cucumber as affected by irradiances with different red: Far-red ratios. *Biologia Plantarum* **59**: 198–200.
- Shimazaki, K., Doi, M., Assmann, S.M., Kinoshita, T. (2007). Light regulation of stomatal movement. *Annual Review of Plant Biology* **58**: 219–247.
- Terashima, I., Fujita, T., Inoue, T., Chow, W.S., Oguchi, R. (2009). Green light drives leaf photosynthesis more efficiently than red light in strong white light: Revisiting the enigmatic question of why leaves are green. *Plant and Cell Physiology* **50**: 684–697.
- Trouwborst, G., Hogewoning, S.W., van Kooten, O., Harbinson, J., van Ieperen, W. (2016). Plasticity of photosynthesis after the “red light syndrome” in cucumber. *Environmental and Experimental Botany* **121**: 75–82.
- von Caemmerer, S., Farquhar, G. (1981). Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. *Planta* **153**: 376–387.
- Walters, R.G. (2005). Towards an understanding of photosynthetic acclimation. *Journal of Experimental Botany* **56**: 435–447.
- Walters, R.G., Horton, P. (1995a). Acclimation of *Arabidopsis thaliana* to the light environment: Regulation of chloroplast composition. *Planta* **197**: 475–481.
- Walters, R.G., Horton, P. (1995b). Acclimation of *Arabidopsis thaliana* to the light environment: Changes in photosynthetic function. *Planta* **197**: 306–312.
- Wientjes, E., Amerongen, H. van, Croce, R. (2013). LHCII is an antenna of both photosystems after long-term acclimation. *Biochimica et Biophysica Acta (BBA)-Bioenergetics* **1827**: 420–426.
- Yano, A., Fujiwara, K. (2012). Plant lighting system with five wavelength-band light-emitting diodes providing photon flux density and mixing ratio control. *Plant Methods* **8**: 1–12.

Zavafer, A., Chow, W.S., Cheah, M.H. (2015). The action spectrum of Photosystem II photoinactivation in visible light. *Journal of Photochemistry and Photobiology B: Biology* **152**: 247–260.