

Growth Analysis and Photosynthesis Measurements of Cucumber Seedlings Grown under Light with Different Red to Far-red Ratios

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Additional index words. biomass allocation, leaf enlargement, net assimilation, photosensitive film, relative growth rate

Abstract. Light with a higher red to far-red ratio (R:FR) than sunlight reduces plant growth, but the cause has not been firmly established. In the present study, cucumber seedlings were grown under normal light (similar to sunlight; R:FR = 1.4) from metal-halide lamps or high-R:FR light (R:FR = 4.3) created by transmitting their light through FR-absorbing film, and then their growth parameters and photosynthesis were compared. The relative growth rate (RGR) at high R:FR was 92% of that under normal R:FR, although the net assimilation rate (NAR) did not differ between the treatments, indicating that changes in net photosynthesis per unit leaf area did not cause the growth inhibition at high R:FR. The CO₂ exchange per unit leaf area did not differ between the treatments, which supports this hypothesis. The leaf area ratio (LAR) of total plant dry weight of high R:FR seedlings to that of normal R:FR seedlings was also 92%. This suggests that growth suppression in the high R:FR seedlings was caused mainly by decreased LAR. The specific leaf area (SLA) and leaf weight ratio (LWR), components of LAR, under high-R:FR light were 89% and 105%, respectively, of those under normal light, indicating that the smaller LAR at high R:FR mainly results from suppressed leaf enlargement per unit leaf dry matter.

Photo-selective films that absorb FR light (FR-absorbing films) have been used to control the growth and development of horticultural crops (Demotes-Mainard et al., 2016; Rajapakse and Shahak, 2007; Rajapakse et al., 1999). Under these films, shoot length, which is an important criterion for the quality of transplants and pot plants, can be shortened without using chemical growth regulators (Cerny et al., 2003; Li et al., 2000; Runkle and Heins, 2002; Wilson and Rajapakse, 2001), thereby improving tolerance to mechanical stress including wind damage (Latimer and Mitchell, 1988). The reduction of shoot elongation is due to the R:FR of the filtered light, which is higher than that of sunlight due to the film's selective

absorption of FR light. This light (hereafter, "high-R:FR light") increases the proportion of active phytochrome and thereby suppresses shoot elongation (Franklin, 2008; Sasidharan et al., 2008; Smith and Whitelam, 1997). In addition to reducing extension growth, the FR-absorbing films also decrease plant dry matter production (Cerny et al., 2003; Fletcher et al., 2005; Li et al., 2000). Several studies have demonstrated that high-R:FR light decreases plant dry matter production even at equivalent photosynthetic photon fluxes (PPFs) (Hogewoning et al., 2010; Li and Kubota, 2009; Shibuya et al., 2010a), but the exact cause of this decrease has not been firmly established.

The purpose of the present study was to determine the factor or factors that limit plant growth under high-R:FR light by analyzing its effects on the components that contribute to plant growth (Hunt et al., 2002; Radford, 1967). In these methods, the RGR is calculated by multiplying the LAR by the NAR, which are correlated with the light interception area per plant and the net photosynthetic rate per unit leaf area, respectively. The high-R:FR light has been shown to alter these growth parameters. There have been many reports that leaf enlargement (correlated with LAR) was inhibited under high-R:FR light (Fletcher et al., 2005; Heraut-Bron et al.,

1999; Hogewoning et al., 2010; Li and Kubota, 2009; Shibuya et al., 2010a). The suppressed leaf enlargement decreases the light-interception area, and this could explain the reduction in dry matter production under high-R:FR light (Fletcher et al., 2005; Li and Kubota, 2009). If so, a smaller LAR can result from decreased leaf enlargement per unit leaf dry matter, decreased allocation of dry matter to the leaves vs. stems resulted from the acceleration of stem elongation, or both (Casal et al., 1987). However, leaf enlargement has not been investigated sufficiently well for plants grown under high R:FR lights to determine which explanation is correct.

Contradictory results have been reported for NAR. Heraut-Bron et al. (1999) demonstrated that the R:FR did not affect photosynthesis per unit leaf area of white clover (*Trifolium repens* L.). However, other reports demonstrated that low-R:FR light reduces the photosynthetic performance per unit leaf area of common bean (*Phaseolus vulgaris* L.), cucumber (*Cucumis sativus* L.), and other several species of different growth habit (Barreiro et al., 1992; Hogewoning et al., 2010; Pons and de Jong-Van Berkel, 2004; Shibuya et al., 2010a, 2012, 2015), although Yang et al. (2013) reported the opposite results for chrysanthemum (*Chrysanthemum ×grandiflorum* Tzvelv). In these reports, photosynthesis of a single leaf was measured under leaf chamber conditions, and thus the results may be different from results of whole-plant photosynthesis under growing conditions, which are more appropriate to explain RGRs.

In the present study, cucumber seedlings were grown under light with a normal R:FR (similar to that of sunlight) or under high-R:FR light created by FR-absorbing film, and their growth parameters were determined by the growth analysis methods. In addition, net and gross photosynthesis per unit leaf area and of the whole plant were evaluated during the growing period to follow the change in photosynthetic performance and validate the results of the growth analysis.

Materials and Methods

Growth conditions. Cucumber cv. Hokushin seeds were sown in plastic pots (60 mm in diameter, 55 mm in height; 1 plant per pot) containing vermiculite. The plants were then grown in a growth chamber. Metal-halide lamps (DR400/TL; Toshiba Lighting & Technology Corp., Yokosuka, Japan) were used with a spectrum similar to that of sunlight (R:FR = 1.4) for illumination. FR-absorbing film (prototype, NIRF-L-PP-10; Yanmar Co., Ltd., Osaka, Japan, and Panac Advance Co., Ltd., Tokyo, Japan) were placed between the lights and half of the seedlings. The R:FR under the FR-absorbing film was 4.3. The R:FR was defined as the ratio of photon flux between 600 and 700 nm (R) to that between 700 and 800 nm (FR). The film transmits ≈40% of PPF. For the other half of the seedlings,

Received for publication 1 Apr. 2016. Accepted for publication 27 Apr. 2016.

This research was supported by a Japan Society for the Promotion of Science Grant-in-Aid for Scientific Research (B) (KAKENHI 24380140, KAKENHI 15H04575), and by a joint research agreement between Osaka Prefecture University and Yanmar Co., Ltd. The authors thank Ryo Matsuda (University of Tokyo) and Keach Murakami (University of Tokyo) for valuable discussion.

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a shade net (4S-SU45, Sekisui Nano Coat Technology Co., Ltd., Gamagori, Japan) that does not change the R:FR were placed between the lights and the plants to reduce the PPF by the same amount. Figure 1 shows the resulting spectra in the two treatments. The PPF at the leaf surface was maintained at 300 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ during plant growth by adjusting the distance between the lamps and the canopy surface daily. The light:dark period was 16:8 h throughout the growing period. The air temperature and relative humidity were maintained at 27 °C and 50%, respectively. The pots were immersed to a depth of 5 to 10 mm in nutrient solution (the A-type recipe of OAT Solution; OAT Agrico Co. Ltd., Tokyo, Japan). The seedlings were arranged with sufficient space to avoid mutual shading among neighboring seedlings.

Growth analysis. Six seedlings in each treatment group were sampled at 6 and 13 d after seeding. On day 13, the cotyledons and first true leaf had expanded, but the second true leaf had not expanded. The self-shading among the leaves were not observed during the experimental period. The leaf area and shoot length were measured, and then the whole-plant and leaf dry weight (DW, measured after 3 d of drying at 80 °C) were determined. The leaf area was measured with an image scanner and “LIA for Win32” image analysis software (K. Yamamoto, Nagoya University, Nagoya, Japan, <http://www.agr.nagoya-u.ac.jp/~shinkan/LIA32/index.html>). The leaf mass per unit area (LMA) were calculated by dividing leaf DW by leaf area 13 d after seeding. Three seedlings for each treatment group were also sampled 7, 9, and 11 d after seeding to measure the whole-plant DW. The RGR (d^{-1}), relative leaf expansion rate (RLER, d^{-1}), NAR ($\text{g}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ DW basis), LAR ($\text{m}^2\cdot\text{g}^{-1}$), SLA ($\text{m}^2\cdot\text{g}^{-1}$), and LWR (dimensionless) were calculated using the following

equations (Granier and Tardieu, 1998; Hunt et al., 2002; Radford, 1967):

$$\text{RGR} = \frac{\ln W_2 - \ln W_1}{t_2 - t_1} = \text{NAR} \times \text{LAR} \quad [1]$$

$$\text{RLER} = \frac{\ln A_2 - \ln A_1}{t_2 - t_1} \quad [2]$$

$$\begin{aligned} \text{NAR} &= \frac{1}{t_2 - t_1} \times \int_{t_1}^{t_2} \frac{1}{A} \times \frac{dW}{dt} dt \\ &= \frac{W_2 - W_1}{A_2 - A_1} \times \frac{\ln A_2 - \ln A_1}{t_2 - t_1} \end{aligned} \quad [3]$$

$$\begin{aligned} \text{LAR} &= \frac{1}{t_2 - t_1} \times \int_{t_1}^{t_2} \frac{A}{W} dt = \frac{A_2 - A_1}{\ln A_2 - \ln A_1} \\ &\times \frac{\ln W_2 - \ln W_1}{W_2 - W_1} = \text{SLA} \times \text{LWR} \end{aligned} \quad [4]$$

$$\begin{aligned} \text{SLA} &= \frac{1}{t_2 - t_1} \times \int_{t_1}^{t_2} \frac{A}{L} dt = \frac{A_2 - A_1}{\ln A_2 - \ln A_1} \\ &\times \frac{\ln L_2 - \ln L_1}{L_2 - L_1} \end{aligned} \quad [5]$$

$$\begin{aligned} \text{LWR} &= \frac{1}{t_2 - t_1} \times \int_{t_1}^{t_2} \frac{L}{W} dt = \frac{L_2 - L_1}{\ln L_2 - \ln L_1} \\ &\times \frac{\ln W_2 - \ln W_1}{W_2 - W_1} \end{aligned} \quad [6]$$

where W_1 and W_2 are the total DW (g/plant) at times t_1 and t_2 (6 and 13 d after seeding, respectively), A_1 and A_2 are the corresponding total leaf areas (m^2/plant), and L_1 and L_2 are the corresponding leaf DW values (g/plant).

Photosynthesis measurements. Seedling photosynthesis was measured once per day from 6 to 13 d after seeding using a CO_2 assimilation chamber (L \times D \times H: 200 \times 200 \times 150 mm) with continuous air flow. The CO_2 exchange rates were determined ≈ 2 –7 h after the start of the photoperiod. The measurements were conducted with three replicate groups for each treatment ($n = 3$). The number of seedlings per group ranged from two to six, which was determined based on seedling size (i.e., fewer seedlings were used as the plants grew larger to avoid mutual shading during the

measurements). An air pump was used to pass air through the chamber (at 4–6 $\text{L}\cdot\text{min}^{-1}$). The CO_2 concentration at the inlet and outlet of the assimilation chamber was sampled alternately at 1-min intervals using another air pump with a flow rate of 1.0 $\text{L}\cdot\text{min}^{-1}$. The CO_2 concentration in the air samples was measured with an LI-7000 IR gas analyzer (LI-COR Inc., Lincoln, NE). The whole-plant CO_2 exchange rate ($\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ per plant) was calculated by multiplying the air flow rate ($\text{m}^3\cdot\text{s}^{-1}$) by the difference in CO_2 concentration between the inlet and outlet of the assimilation chamber ($\text{mol}\cdot\text{m}^{-3}$) and then dividing this difference by the number of plants. The CO_2 concentrations were averaged over 10 samples (i.e., over a 20-min period). The CO_2 exchange rate was also measured in the dark, with darkness created by temporarily covering the chamber with shade cloth. The CO_2 concentration and relative humidity in the assimilation chamber were stable during the measurement.

The CO_2 exchange rates under light and dark conditions represented the whole-plant net photosynthetic rate (P_N) and the dark respiration rate (R_D), respectively. R_D did not differ significantly between the two light treatments, so we have not presented or discussed that data. The gross photosynthetic rate (P_G) was determined by subtracting R_D from P_N to compare the photosynthetic performance between the treatments. To determine the P_N , R_D , and P_G per unit leaf area, the leaf areas of the seedlings used for the CO_2 exchange measurement were estimated from the leaf length and width by using a linear relationship between leaf area and length \times width that had been determined in a preliminary experiment.

The NAR ($\text{g}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, DW basis) was also calculated from the CO_2 exchange rates (for comparison with the NAR calculated based on the growth analysis) using the following equation:

$$\begin{aligned} \text{NAR} &= \sum_{t=6}^{13} (P_{Nt} \times \text{PP} + R_{Dt} \times \text{DP}) \\ &\times 44 \times \frac{1}{1.63} \times \frac{1}{8} \end{aligned} \quad [7]$$

where P_{Nt} and R_{Dt} are the net photosynthetic rate and dark respiration rate per unit leaf area ($\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, CO_2 basis) at t days after seeding, PP and DP are the photoperiod (16 h = 57,600 s) and dark period (8 h = 28,800 s), respectively, and 44, 1.63, and 8 are the molar weight of CO_2 ($\text{g}\cdot\text{mol}^{-1}$), the CO_2 assimilation per unit DW [CO_2/DW (g/g)], and measuring period (d), respectively.

Statistical analysis. Significant differences between treatment means were identified using

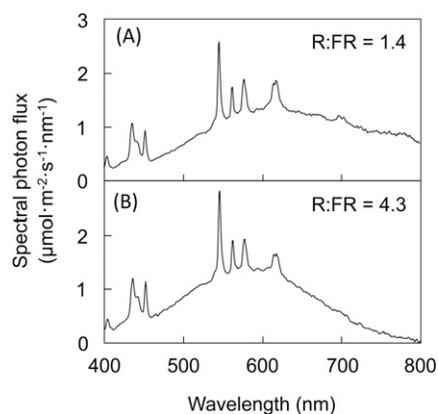


Fig. 1. Spectra of (A) light from metal-halide lamps (MHLs) transmitted through a shade net that did not change the light quality, and (B) light from MHLs transmitted through the far-red-light-absorbing film. The red to far-red ratio (R:FR) was defined as the ratio of photon flux between 600 and 700 nm (R) to that between 700 and 800 nm (FR).

Table 1. The dry weights (DWs), leaf area, leaf mass per unit area (LMA), and shoot length of cucumber seedlings grown under light with a high red to far-red ratio (R:FR = 4.3) or natural R:FR (1.4), 13 d after seeding.

Treatment	DW (mg/plant)				Leaf area (cm^2/plant)	LMA ($\text{m}^2\cdot\text{g}^{-1}$)	Shoot length (mm)
	Leaf	Hypocotyl and petiole	Root	Total			
High R:FR	254 \pm 6	37 \pm 1	52 \pm 2	343 \pm 7	167 \pm 6	16.1 \pm 0.2	26.7 \pm 1.0
Normal R:FR	300 \pm 7	60 \pm 3	62 \pm 3	421 \pm 12	232 \pm 5	14.2 \pm 0.2	37.5 \pm 1.8
P value	<0.001	<0.001	0.019	<0.001	<0.001	<0.001	<0.001

Data are the average \pm SE for six plants ($n = 6$).

Student's *t* test. The interaction effects of the determination method (growth vs. photosynthetic analysis) and the treatment on values of NAR were determined by two-way analysis of variance. The statistical analyses were performed using the Statcel 2 software (OMS Publishing Inc., Tokorozawa, Japan).

Results and Discussion

The total DW and leaf area of the high-R:FR seedlings were 81% and 72%, respectively, of those of the seedlings grown under normal light 13 d after seeding (Table 1). These results confirmed the general finding that growth and leaf expansion are suppressed under high-R:FR light. The LMA and shoot length of the high-R:FR seedlings were greater (113%) and shorter (71%), respectively, than those of the normal R:FR seedlings. These morphological traits of the high-R:FR seedlings agree with previous reports (Hogewoning et al., 2010; Shibuya et al.,

2010a, 2012, 2015), and suggest that the plants would have improved tolerance to the environmental stress (Itagaki et al., 2016; Latimer and Mitchell, 1988; Shibuya et al., 2010b, 2011) when they are used as transplants.

The DW and leaf area of the seedlings increased exponentially during the treatment. However, the increases of the rates under high-R:FR light were both less than those under normal R:FR (Fig. 2); the differences were significant after 10 and 6 d, respectively. The RGR and RLER under high-R:FR light were 92% and 85%, respectively, of those under normal R:FR. There was no significant difference in NAR between the treatments (Table 2), indicating that differences in net dry-matter assimilation (i.e., net photosynthesis) did not explain the difference in RGR between the treatments. The LAR of the high-R:FR seedlings was less than that of normal R:FR seedlings, and the proportion (92%) was the same as for the RGR (Table 2). This suggests that growth of the high-R:FR seedlings was mainly suppressed by decreased LAR, which is the other component of RGR ($RGR = NAR \times LAR$).

SLA and LWR, which are components of LAR ($LAR = SLA \times LWR$), under high-R:FR light were 89% and 105%, respectively, of those under normal R:FR light (Table 2). This indicates that the smaller LAR under high-R:FR light, which is the main factor responsible for the smaller RGR, resulted from decreased SLA. In other words, the inhibition of dry matter production under high-R:FR light resulted mainly from suppressed leaf enlargement per unit leaf dry matter but not from a change in the allocation of dry matter between the leaves and other plant parts. This hypothesis has been proposed in previous reports (Fletcher et al., 2005; Li and Kubota, 2009), and was confirmed using the growth analysis results in the present study. The slightly but significantly greater LWR of high-R:FR seedlings (Table 2), which is probably due to decreased biomass allocation to hypocotyl and petiole (Table 1), mitigated the inhibition of dry matter production under high-R:FR light. Casal et al. (1987) suggested that leaf expansion is reduced by FR light due to leaf competition with the stem tissues for photosynthate. The effect of increasing R:FR on leaf expansion and subsequent dry matter production is probably due to the range of R:FR values, which may determine the degree of competition between leaf enlargement and shoot elongation.

In the photosynthesis measurements, P_G (Fig. 3A) and P_N (data not shown) per unit leaf area remained relatively constant during the treatment period. There was also no difference in P_G and P_N (data not shown) per unit leaf area between the treatments, except 13 d after seeding (Fig. 3A). This agrees with a previous finding that the R:FR did not affect the photosynthesis per unit leaf area (Heraut-Bron et al., 1999). The reason for the difference in photosynthesis on day 13 is unclear, but the difference was relatively small and may not significantly contribute the total dry matter production. The values of NAR determined from the photosynthesis measurements were $5.49 \pm 0.11 \text{ g}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ and $5.78 \pm 0.28 \text{ g}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ under high- and normal-R:FR light, respectively (average \pm SE, $n = 3$); they did not significantly differ ($P = 0.400$). There was no significant interaction effect between the treatment and evaluation method ($P = 0.527$), which means that the NAR results in the growth analysis were validated by the NAR results from the photosynthesis measurements.

The whole-plant P_G increased exponentially after the treatment began (Fig. 3B). The rate of increase under normal R:FR was greater than that under high-R:FR light, and the difference was significant throughout the treatment period. The whole-plant P_G was significantly and positively correlated with whole-plant leaf area (Fig. 4). The relationships were equally strong under both light conditions, indicating that the whole-plant P_G was determined mainly by the leaf area, which defines the plant's light interception capacity. This also supports the result of the growth analysis, in which RGR was determined mainly by LAR in both treatments. Previous studies demonstrated that the photosynthetic capacity per unit leaf area of cucumber could be improved under high-R:FR light (Hogewoning et al., 2010; Shibuya et al., 2010a, 2012, 2015), but photosynthesis did not differ between the treatments in the present study. This is probably due to the relatively low *PPF* ($300 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), which may have concealed differences in photosynthetic capacity that might have appeared under stronger light. Thus, the disadvantage in dry matter production under the light with high-R:FR seedlings may decrease at higher *PPF*.

In the present study, the seedlings were grown until the first leaf stage to avoid self-shading among the leaves, and were arranged with sufficient space to avoid mutual shading among the neighbors. If the seedlings were grown further or densely, NAR of the normal-R:FR seedlings may be decreased earlier than that of the high-R:FR seedlings by self- or mutual-shading, respectively, because of faster leaf enlargement under normal R:FR. In addition, the results would differ among species, because morphological traits including degree of self-shading are often species-specific (Falster and Westoby, 2003).

In conclusion, the present study confirmed that the dry matter production of cucumber seedlings was suppressed under high-R:FR light, mainly due to a reduction of light

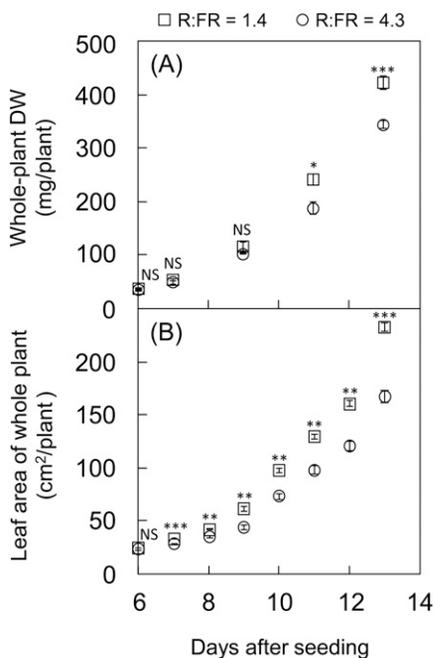


Fig. 2. Time courses of whole-plant dry weight (DW) and leaf area in cucumber seedlings under light with a high red to far-red ratio (R:FR = 4.3) or natural R:FR (1.4). Data are the average \pm SE (DW, days 6 and 13, $n = 6$; DW, day 7 to 12, $n = 3$; leaf area, $n = 6$). Leaf areas from day 7 to 12 were estimated from the leaf length and width. NS, no significant difference between treatments; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$ (*t* test).

Table 2. The relative growth rate (RGR), relative leaf expansion rate (RLER), net assimilation rate (NAR, dry weight basis), leaf area ratio (LAR), specific leaf area (SLA), and leaf weight ratio (LWR) of cucumber seedlings grown under light with a high red to far-red ratio (R:FR = 4.3) or natural R:FR (1.4) during the experimental period.

Treatment	RGR (d ⁻¹)	RLER (d ⁻¹)	NAR (g·m ⁻² ·d ⁻¹)	LAR (m ² ·g ⁻¹)	SLA (m ² ·g ⁻¹)	LWR
High R:FR	0.324 \pm 0.03	0.278 \pm 0.05	5.96 \pm 0.05	0.0543 \pm 0.0006	0.0715 \pm 0.007	0.760 \pm 0.004
Norm. R:FR	0.353 \pm 0.04	0.327 \pm 0.03	6.03 \pm 0.12	0.0585 \pm 0.0006	0.0807 \pm 0.008	0.726 \pm 0.004
<i>P</i> value	<0.001	<0.001	0.609	<0.001	<0.001	<0.001

Data are the average \pm SE for six plants ($n = 6$).

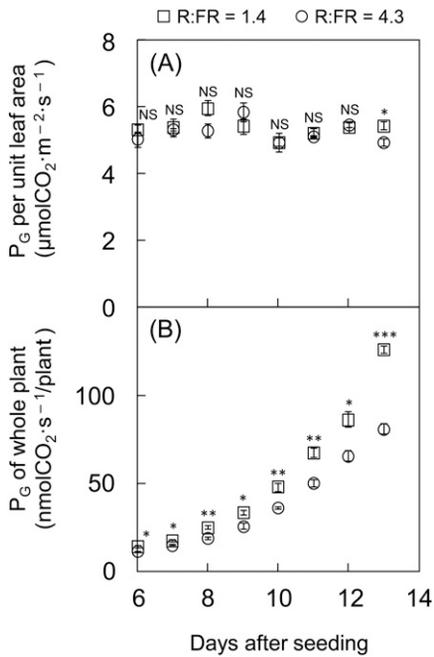


Fig. 3. Time courses of gross photosynthetic rates (P_G) per unit leaf area and of whole-plant in cucumber seedlings grown under light with a high red to far-red ratio (R:FR = 4.3) or natural R:FR (1.4). Data are the average \pm SE of three replicates. NS, no significant difference between the treatment; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$ (t test).

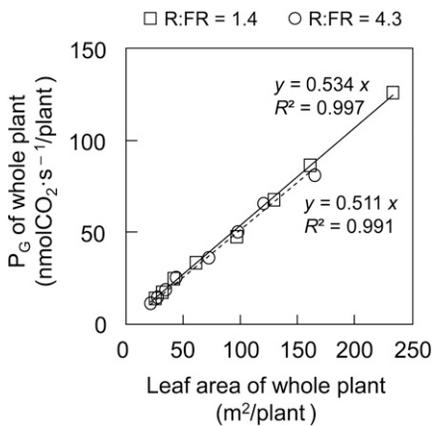


Fig. 4. Relationships between gross photosynthetic rates (P_G) of whole-plant and leaf area in cucumber seedlings grown under illumination with a high red to far-red ratio (R:FR = 4.3) or natural R:FR (1.4) during the experimental period.

interception that resulted from inhibition of leaf enlargement per unit leaf dry matter. This reduction may have been caused by reduction of cell-wall extensibility, which would also accelerate shoot elongation (Franklin, 2008; Sasidharan et al., 2008). Therefore, the shorter shoots and the faster dry matter accumulation,

which are both required in transplant and pot-plant production, cannot be simultaneously obtained by modifying the R:FR of the light. In controlling R:FR for the plant production, the growers may need to consider which of the advantages is more important.

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