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High-light-like photosynthetic responses of *Cucumis sativus* leaves acclimated to fluorescent illumination with a high red:far-red ratio: interaction between light quality and quantity

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Abstract

This study evaluated the photosynthetic responses of *Cucumis sativus* leaves acclimated to illumination from three-band white fluorescent lamps with a high red:far-red (R:FR) ratio (R:FR = 10.5) and the photosynthetic responses of leaves acclimated to metal-halide lamps that provided a spectrum similar to that of natural light (R:FR = 1.2) at acclimation photosynthetic photon flux density (PPFD) of 100 to 700 µmol m^{-2} s^{-1}. The maximum gross photosynthetic rate (P_G) of the fluorescent-acclimated leaves was approximately 1.4 times that of the metal-halide-acclimated leaves at all acclimation PPFDs. The ratio of quantum efficiency of photosystem II (Φ_{PSII}) of the fluorescent-acclimated leaves to that of the metal-halide-acclimated leaves tended to increase with increasing acclimation PPFD, whereas the corresponding ratios for the leaf mass per unit area tended to decrease with increasing acclimation PPFD. These results suggest that the greater maximum P_G of the fluorescent-acclimated leaves resulted from an interaction between the acclimation light quality and quantity, which was mainly caused by the greater leaf biomass for photosynthesis per area at low acclimation PPFDs and by the higher Φ_{PSII} as a result of changes in characteristics and distribution of chloroplasts, or a combination of these factors at high acclimation PPFDs.

Additional key words: fluorescent lamp, gross photosynthetic rate, leaf mass per unit area, light quality, quantum efficiency of photosystem II.

Introduction

Plants grown under typical commercial fluorescent lamps have unusual morphological characteristics, such as shorter shoots, thicker leaves, and deeper leaf color than those grown under normal-spectrum lights (*e.g.*, Hogewoning *et al.* 2010, Shibuya *et al.* 2010a, 2010b, 2011). These morphological characteristics result from the high red:far-red (R:FR) ratios of typical commercial fluorescent lamps, which emit little FR radiation, because these morphological characteristics can be normalized by increasing the FR content of the light from these lamps (Deutch and Rasmussen 1974, Murakami *et al.* 1991, Shibuya *et al.* 2010a, 2011). The use of illumination with a high R:FR ratio also often suppresses quantitative aspects of plant growth, including shoot elongation, leaf expansion, and consequent biomass production (Li and Kubota 2009, Hogewoning *et al.* 2010, Shibuya *et al.* 2010a). Therefore, illumination with a high R:FR ratio is typically considered unsuitable for plant growth.

On the other hand, the plants grown under fluorescent lamps have a greater potential photosynthetic ability (*i.e.* a higher photosynthetic rate at high light intensity) than plants grown under normal lights (Hogewoning *et al.* 2010, Shibuya *et al.* 2010a), despite the growth suppression that occurs under the fluorescent light. The acclimation of photosynthesis to light at higher than natural R:FR ratios has not been well investigated, except for two recent reports (Hogewoning *et al.* 2010, Shibuya *et al.* 2010a), although the typical commercial fluorescent lamps have been often used for horticultural production and plant-physiology studies. The impacts of a low R:FR

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Abbreviations: *ANOVA* – analysis of variance; Chl – chlorophyll; g_s – stomatal conductance; LMA – leaf mass per unit area; P_G – gross photosynthetic rate; P_N – net photosynthetic rate; PPFD – photosynthetic photon flux density; R:FR – red:far-red ratio; Φ_{PSII} – quantum efficiency of photosystem II.

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ratio have been investigated in ecological science studies (Corré 1983, Turnbull *et al.* 1993, Murchie and Horton 1997, Maliakal *et al.* 1999, Sleeman and Dudley 2001, Sleeman *et al.* 2002). To analyze the mechanisms that underlie responses of a plant to light, it is necessary to account for the interaction between light quality and quantity, since both parameters affect morphological and physiological characteristics of a plant (*e.g.* Ballaré *et al.* 1991) and since the interaction is often complex. However, previous research investigated only one level of light intensity used for acclimation, with a PPFD of 100 µmol m^{-2} s^{-1} (Hogewoning *et al.* 2010) or 350 µmol m^{-2} s^{-1} (Shibuya *et al.* 2010a). The present study investigated the photosynthetic responses and morphological characteristics of *Cucumis sativus* leaves acclimated to illumination from three-band white fluorescent lamps with a high R:FR ratio or from metal-halide lamps that provided a spectrum similar to that of natural light after acclimation at various light intensities.

Materials and methods

Cucumis sativus cv. 'Hokushin' seedlings were acclimated to fluorescent lamps with a high R:FR ratio (*FPL55EX-N; 55 W; Panasonic Corp*., Kadoma, Japan) or to metal-halide lamps providing a spectrum similar to that of natural (*DR400/TL; 400 W; Toshiba Lighting & Technology Corp*., Yokosuka, Japan) by growing them under the different lamps after germination until the first true leaves had expanded. The acclimation PPFD at the leaf surfaces was maintained at 100, 300, 500, or 700 µmol m^{-2} s^{-1} by adjusting the distance between the light source and the leaves. The metal-halide and fluorescent lamps were arranged at a density of 17 and 25 lamps m^{-2}, respectively. The distance between the lamps and the leaves at a PPFD of 700 µmol m^{-2} s^{-1} was approximately 250 and 150 mm for the metal-halide and fluorescent lamps, respectively. A water filter (20 mm depth) was placed under the metal-halide lamps to prevent biasing effects as a result of increases in leaf temperature caused by the long-wave radiation from these lamps. A glass plate was placed under the fluorescent lamps. The leaf-air temperature difference during the acclimation was within ± 0.5ºC under each illumination type. The light:dark period was 12:12 h throughout the acclimation period. The spectrum under each light source (Fig. 1) was measured using a *BLK-CXR-SR* spectrometer (*StellarNet Inc.,* Tampa, FL, USA) at the level of the leaf surface. The ratio of photon flux at red wavelengths (600 to 700 nm) to that at far-red wavelengths (700 to 800 nm), hereafter referred to as the R:FR ratio, was 10.5 for the fluorescent lamps and 1.2 for the metal-halide lamps. The measured R:FR ratio produced by the fluorescent lamps was higher than that (7.0) in previous studies (Shibuya *et al.* 2010a, 2010b, 2011), even though the same type of lamps were used. The previous fluorescent R:FR value was probably underestimated as a result of measurement noise in the FR range.

Plants were grown in plastic pots (60 mm in diameter, 55 mm in height) containing vermiculite. Nutrient solution (*A-type Otsuka House Solution*; *Otsuka AgriTechno Co. Ltd*., Osaka, Japan) was supplied to the bottoms of the pots continuously by standing the pots in a solution 5 to 10 mm deep. Air temperature and relative humidity in the growth chambers were maintained at 28°C and 50%, respectively.

After the first true seedling leaves had expanded, the net photosynthetic rate (P_N) and the quantum efficiency of photosystem II (Φ_{PSII}; Maxwell and Johnson 2000) of the first true leaves acclimated to two different lamps at various light intensities were measured with a photosynthesis and fluorescence measuring system (*LI-6400-40; LI-COR Inc*., Lincoln, NE, USA) at PPFDs of 100, 300, 600; 1,200; and 1,800 µmol m^{-2} s^{-1}. Five seedlings in each treatment group were sampled for measuring. The seedlings under each treatment had one expanded true leaf (average area was approximately 45 cm^{2}), one nonexpanded true leaf, and two cotyledons. During these measurements, the PPFD was increased from the low PPFD to the high one. The minimum waiting time for measurement at each PPFD was 3 min, and the maximum was 10 min. This maximum waiting time was enough to make an activation state stable. Illumination was supplied

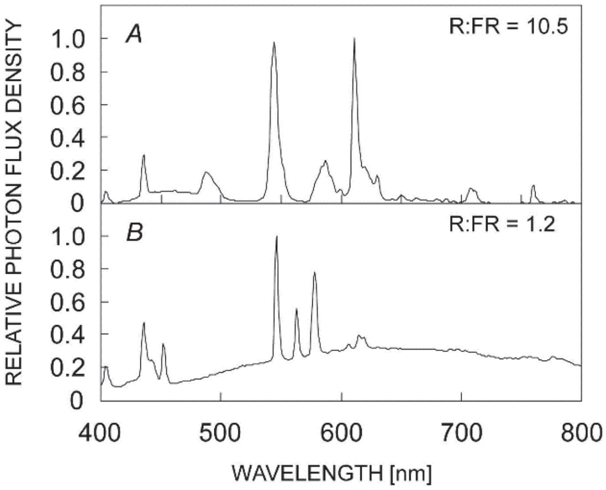

Fig. 1. Spectra of light produced by the (*A*) fluorescent lamps with a high red:far-red (R:FR) ratio and (*B*) metal-halide lamps that provided a spectrum similar to that of natural light measured at the leaf surface. Relative photon flux densities were expressed in values relative to the maximum. R:FR ratio was estimated by dividing the cumulative photon flux density [µmol m^{-2} s^{-1}] from red light (600 to 700 nm) by that from far-red light (700 to 800 nm) light. The plants were shielded from the metal-halide light by a water filter to avoid leaf temperature increases.

by red (peak wavelength = 635 nm) and blue (peak = 465 nm) LEDs at a ratio of 9:1 during the measurements. The PPFD and duration of saturating pulse used for measuring Φ_{PSII} was approximately 7,000 µmol m^{-2} s^{-1} and 0.8 s, respectively. After measuring P_N and Φ_{PSII}, the dark respiration rate of the leaves was measured with the same system at a PPFD of 0 µmol m^{-2} s^{-1}. P_G at a given PPFD was estimated by summing the dark respiration rate and the P_N. In the leaf chamber of the measuring system, the leaf temperature was maintained at 28°C, the relative humidity at 50%, and the CO_2 concentration at 400 µmol mol^{-1}. The absorbance of leaves was estimated from a relative chlorophyll (Chl) content determined with a Chl meter (*SPAD-502; Konica Minolta Sensing Inc.*, Sakai, Japan) as follows. The relative Chl content of several seedlings' leaves was evaluated with the Chl meter in a preliminary experiment. An absorbance of the leaves was also evaluated from a spectral reflectance and transmittance determined with the spectrometer. From these values, the linear relationship (n = 77, P<0.001, data not shown) between relative Chl content and absorbance was determined, and then, the absorbance of sampled leaves could be estimated from the relative Chl contents with this relationship. Because the ratio of PSII to PSI could vary with the ratio of FR illumination (Walter and Horton 1995, Leong and Anderson 1996), this study did not estimate the photosynthetic electron transport rate from Φ_{PSII}, PPFD, and leaf absorption by the method of Genty *et al.* (1989) in which the partitioning of energy between PSII and PSI is assumed constant. The stomatal conductance (g_s) measured by the photosynthesis measuring system was also not analyzed, because there was a measurement error of unknown origins (it may be caused by instability of water vapor concentrations in the sample and/or reference gas) for the g_s estimation that cannot be compensated. The thickness of the first true leaves in the samples was measured for the same part of the leaf used to measure the photosynthetic parameters using a *G2-205M* digital thickness gauge (*OZAKI MFG Co. Ltd.*, Tokyo, Japan). The leaf area of the first true leaves was measured by an image scanner and an image analysis software *LIA for win32* (K. Yamamoto, Nagoya University, Nagoya, Japan) and then the leaf dry mass was measured by oven-drying at 80°C for 72 h, from which the leaf mass per unit area (LMA) was calculated. Another 10 seedlings acclimated to each illumination regime were sampled, and then Chl *a*/*b* ratio of their first true leaves was determined by the procedure of Porra *et al.* (1989).

Two-way analysis of variance (*ANOVA*) was used to examine the effects of acclimated illumination on maximum P_G, Φ_{PSII} at maximum P_G, relative Chl content, Chl *a*/*b* ratio, leaf thickness, and LMA. The statistical analyses were performed using a software package *Statcel 2* (*OMS Publishing Inc.*, Tokorozawa, Japan).

Results

There were significant effects of illumination type and acclimation PPFD on maximum P_G and Φ_{PSII} at maximum P_G, relative Chl content, Chl *a*/*b* ratio, leaf thickness, and LMA (Table 1). The interaction effects between illumination type and acclimation PPFD on them were also significant except for the Chl *a*/*b* ratio.

Table 1. Results of analysis of variance (*ANOVA*) to test significant effects of illumination type and acclimation photosynthetic photon flux density (PPFD) on maximum gross photosynthetic rate (P_G), quantum efficiency photosystem II (Φ_{PSII}) at maximum P_G, relative chlorophyll (Chl) content, Chl *a*/*b* ratio, leaf thickness, and leaf mass per area (LMA) of *Cucumis sativus* leaves.

		Maximum P_G		Φ_{PSII} at maximum P_G		Relative Chl content		Chl *a*/*b* ratio		Leaf thickness		LMA	
Source	df	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Illumination type (A)	1	524.83	<0.001	189.52	<0.001	190.95	<0.001	8.23	<0.010	124.80	<0.001	31.97	<0.001
Acclimation PPFD (B)	3	213.56	<0.001	99.29	<0.001	10.67	<0.001	43.45	<0.001	81.69	<0.001	311.36	<0.001
A × B	3	6.70	0.001	7.68	<0.001	12.25	<0.001	1.94	0.125	3.14	0.039	12.32	<0.001

The P_G of leaves acclimated to illumination from both types of lamp increased and approached saturation as PPFD increased from 0 to 1,800 µmol m^{-2} s^{-1} (Fig. 2). The P_G of the fluorescent-acclimated leaves was greater than that of metal-halide-acclimated leaves at the same combination of measurement PPFD and acclimation PPFD. The tendency for photosynthesis to exhibit saturation seemed to be stronger under the metal-halide illumination. The maximum P_G (at a PPFD of 1,800 µmol m^{-2} s^{-1}) increased with increasing acclimation PPFD for both types of leaves (Fig. 3*A*), and was greater in the fluorescent-acclimated leaves. The maximum P_G of the fluorescent-acclimated leaves was approximately 1.4 times that of the metal-halide-acclimated leaves at all acclimation PPFDs. The Φ_{PSII} at maximum P_G increased with increasing acclimation PPFD for both types of

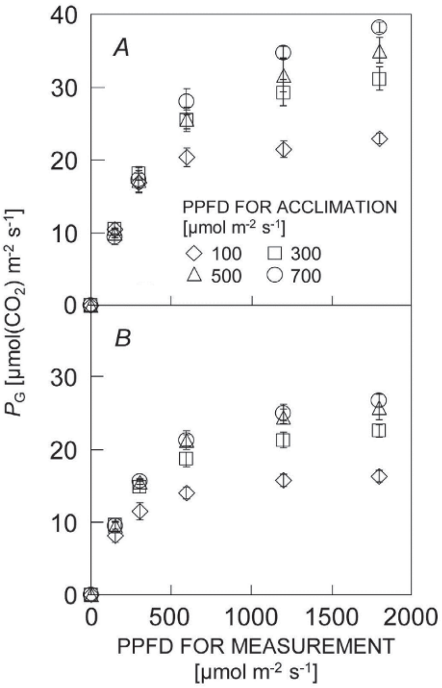

Fig. 2. Photosynthetic light-response curves for *Cucumis sativus* leaves acclimated to illumination from (*A*) fluorescent lamps with a high red:far-red ratio (R:FR = 10.5) and (*B*) metal-halide lamps that provided a spectrum similar to that of natural light (R:FR = 1.2) during acclimation to a range of photosynthetic photon flux densities (PPFDs). P_G: gross photosynthetic rate. Data are means ± SD ($n = 5$).

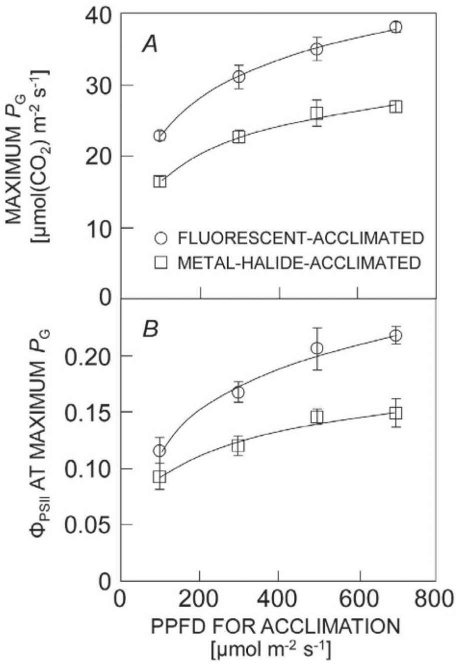

Fig. 3. (*A*) Maximum gross photosynthetic rate (P_G) and (*B*) quantum efficiency of photosystem II (Φ_{PSII}) at the maximum P_G for *Cucumis sativus* leaves acclimated to illumination from fluorescent lamps with a high red:far-red ratio (R:FR = 10.5) or from metal-halide lamps that provided a spectrum similar to that of natural light (R:FR = 1.2) at various acclimation photosynthetic photon flux densities (PPFDs). The maximum P_G was the value measured at a PPFD of 1,800 μmol m^{-2} s^{-1}. Data are means ± SD ($n = 5$). Exponential functions were used for curve fitting.

leaves (Fig. 3*B*). The ratio of Φ_{PSII} of the fluorescent-acclimated leaves to that of the metal-halide-acclimated leaves tended to increase with increasing acclimation PPFDs of 100, 300, 500, and 700 μmol m^{-2} s^{-1}, respectively.

The relative Chl content was greater in the fluorescent-acclimated leaves at all acclimation PPFDs (Fig. 4*A*). The relative Chl content of the metal-halide-acclimated leaves increased with increasing acclimation PPFD, whereas that of the fluorescent-acclimated leaves was stable. The ratio of relative Chl content of the fluorescent-acclimated leaves to that of the metal-halide-acclimated leaves decreased with increasing acclimation PPFD; the ratio was 1.38, 1.43, 1.18, and 1.09 at acclimation PPFDs of 100, 300, 500, and 700 μmol m^{-2} s^{-1}, respectively. The leaf absorbance estimated from the relative Chl content varied from 91.1% to 92.7% in the fluorescent-acclimated leaves, from 84.9% to 89.2% in the metal-halide-acclimated leaves. The Chl *a*/*b* ratio increased with increasing acclimation PPFD for both types of leaves, and was higher in the metal-halide-acclimated leaves at all acclimation PPFDs (Fig. 4*B*). The effect of illumination type on Chl *a*/*b* ratio was relatively small compared with that of acclimation PPFD. The leaf thickness increased with increasing acclimation PPFD in both types of leaves (Fig. 5*A*), but was greater in the fluorescent-acclimated leaves at all acclimation PPFDs. The LMA increased linearly with increasing acclimation PPFD in both types of leaves (Fig. 5*B*). The LMA of the fluorescent-acclimated leaves was 1.32 and 1.22 times that of the metal-halide-acclimated leaves at acclimation PPFDs of 100 and 300 μmol m^{-2} s^{-1}, respectively, but did not differ between the two types of leaves at acclimation PPFDs of 500 and 700 μmol m^{-2} s^{-1}.

Discussion

The differences in the photosynthetic and morphological characteristics between fluorescent- and metal-halide-acclimated leaves are probably due primarily to difference in proportion of active phytochrome which is correlated with R:FR ratio (Franklin and Whitelam 2007), since similar relationships could be observed between fluorescent lamps with high and natural (R:FR = 1.1) R:FR ratios in which only the FR photon flux was modified (Shibuya *et al.* 2010a).

The photosynthetic light-response curves of the

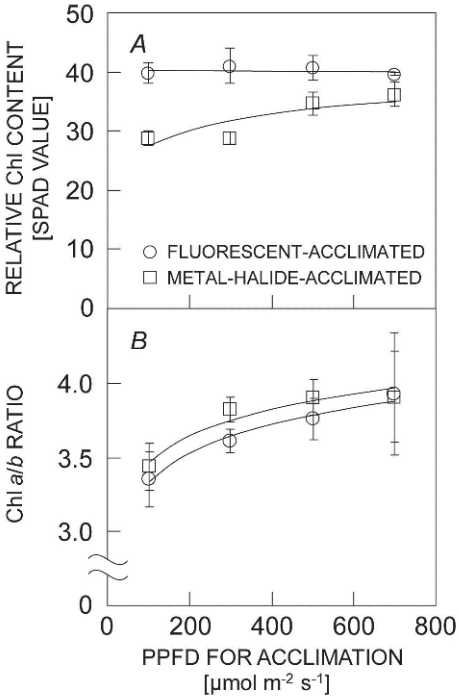

Fig. 4. (*A*) Relative chlorophyll (Chl) content and (*B*) Chl *a*/*b* ratio of *Cucumis sativus* leaves acclimated to illumination from fluorescent lamps with a high red:far-red ratio (R:FR = 10.5) or from metal-halide lamps that provided a spectrum similar to that of natural light (R:FR = 1.2) at various acclimation photosynthetic photon flux densities (PPFDs). Relative Chl content was obtained using a *SPAD-502* Chl meter. Data are means ± SD (relative Chl content; *n* = 5, Chl a/b ratio; *n* = 10). Exponential functions were used for curve fitting.

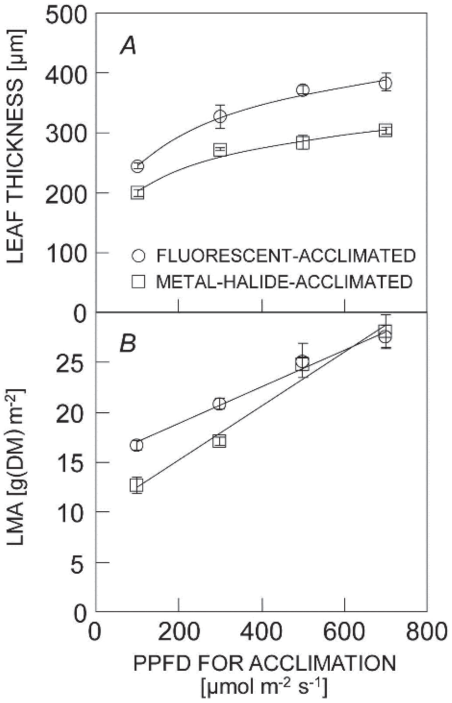

Fig. 5. (*A*) Leaf thickness and (*B*) leaf mass per unit area (LMA) of *Cucumis sativus* leaves acclimated to illumination from fluorescent lamps with a high red:far-red ratio (R:FR = 10.5) or from metal-halide lamps that provided a spectrum similar to that of natural light (R:FR = 1.2) at various acclimation photosynthetic photon-flux densities (PPFDs). Data are means ± SD (*n* = 5). Exponential function and linear function were used for fitting of the leaf thicknesses and the LMAs respectively.

fluorescent-acclimated leaves in the present study were similar to those of sun leaves, whereas the curves for the metal-halide-acclimated leaves were similar to those of shade leaves (Lichtenthaler *et al.* 1981) when both responses were compared at the same acclimation PPFD. The R:FR ratio under fluorescent light (10.5) was much higher than that of solar radiation, and generally does not exist in nature. With a lower R:FR ratio that occurs with natural light, leaf thickness and Chl content decrease as a result of investing resources in the most efficient way into elongating organs, to compensate for the adverse effects (Smith and Whitelam 1997, Franklin 2008). In addition, plant leaves acclimated to light with a low R:FR ratio have low potential photosynthetic ability (Maliakal *et al.* 1999, Sleeman and Dudley 2001, Sleeman *et al.* 2002). The potential photosynthetic abilities of fluorescent-acclimated leaves probably improved as a result of a better acclimation to received light because the opposite physiological and morphological responses to those that are typical of shade avoidance occurred in the fluorescent-acclimated leaves.

The greater Chl content and consequently higher absorbance of the fluorescent-acclimated leaves is probably not a main reason for the greater potential photosynthetic ability; because a light-saturated photosynthetic rate is generally not limited by light harvesting by Chl in C_3 species (Dowdell and Dodge 1970), and the absorbance difference between the two types of leaves was relatively small compared to the difference in maximum P_G. In addition, the initial slopes of the light response curves in the two types of leaves were almost the same. Part of reason for the greater potential photosynthetic ability of the fluorescent-acclimated leaves may be the higher Φ_{PSII} as a result of changes in characteristics of chloroplasts. The chloroplast characteristics may differ in response to a changing R:FR ratio in the way that it does in sun and shade leaves (Öquist *et al.* 1992). In general, the chloroplasts in sun leaves have a higher capacity for photosynthetic light conversion at light saturation than those in shade leaves with their low grana stacks and less light-harvesting Chl *a*/*b* protein complex (*i.e.* higher Chl *a*/*b* ratio) (Lichtenthaler *et al.* 1981). However, the ratio of light-harvesting Chl complex was probably not the main reason for the difference in potential photosynthetic ability between the two types of leaves in the present study, because the Chl *a*/*b* ratio was decreased by fluorescent acclimation rather than be increased. The Chl *a*/*b* ratio is probably regulated by PPFD, but in a manner which is independent of R:FR.

The differences in the vertical distribution of chloroplasts within the leaf between the two types of leaves may explain the difference in Φ_{PSII} at high measurement PPFDs. It is supposed that the chloroplasts were distributed more widely in the fluorescent-acclimated leaves based on the relationship among Chl content, LMA, and leaf thickness. This hypothesis is supported by results of the previous report (Shibuya *et al.* 2011) in which the palisade and spongy tissues in fluorescent-acclimated leaves were thicker than those in metal-halide acclimated leaves in a similar way as the sun leaves. The quantum efficiency of photosynthesis could be lower in chloroplasts located near the irradiated surface than in chloroplasts deeper within the leaf (Terashima *et al.* 2009). Thus, when chloroplasts are distributed widely from the upper to the lower layers of thicker leaves, such as in the fluorescent-acclimated leaves, the total quantum efficiency per unit leaf area can be improved by having a higher quantum efficiency in the lower chloroplasts than would be the case in thinner leaves, in which the chloroplasts may be distributed near the irradiated surface. It should be noted that the role of chloroplast characteristics and distribution is still a hypothesis based on indirect experimental evidence. To clarify these mechanisms, a detailed physiological and anatomical analysis of chloroplast will be necessary.

The LMA difference between the two types of leaves could also partly explain the changes in the photosynthetic response, because there is often a tight relationship between photosynthetic capacity and LMA; a greater leaf biomass for photosynthesis per area enhances the photosynthetic capacity at high light intensity (Poorter *et al.* 2009). The greater LMA in the fluorescent-acclimated leaves at acclimation PPFDs of 100 and 300 µmol m^{-2} s^{-1} generally agreed with previous reports, in which greater potential photosynthetic ability was observed in plants acclimated to fluorescent illumination at a PPFD of 100 µmol m^{-2} s^{-1} (Hogewoning *et al.* 2010) or 350 µmol m^{-2} s^{-1} (Shibuya *et al.* 2010a). The LMA difference between the two types of leaves probably resulted from differences in the R:FR ratio of the acclimation illumination, although it was previously reported that changes in the R:FR ratio can alter LMA to a minor degree (Poorter *et al.* 2009); similar relationships were observed in previous studies in which only the FR photon flux was modified (Shibuya *et al.* 2010a, 2011). However, there was no LMA difference between the two types of leaves at high acclimation PPFDs. It is therefore possible that the effects of LMA on photosynthetic responses were related to the acclimation light intensity. The leaf thickness value and the leaf mass provided similar results in general, yet they did not always do so. It is supposed that the dry mass concentration per leaf volume was lower in the fluorescent-acclimated leaves than the metal-halide-acclimated leaves at the high PPFDs based on the relationship between LMA and leaf thickness, or, in other words, that the greater thickness of fluorescent acclimated leaves at high PPFD resulted in part from larger, swollen cells with a greater water content, possibly with larger vacuoles but also and/or enlarged cytoplasm allowing for space for chloroplast redistribution.

There is another possibility that the difference in g_s between the two types of leaves was one of reason for the difference in potential photosynthetic ability, even though we could not analyze a relationship between P_G and g_s in the present study. For example, Boccalandoro *et al.* (2009) reported that illumination with higher R:FR that enhance the proportion of active phytochrome also enhance stomatal density and consequent CO_2 uptake at high light intensity.

From these results, it can be concluded that the potential photosynthetic ability of *Cucumis sativus* leaves could be improved by acclimation to fluorescent illumination, regardless of the acclimation light intensity. The ratios of Φ_{PSII} in the fluorescent-acclimated leaves to those in the metal-halide-acclimated leaves tended to increase with increasing acclimation PPFD, whereas the corresponding ratios for relative Chl content and LMA tended to decrease with increasing acclimation PPFD. Thus, the mechanisms responsible for the greater maximum P_G of the fluorescent-acclimated leaves may relate to an interaction between the acclimation light quality and quantity, and may have been mainly caused by a greater leaf biomass for photosynthesis per area at low acclimation PPFDs and by the greater Φ_{PSII} and as a result of changes in characteristics and distribution of chloroplasts, or a combination of these factors at high acclimation PPFDs. This implies two separate responses, one for LMA (or cellular characteristics) and one for Φ_{PSII} (or chloroplast characteristics), with separate light perception mechanisms. The facts that plants acclimated to fluorescent illumination with high R:FR ratio show the heightened photosynthetic acclimation to light intensities would be considerable when photosynthetic results obtained under the fluorescent illumination are applied to field grown plants. In horticultural production, this improved acclimation would be useful in particular for the production of transplants under artificial lights (Kozai *et al.* 2006, Kozai 2007), since the high quality transplants with sun-leaf-like leaves could be raised at relatively low light intensity.

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