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 (FLH) 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 (FLL). The seedlings were grown under FLH (R:FR = 7.0), ML (R:FR = 1.2), or FLL (R:FR = 1.1) at a photosynthetic photon flux density (PPFD) of 350 μmol m−2 s−1. The gross photosynthetic rate (Pg), quantum yield of photosystem II (ΦPSII), and photosynthetic electron transfer rate (ETR) of the foliage leaves were then evaluated at PPFDs ranging from 0 to 1000 μmol m−2 s−1. The photosynthetic light response of FLH seedlings was similar to those of sun leaves, and the responses of ML and FLL seedlings were similar to those of shade leaves. The Pg, ETR, and ΦPSII of FLH seedlings at PPFD of 1000 μmol m−2 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 FLL seedlings. The Pg was closely correlated with ETR in each treatment. FLH seedlings had thicker leaf and greater chlorophyll content per leaf area than ML and FLL seedlings. The greater Pg of FLH 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 high light provided by the fluorescent lamps used in these systems have less shoot elongation than those grown under natural light (Ohyama 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; Murry 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. ‘Hokusshin’ was sown in plastic pots (60 mm diameter, 55 mm height) containing vermiculite and 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 μmol m−2 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.) (FLH) 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 FLH 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 μmol m−2 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 FLH or 6 d under ML, sample seedlings from each treatment group were taken to measure the net photosynthetic rate (Pn) and quantum yield of photosystem II (ΦPSII; Maxwell and Johnson, 2000). Because of the faster development of leaves under ML than under FLH, FLH 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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humidity at 50% ± 10%, and CO₂ concentration at 400 ppm.

In the leaf chamber of the measuring system, the air temperature was maintained at 28 °C and the leaf temperature 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 fluorescent lamps. Cucumber seedlings were grown in growth chambers illuminated with FLH or fluorescent lamps with low R:FR light (FL20S-FL-P; Panasonic Corp.) (FLL), 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 FLH was similar to that of FLL, except that there was higher photon flux at FR (Fig. 1). The R:FR of FLL 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 FLL and 8 d under FLH 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 Pn 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 FLH or FLL for 4, 6, and 8 d after the cotyledons had fully expanded, and then Pn of them was measured at a PPFD of 1000 μmol·m⁻²·s⁻¹. Measuring methods and conditions (with the exception of PPFD level) were the same as in Expt. 1.
Results

Expt. 1. The $P_g$ of seedlings grown under either FLH or ML increased with a tendency of saturation as $PPFD$ was raised from 0 to 1000 $\mu$mol-m$^{-2}$-s$^{-1}$ (Fig. 2A). The tendency of saturation was stronger in ML than FLH. The $P_g$ of FLH seedlings was 1.18, 1.15, 1.20, and 1.31, and 1.38 times that of ML seedlings at $PPFD$s of 50, 100, 250, 500, and 1000 $\mu$mol-m$^{-2}$-s$^{-1}$, respectively. The light compensation point, estimated from the light-response curve of $P_g$ (data not shown), was 35 $\mu$mol-m$^{-2}$-s$^{-1}$ in FLH seedlings and 33 $\mu$mol-m$^{-2}$-s$^{-1}$ in ML seedlings. The ratio of $P_g$ of the FLH seedlings to that of the ML seedlings increased with increasing $PPFD$. The ETR of seedlings grown under FLH or ML increased with increasing $PPFD$ from 0 to 1000 $\mu$mol-m$^{-2}$-s$^{-1}$ in the same way as $P_g$ (Fig. 2A). The ETR of FLH seedlings was 1.08, 1.10, 1.14, 1.22, and 1.32 times that of ML seedlings at $PPFD$s of 50, 100, 250, 500, and 1000 $\mu$mol-m$^{-2}$-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 FLH seedlings at the same ETR. The $\Phi_{PSII}$ of FLH seedlings was 1.05, 1.07, 1.11, 1.19, and 1.28 times that of ML seedlings at $PPFD$s of 50, 100, 250, 500, and 1000 $\mu$mol-m$^{-2}$-s$^{-1}$, respectively (Fig. 5A). The ratio of the $\Phi_{PSII}$ of the FLH seedlings to those of the ML seedlings increased with increasing $PPFD$. There was no significant difference in leaf fresh weight or leaf area between FLH and ML seedlings ($P > 0.05$; Table 1). The fresh weight per leaf area, relative chlorophyll content, and shoot length in FLH 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 FLH leaves was 89.4% and that in ML leaves was 86.9%.

Expt. 2. The ETR and $\Phi_{PSII}$ of FLH seedlings in Expt. 2 were greater than those in Expt. 1 (Figs. 3 and 5), although the environmental conditions were almost the same for FLH seedlings in the two experiments. The growth parameters of FLH 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 absolute values obtained in each experiment could not be compared directly.

The $P_g$ of seedlings grown under either FLH or FLL increased with a tendency of saturation as $PPFD$ was raised from 0 to 1000 $\mu$mol-m$^{-2}$-s$^{-1}$ (Fig. 2B). The tendency of saturation was stronger in FLH than FLL. The ratio of the $P_g$ of the FLH seedlings to that of the FLL seedlings increased with increasing $PPFD$ in the same way as the relationship between FLH and ML in Expt. 1. The $P_g$ of FLH seedlings was 0.97, 1.04, 1.11, 1.28, and 1.40 times that of FLL seedlings at $PPFD$s of 50, 100, 250, 500, and 1000 $\mu$mol-m$^{-2}$-s$^{-1}$, respectively. The light compensation point, estimated from the light-response curve of $P_n$ (data not shown), was 50 $\mu$mol-m$^{-2}$-s$^{-1}$ in FLH seedlings and 47 $\mu$mol-m$^{-2}$-s$^{-1}$ in FLL seedlings. The ETR of seedlings grown under FLH or FLL increased with increasing $PPFD$ from 0 to 1000 $\mu$mol-m$^{-2}$-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 FLH seedlings at higher ETR, whereas it was almost constant in FLH seedlings.
The \( P_n \) in FL\(_L\) seedlings was lower than in FL\(_H\) seedlings at high ETRs (from \( \approx 100 \mu\text{mol-m}^{-2}\cdot\text{s}^{-1} \)). The \( \Phi_{\text{PSII}} \) of FL\(_H\) seedlings was greater than that of FL\(_L\) seedlings at PPFDs of 500 and 1000 \( \mu\text{mol-m}^{-2}\cdot\text{s}^{-1} \) but smaller than that of FL\(_L\) seedlings at PPFDs of 50 and 100 \( \mu\text{mol-m}^{-2}\cdot\text{s}^{-1} \) (Fig. 5B). The ratios of the ETR and \( \Phi_{\text{PSII}} \) 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.

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 \( \approx 1.2 \) 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 seedlings probably did not affect their growth stage of ML or FL\(_L\) seedlings at Day 6 and Day 8 was almost same and was greater than those of FL\(_H\) 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 PPFDs was higher in FL\(_H\) seedlings than in ML and FL\(_L\) seedlings grown at the same PPFDs (Fig. 2).

This means that, at high PPFDs, 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\(_L\) seedlings because, like in sun leaves versus shade leaves, the light compensation point of FL\(_H\) seedlings was higher than...
those of ML and FL\textsubscript{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\textsubscript{H} seedlings was greater than that in FL\textsubscript{L} seedlings at high PPFD\textsubscript{S}, 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 PPFD\textsubscript{S}. 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\textsubscript{H} seedlings at high PPFD\textsubscript{S} 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\textsubscript{H} seedlings than of ML and FL\textsubscript{L} seedlings was the higher relative chlorophyll content per leaf area. Another reason is probably the higher efficiency of PSII photochemistry in FL\textsubscript{H} seedlings than in ML and FL\textsubscript{L} seedlings at high PPFD\textsubscript{S} (Fig. 5). The function of chlorophyll may differ with the R:FR in the same way as we also observed here. On the other hand, the photosynthetic efficiency of FL\textsubscript{H} seedlings at high PPFD\textsubscript{S} was probably induced under high PPFD\textsubscript{S}; consequently, the linear relationship between ETR and $P_g$ was maintained. This would be supported by the decrease in $\Phi_{PSII}$ 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\textsubscript{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\textsubscript{S}. 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\textsubscript{H} than under ML or FL\textsubscript{L}. The R:FR under FL\textsubscript{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 can improve potential photosynthesis compared with those of ML and FL\textsubscript{L}. The photosynthetic efficiency of FL\textsubscript{H} seedlings at high PPFD\textsubscript{S} 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; Korbee et al., 2005; Pausch et al., 1991; Yorio 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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