Potential Photosynthetic Advantages of Cucumber (*Cucumis sativus* L.) Seedlings Grown under Fluorescent Lamps with High Red:far-red Light

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Abstract. To evaluate the effect of fluorescent lamps with a high red:far-red (R:FR) light on the potential photosynthesis of transplants, we investigated the photosynthetic light responses of cucumber (*Cucumis sativus* L.) seedlings grown under fluorescent lamps with high R:FR light (FL_H) and compared them with the responses of the seedlings grown under metal-halide lamps (ML) that provided a spectrum similar to that of natural light and under a fluorescent lamp with low R:FR light (FL_L). The seedlings were grown under FL_H (R:FR = 7.0), ML (R:FR = 1.2), or FL_L (R:FR = 1.1) at a photosynthetic photon flux density (PPFD) of 350 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. The gross photosynthetic rate (P_g), quantum yield of photosystem II (Φ_{PSII}), and photosynthetic electron transfer rate (ETR) of the foliage leaves were then evaluated at PPFDs ranging from 0 to 1000 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. The photosynthetic light response of FL_H seedlings was similar to those of sun leaves, and the responses of ML and FL_L seedlings were similar to those of shade leaves. The P_g , ETR, and Φ_{PSII} of FL_H seedlings at PPFD of 1000 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ was 1.38, 1.32, and 1.28 times, respectively, those of ML seedlings, and was 1.40, 1.23, and 1.22 times, respectively, those of FL_L seedlings. The P_g was closely correlated with ETR in each treatment. FL_H seedlings had thicker leaf and greater chlorophyll content per leaf area than ML and FL_L seedlings. The greater P_g of FL_H seedlings than in the other two groups of seedlings at high PPFD was probably the result of the improved ETR resulting from physiological and morphological changes in response to the high R:FR light.

High-performance production systems unconstrained by weather conditions have recently been developed to produce high-quality transplants under artificial light (Kozai, 2007; Kozai et al., 2006). Seedlings grown under light provided by the fluorescent lamps used in these systems have less shoot elongation than those grown under natural light (Ohya et al., 2003). The reduced shoot elongation seems to be the result of the high red to far-red ratios (R:FR) of typical commercial fluorescent lamps, which emit little FR irradiance. Elongation of plant shoots could be improved by increasing the FR content of the light from these lamps (Murakami et al., 1991). In natural ecosystems, shoot elongation and leaf expansion are increased and leaf thickness and chlorophyll content reduced by a reduction in the R:FR resulting from absorption of red irradiation by neighboring vegetation (Smith

and Whitelam, 1997). This morphological response is called shade avoidance and is used by plants to tolerate or avoid shading (Franklin, 2008). In contrast, the higher-than-natural R:FR of fluorescent lamps may improve adaptability to high irradiation levels because seedlings under such lamps show morphological responses that are inverse to shade avoidance. At high irradiation levels, leaves adapted to high irradiation (sun leaves) have greater photosynthetic light-use efficiency than shaded leaves (Lichtenthaler et al., 1981). If adaptation of seedlings to high irradiation could be improved by growth under fluorescent lamps, then the photosynthetic efficiency and consequent growth at high irradiation could be improved. However, photosynthetic acclimation to light at higher-than-natural R:FR has not been well investigated, although that at lower R:FR has been investigated in ecological science studies (Corré, 1983; Maliakal et al., 1999; Murchie and Horton, 1997; Sleeman and Dudley, 2001; Sleeman et al., 2002; Turnbull et al., 1993). To evaluate the effect of adaptation to fluorescent light with high R:FR light on the potential photosynthetic advantage of transplants, we investigated the photosynthetic

light responses of cucumber (*Cucumis sativus* L.) seedlings grown under fluorescent lamps with high R:FR light and compared them with the responses of the seedlings grown under metal-halide lamps that provided a spectrum similar to that of natural light and under a fluorescent lamp with low R:FR light.

Materials and Methods

Expt. 1: Comparison of high red:far-red fluorescent lamps with metal-halide lamps. *Cucumis sativus* L. 'Hokushin' was sown in plastic pots (60 mm diameter, 55 mm height) containing vermiculite medium and then germinated in a chamber maintained at an air temperature of 26 to 28 °C, a relative humidity of 60%, and a photosynthetic photon flux density (PPFD) of 250 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ under fluorescent lamps (FHF32EX-N-H; Panasonic Corp., Kadoma, Japan) with a light:dark photoperiod of 12:12 h. After the cotyledons had fully expanded, the seedlings were moved to growth chambers illuminated with fluorescent lamps with high R:FR light (FPL55EX-N; Panasonic Corp.) (FL_H) or with metal-halide lamps (DR400/TL; Toshiba Lighting & Technology Corp., Yokosuka, Japan) (ML) providing a spectrum similar to that of natural light. The R (wavelength 600 to 700 nm):FR (700 to 800 nm) of FL_H was 7.0 and that of ML was 1.2. The spectrum of ML was similar to that of natural light, except that ML had strong peaks at wavelengths of 540 to 570 nm (Fig. 1). The spectra were measured by a spectrometer (BLK-CXR-SR; StellarNet Inc., Tampa, FL).

Nutrient solution (A-type recipe of Otsuka House Solution; Otsuka Chemical 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. The composition of the solution in grams per 1000 L of tap water was: total nitrogen, 260; P₂O₅, 120; K₂O, 405; CaO, 230; MgO, 60; MnO, 1.5; B₂O₃, 1.5; iron, 2.7; copper, 0.03; zinc, 0.09; and molybdenum, 0.03. Electrical conductivity was ≈ 2.6 mS/cm, and the pH value was ≈ 6.5 . The growth conditions were: air temperature 27 to 28 °C, relative humidity 50%, and PPFD 350 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at the canopy surface with a light:dark photoperiod of 12:12 h. The PPFD at the canopy was maintained by adjusting the distance between the light sources and the plant canopy during the growing period. A water filter (20-mm depth) was placed under the ML to prevent increases in leaf temperature from the long-wave radiation from the ML.

After being grown for 8 d under FL_H or 6 d under ML, sample seedlings from each treatment group were taken to measure the net photosynthetic rate (P_n) and quantum yield of photosystem II photochemistry (Φ_{PSII} ; Maxwell and Johnson, 2000). Because of the faster development of leaves under ML than under FL_H, FL_H seedlings took 2 d longer to equal the growth stage of ML seedlings for measurement. The seedlings under each treatment had one full-expanded

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Fig. 1. Fluorescent lamp with high red:far-red (R:FR) light (FL_H), fluorescent lamp with low R:FR light (FL_L), and metal-halide lamp (ML) spectra used in the experiment. Photon fluxes per unit wavelength are expressed in values relative to a maximum. R:FR was estimated by dividing the accumulated photon flux from red (wavelength 600 to 700 nm) by that from far-red (700 to 800 nm) light. The spectrum of ML was measured below the water filter.

foliage leaf, one unexpanded foliage leaf, and two cotyledons. P_n and Φ_{PSII} of the first foliage leaves were measured with a photosynthesis and fluorescence measuring system (LI-6400-40; LI-COR Inc., Lincoln, NE) at $PPFD_s$ of 1000, 500, 250, 100, and 50 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$; the $PPFD$ was changed in the order of high to low. After the measurement of P_n and Φ_{PSII} , the dark respiration rate of the leaves was measured with the same system at a $PPFD$ of 0 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Gross photosynthetic rate (P_g) was estimated by summing the dark respiration rate and the P_n . The minimum waiting time for measurement at each $PPFD$ was 3 min, and the maximum was 10 min. Illumination was supplied by red (peak = 635 nm) and blue (peak = 465 nm) light-emitting diodes in a combination ratio of 9:1. In the leaf chamber of the measuring system, the air temperature was maintained at $30 \pm 3^\circ\text{C}$, leaf temperature at 28°C , relative humidity at $50\% \pm 10\%$, and CO_2 concentration at $400 \mu\text{mol}\cdot\text{mol}^{-1}$. The photosynthetic electron transport rate (ETR) was then estimated from Φ_{PSII} , $PPFD$, and leaf absorption in accordance with the method of Genty et al. (1989). The absorbance of leaves was estimated from a relative chlorophyll content

determined with a chlorophyll meter (SPAD-502; Konica Minolta Sensing Inc., Sakai, Japan) as follows. The relative chlorophyll content of several seedlings' leaves was evaluated with the chlorophyll meter in a preliminary experiment. Absorbance of the leaves was also evaluated from spectral reflectance and transmittance determined with the spectrometer. From these values, the linear relationship between relative chlorophyll content and leaf absorption was determined. Finally, we could estimate the absorbance of sampled leaves from the relative chlorophyll content with this relationship. The measurements of the photosynthetic parameters were conducted for five seedlings in each treatment without replication.

Samples of 10 seedlings in each treatment group were taken to measure the fresh weight, area, and chlorophyll content of the first foliage leaf and the shoot length. The relative chlorophyll content was evaluated with the chlorophyll meter. Fresh weight per leaf area was estimated as an index of leaf thickness. Significance between means of the growth parameters was determined by Student's *t* test at $P = 0.05$ and 0.01 .

Expt. 2: Comparison of high red:far-red fluorescent lamps with low red:far-red

Fig. 2. Light-response curves of gross photosynthetic rate (P_g) of (A) cucumber seedlings grown under fluorescent lamps with high red:far-red (R:FR) light (FL_H) or metal-halide lamps (ML) (Expt. 1); and (B) those grown under FL_H or fluorescent lamps with low R:FR light (FL_L) (Expt. 2). Values represent means $\pm$ SE ($n = 5$). Measurements were conducted at a leaf temperature of 28°C and a CO_2 concentration of $400 \mu\text{mol}\cdot\text{mol}^{-1}$. Illumination was supplied by red and blue light-emitting diodes in a combination ratio of 9:1 during the measurement.

fluorescent lamps. Cucumber seedlings were grown in growth chambers illuminated with FL_H or fluorescent lamps with low R:FR light (FL20S-FR-P; Panasonic Corp.) (FL_L), and then the photosynthetic light-response curve and growth characteristics of the seedlings were evaluated in the same way as Expt. 1. The spectrum of FL_H was similar to that of FL_L, except that there was higher photon flux at FR (Fig. 1). The R:FR of FL_L was 1.1. The growing conditions (with the exception of the light source) and measuring methods were the same as in Expt. 1. It took 6 d under FL_L and 8 d under FL_H for seedlings to reach an equal growth stage for measurement.

Expt. 3: Effects of seedlings' age on net photosynthetic rate at high photosynthetic photon flux density. We evaluated P_n of seedlings at varied age to prove that the difference in age of seedlings does not affect the photosynthetic light response. The seedlings were grown under FL_H or FL_L for 4, 6, and 8 d after the cotyledons had fully expanded, and then P_n of them was measured at a $PPFD$ of $1000 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Measuring methods and conditions (with the exception of $PPFD$ level) were the same as in Expt. 1.

Fig. 3. Light-response curves of photosynthetic electron transfer rate (ETR) of (A) cucumber seedlings grown under fluorescent lamps with high red:far-red (R:FR) light (FL_H) or metal-halide lamps (ML) (Expt. 1); and (B) those grown under FL_H or fluorescent lamps with low R:FR light (FL_L) (Expt. 2). Values represent means $\pm$ SE ($n = 5$). For measurement conditions, see Figure 2.

Results

Expt. 1. The P_g of seedlings grown under either FL_H or ML increased with a tendency of saturation as PPFD was raised from 0 to 1000 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Fig. 2A). The tendency of saturation was stronger in ML than FL_H. The P_g of FL_H seedlings was 1.18, 1.15, 1.20, 1.31, and 1.38 times that of ML seedlings at PPFDs of 50, 100, 250, 500, and 1000 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, respectively. The light compensation point, estimated from the light-response curve of P_n (data not shown), was 35 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in FL_H seedlings and 33 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in ML seedlings. The ratio of P_g of the FL_H seedlings to that of the ML seedlings increased with increasing PPFD. The ETR of seedlings grown under FL_H or ML increased with increasing PPFD from 0 to 1000 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in the same way as P_g (Fig. 3A). The ETR of FL_H seedlings was 1.08, 1.10, 1.14, 1.22, and 1.32 times that of ML seedlings at PPFDs of 50, 100, 250, 500, and 1000 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, respectively. An almost linear relationship between ETR and P_g was observed in each treatment group (Fig. 4A). The P_g in ML seedlings tended to

be lower than in FL_H seedlings at the same ETR. The Φ_{PSII} of FL_H seedlings was 1.05, 1.07, 1.11, 1.19, and 1.28 times that of ML seedlings at PPFDs of 50, 100, 250, 500, and 1000 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, respectively (Fig. 5A). The ratio of the Φ_{PSII} of the FL_H seedlings to those of the ML seedlings increased with increasing PPFD. There was no significant difference in leaf fresh weight or leaf area between FL_H and ML seedlings ($P > 0.05$; Table 1). The fresh weight per leaf area, relative chlorophyll content, and shoot length in FL_H seedlings were 1.11, 1.25, and 0.47 times, respectively, those of ML seedlings ($P < 0.01$; Table 1). The absorbance of red and blue mixed light in FL_H leaves was 89.4% and that in ML leaves was 86.9%.

Expt. 2. The ETR and Φ_{PSII} of FL_H seedlings in Expt. 2 were greater than those in Expt. 1 (Figs. 3 and 5), although the environmental conditions were almost the same for FL_H seedlings in the two experiments. The growth parameters of FL_H seedlings in each experiment also differed (Tables 1 and 2). These differences were probably the result of differences in the timing of the experiment, although the true reasons are not clear. The

Fig. 4. Relationships between photosynthetic electron transfer rate (ETR) and gross photosynthetic rate (P_g) of (A) cucumber seedlings grown under fluorescent lamps with high red:far-red (R:FR) light (FL_H) or metal-halide lamps (ML) (Expt. 1); and (B) those grown under FL_H or fluorescent lamps with low R:FR light (FL_L) (Expt. 2). Values represent means $\pm$ SE ($n = 5$).

absolute values obtained in each experiment could not be compared directly.

The P_g of seedlings grown under either FL_H or FL_L increased with a tendency of saturation as PPFD was raised from 0 to 1000 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Fig. 2B). The tendency of saturation is stronger in FL_L than FL_H. The ratio of the P_g of the FL_H seedlings to that of the FL_L seedlings increased with increasing PPFD in the same way as the relationship between FL_H and ML in Expt. 1. The P_g of FL_H seedlings was 0.97, 1.04, 1.11, 1.28, and 1.40 times that of FL_L seedlings at PPFDs of 50, 100, 250, 500, and 1000 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, respectively. The light compensation point, estimated from the light-response curve of P_n (data not shown), was 50 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in FL_H seedlings and 47 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in FL_L seedlings. The ETR of seedlings grown under FL_H or FL_L increased with increasing PPFD from 0 to 1000 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in the same way as P_g (Fig. 3B). A strong correlation was observed between ETR and P_g in each treatment group (Fig. 4B). P_g increased linearly with ETR; however, the slope became gentler in FL_L seedlings at higher ETR, whereas it was almost constant in FL_H seedlings.

The P_n in FL_L seedlings was lower than in FL_H seedlings at high ETRs (from $\approx 100 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). The Φ_{PSII} of FL_H seedlings was greater than that of FL_L seedlings at $PPFD$ s of 500 and $1000 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ but smaller than that of FL_L seedlings at $PPFD$ s of 50 and $100 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Fig. 5B). The ratios of the ETR and Φ_{PSII} of FL_H seedlings to those of FL_L seedlings increased with increasing $PPFD$ in the same way as these ratios for FL_H to ML in Expt. 1. The relationships between the photosynthetic light response of FL_H and FL_L were therefore similar to those of FL_H and ML in Expt. 1, but ETR and Φ_{PSII} of FL_H were greater than in Expt. 1.

There were no significant differences in leaf fresh weight and leaf area between FL_H and FL_L seedlings ($P > 0.05$; Table 2). The fresh weight per leaf area in FL_H seedlings was 1.09 times that in FL_L seedlings ($P < 0.05$; Table 2). The relative chlorophyll content and shoot length in FL_H seedlings were 1.28 and 0.56 times, respectively, those in FL_L seedlings ($P < 0.01$; Table 2). The relationship between the growth characteristics of FL_H and FL_L were therefore similar to those of FL_H and ML in Expt. 1, but the growth parameters of FL_H seedlings were greater than in Expt. 1. The absorbance of red and blue mixed light in FL_H leaves was 90.0% and that in FL_L leaves was 89.6%.

Expt. 3. The P_n of seedlings grown under either FL_H or ML was increased from Day 4 to Day 6 and then was maintained almost constant from Day 6 to Day 8 (Fig. 6). The P_n of FL_H seedlings was greater than those of FL_L regardless of their age and was ≈ 1.2 times those of FL_L at the same age. The P_n in this experiment was greater than those in Expt. 2 (data not shown).

Discussion

The differences in the photosynthetic light response and morphological characteristics between FL_H and ML seedlings seemed to be the result of the difference in R:FR between the two lamps because similar relationships were observed between FL_H and FL_L in Expt. 2 in which virtually only the FR photon flux was modified.

The FL_H seedlings took 2 d longer (8 d) to equal the growth stage of ML or FL_L seedlings for measurement. This difference in age of seedlings probably did not affect their photosynthetic light response because the P_n of FL_H seedlings at high $PPFD$ on Day 6 and Day 8 was almost same and was greater than those of FL_L seedlings at the same age (Fig. 6). However, why the P_n in Expt. 3 was greater than those in Expt. 2 is unknown.

Comparison with the results of another experiment revealed that the photosynthetic light response of FL_H seedlings was similar to those of sun leaves, and the curves of ML and FL_L seedlings were similar to those of shade leaves (Lichtenthaler et al., 1981); photosynthetic light-use efficiency at high $PPFD$ s was higher in FL_H seedlings than in ML and FL_L seedlings grown at the same $PPFD$ s (Fig. 2).

Fig. 5. Light-response curves of quantum yield of photosystem II (Φ_{PSII}) of (A) cucumber seedlings grown under fluorescent lamps with high red:far-red (R:FR) light (FL_H) or metal-halide lamps (ML) (Expt. 1); and (B) those grown under FL_H or fluorescent lamps with low R:FR light (FL_L) (Expt. 2). Values represent means $\pm$ SE ($n = 5$). For measurement conditions, see Figure 2.

Table 1. Leaf fresh weight, leaf area, relative chlorophyll content of first leaf, and shoot length in cucumber seedlings grown under fluorescent lamps with high red:far-red light (FL_H) or metal-halide lamps (ML) (Expt. 1).

Treatment	Leaf fresh wt (mg)	Leaf area (cm^2)	Fresh wt per leaf area ($\text{mg}\cdot\text{cm}^{-2}$)	Relative chlorophyll content (SPAD value)	Shoot length (mm)
FL_H	509 ± 14	28.6 ± 0.6	17.8 ± 0.3	38.7 ± 0.5	31.2 ± 2.9
ML	475 ± 11	29.6 ± 0.6	16.1 ± 0.1	30.9 ± 0.5	67.0 ± 3.7
Significance	NS	NS	**	**	**

Values are means $\pm$ SE ($n = 10$). Relative chlorophyll content was the chlorophyll meter value (SPAD-502; Konica Minolta Sensing Inc., Sakai, Japan).

NS = nonsignificant at $P = 0.05$; **significantly different between the treatments at $P = 0.01$, respectively, according to Student's t test.

Table 2. Leaf fresh weight, leaf area, relative chlorophyll content of first leaf, and shoot length in cucumber seedlings grown under fluorescent lamps with high red:far-red (R:FR) light (FL_H) or fluorescent lamps with low R:FR light (FL_L) (Expt. 2).

Treatment	Leaf fresh wt (mg)	Leaf area (cm^2)	Fresh wt per leaf area ($\text{mg}\cdot\text{cm}^{-2}$)	Relative chlorophyll content (SPAD value)	Shoot length (mm)
FL_H	810 ± 23	40.5 ± 1.9	20.2 ± 0.6	43.1 ± 1.1	33.5 ± 1.1
FL_L	759 ± 23	39.4 ± 1.0	18.6 ± 0.4	33.8 ± 1.5	60.1 ± 2.0
Significance	NS	NS	*	**	**

Values are means $\pm$ SE ($n = 10$). Relative chlorophyll content was the chlorophyll meter value (SPAD-502; Konica Minolta Sensing Inc., Sakai, Japan).

NS = nonsignificant at $P = 0.05$; * and **significantly different between the treatments at $P = 0.05$ and $P = 0.01$, respectively, according to Student's t test.

This means that, at high $PPFD$ s, seedlings grown in a closed system under FL_H would fix more CO_2 per leaf area than seedlings grown under natural light at the same $PPFD$.

In contrast, a low $PPFD$ would be unfavorable to FL_H seedlings because, like in sun leaves versus shade leaves, the light compensation point of FL_H seedlings was higher than

Fig. 6. Changes in net photosynthetic rate (P_n) of cucumber seedlings grown under fluorescent lamps with high red:far-red (R:FR) light (FL_H) or fluorescent lamps with low R:FR light (FL_L) after starting treatment (Expt. 3). Values represent means $\pm$ SE (Day 4, $n = 5$; Day 6, $n = 4$; Day 8, FL_H: $n = 5$, FL_L: $n = 4$). Measurements were conducted at a photosynthetic photon flux density of $1000 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, a leaf temperature of 28°C , and a CO_2 concentration of $400 \mu\text{mol}\cdot\text{mol}^{-1}$. Illumination was supplied by red and blue light-emitting diodes in a combination ratio of 9:1 during the measurement.

those of ML and FL_L seedlings. Illumination with low R:FR light is advantageous for improving the growth of seedlings because plants often grow faster at lower R:FR (Murakami et al., 1991; Pausch et al., 1991), as we also observed here. On the other hand, the photosynthetic efficiency in FL_H seedlings was greater than that in FL_L seedlings at high PPFDs, although the growth rate in the former was lower. Therefore, a high R:FR light is probably advantageous when seedlings are to be moved to high PPFD conditions, for example, as transplants. There is, therefore, a tradeoff between faster growth and improved photosynthetic efficiency at high PPFDs. In selecting artificial light for plant production, we need to consider which of the two advantages is more important.

The higher P_g of FL_H seedlings at high PPFDs was probably the result of the higher ETR, because P_g was closely correlated with ETR (Fig. 4). One reason for the higher ETR of FL_H seedlings than of ML and FL_L seedlings was the higher relative chlorophyll content per leaf area. Another reason is probably the higher efficiency of PSII photochemistry in FL_H seedlings than in ML seedlings and in FL_L seedlings at high PPFDs (Fig. 5). The function of chlorophyll may differ with the R:FR in the same way as it differs in sun and shade leaves (Öquist et al., 1992). However, we do not know the reason for the improved Φ_{PSII} in FL_H seedlings compared with ML and FL_L seedlings at high PPFDs (Fig. 5). A linear relationship between ETR and P_g was observed over a wide range of them in Expt. 1, meaning that CO_2 fixation efficiency per electron transport remained constant. The efficiency of CO_2 fixation in C_3 plants is reduced because of photorespiration when CO_2 fixation is saturated (Kato et al., 2003). In Expt. 1, strong nonphotochemical heat dissipation was probably induced under high PPFD; consequently, the linear relationship between

ETR and P_g was maintained. This would be supported by the decrease in Φ_{PSII} under higher PPFD. On the other hand, the development of a nonlinear relationship in Expt. 2 was probably the result of the greater P_g and ETR than those in Expt. 1. The gentle slope in the relationship between ETR and P_g in FL_L seedlings at high ETR (Fig. 4B) seemed to be the result of the reduction of the CO_2 fixation efficiency at a high PPFD. The reduction of CO_2 fixation efficiency could also be reduced by acclimating to high PPFD (Kato et al., 2003). Our results suggest that both a high R:FR light and high PPFD act by the same mechanism to reduce the reduction of CO_2 fixation efficiency. To clarify these mechanisms, a detailed analysis of chlorophyll function will be necessary.

From the values of fresh weight per leaf area and relative chlorophyll content (Tables 1 and 2), we assumed that leaf thickness and chlorophyll content per leaf area were greater in growth under FL_H than under ML or FL_L. The R:FR under FL_H (7.0) is much higher than that of solar radiation and does not exist in nature. With a lower R:FR than occurs with natural light, shoot elongation and leaf expansion rates increase so that the plant can avoid shade and chlorophyll content declines (Smith and Whitelam, 1997). In addition, plant leaves adapted to low R:FR light have low net photosynthetic rates (Maliakal et al., 1999; Sleeman and Dudley, 2001; Sleeman et al. 2002). In FL_H seedlings, the inverse physiological and morphological responses (i.e., increased leaf thickness and chlorophyll content and reduced shoot elongation) to those typical of shade avoidance seemed to be the result of heightened adaptation to the higher PPFD induced by the high R:FR of FL_H. The photosynthetic efficiency of FL_H seedlings at high PPFDs was probably improved as a result of this heightened adaptation to sun.

From these data, we concluded that growth of cucumber seedlings under fluorescent lamps with high R:FR light can improve potential photosynthesis compared with that under low R:FR illumination. Photosynthetic responses under light of different qualities have been well investigated (Goins et al., 1997; Korbbe et al., 2005; Pausch et al., 1991; Yorino et al., 2001). The fact that light quality affects photosynthetic light response should be considered in selecting a light source for plant production under artificial light when postproduction characteristics are vital such as in transplant production.

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