Photosynthesis and Morphology of Leaf Lettuce (Lactuca sativa L. cv. Greenwave) Grown under Alternating Irradiation of Red and Blue Light

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The mechanism for accelerating leaf lettuce growth by alternating irradiation of red (R) and blue (B) lights was investigated in this study. Leaf lettuce was cultivated under nine light conditions with different time ratios of R/B alternate irradiation; R0B24, R3B21, R6B18, R9B15, R12B12, R15B9, R18B6, R21B3 and R24B0. As a result, R21B3 treatment (21 hours of R irradiation and 3 hours of B irradiation, in an alternating pattern without a dark period) was determined to be the optimum condition for leaf lettuce growth, since shoot fresh weight under this treatment was significantly the highest. Moreover, photosynthetic ability and morphology were studied under alternating irradiation (R21B3 and R12B12) and simultaneous irradiation (RB24; simultaneous irradiation of R and B lights without a dark period). Photosynthetic ability of lettuce grown under R21B3 and R12B12 was significantly higher than that under RB24. A morphological index, PA/LA (Projected Area divided by Leaf Area), was greater in R21B3 and R12B12 than in RB24. This result suggested that alternating irradiation causes plants to have an effective posture for receiving light. Therefore, it seems reasonable to conclude that growth acceleration of plants under alternating radiation was caused by high photosynthetic ability and morphological superiority.

Keywords: light emitting diode, light quality, plant factory, simultaneous irradiation

INTRODUCTION

Plant factories are production facilities where vegetables are cultivated in a controlled environment and the sowing, transplant, harvest and shipping occurs throughout the year. Therefore, growers can produce vegetables without considering the weather, this makes stable production possible. On the other hand, some of the growers find it difficult to make a profit because of the high initial investment and the high cost of the electricity needed to control the production environment. In order to solve this problem, numerous studies have been conducted to determine ways to control light to achieve optimum plant growth. In particular, the development of LEDs that have a narrow band spectrum has enabled a more precise observation of plant responses to each light spectra more clearly. Stutte et al. (2009) reported that the synthesis of anthocyanin in red leaf lettuce was promoted by increasing the ratio of blue light the leaves were exposed to. In addition, it was found that leaf lettuce cultivated under light conditions with a high ratio of blue light had a high antioxidant capacity (Son et al., 2013). As the previous studies have confirmed, high quality vegetables can be produced by controlling light quality. Moreover, using this technique to encourage growth acceleration, more increase of yield was promising. Because plant factories are not influenced by outside weather, and can cultivate vegetables year-round, this technique may prove usefulness for production.

To obtain growth acceleration in plants, a particular method is used; this involves alternating use of red (R) and blue (B) lights (alternating irradiation). The fresh weight of leaf lettuce grown under alternating irradiation of R and B was greater than that of lettuce grown under simultaneous irradiation with R and B, and white fluorescent lamps (Shimokawa et al., 2014; Ohtake et al., 2015). Furthermore, seedlings of leaf lettuce were grown under four irradiation patterns, consisting of a 12 hours photoperiod (RB 12 h/dark period 12 hours), a 4 hours shifted irradiation of B light (R 4 h/ RB 8 h/B 4 h/dark period 8 hours), a 8 hours shifted irradiation of B light (R 8 h/RB 4 h/B 8 h/dark period 4 hours), or an alternating irradiation pattern (R 12 h/B 12 h) (Kuno et al., 2017). The results indicated that the fresh weight of leaf lettuce increased with an increasing shift in irradiation time. As described above, previous studies have demonstrated that alternating irradiation was an effective irradiation pattern for the growth of plants, but the details of the mechanism of growth promotion are still unknown (Ibaraki, 2018).

In the present study, the objective was to reveal how alternating irradiation accelerates the growth of leaf lettuce. First, we studied the optimum time ratio of R/B irradiation for leaf lettuce. Leaf lettuce grown under alternating irradiation can be considered to have some special characteristic. In particular, leaf lettuce under the optimum alternating treatment should have strong characteristics. Next, the mechanism of how alternating irradiation accelerates the plant growth was discussed using the optimum
R/B treatment from both a photosynthetic ability and morphological point of view.

MATERIALS AND METHODS

Plant material and cultivation method

Experiments were conducted in an environmental controlled room (3 m×4 m×4 m). Environmental conditions at each growth stage are shown in Table 1. Seeds of leaf lettuce (*Lactuca sativa* L. cv. Greenwave, ALE539; TAKII & Co., Ltd., Kyoto, Japan) were sown on urethane sponge in the plastic tray (24 cm width×30 cm depth×4 cm height) and irrigated with tap water in the refrigerator (NR-A80W, Panasonic, Tokyo, Japan) for 24 hours. The next day, they were taken from the refrigerator and put into the dark area for 24 hours. Next, there was a one week germination period under white LEDs (EM1134660, ESPEC MIC Co., Aichi, Japan) at the same place as the next nursing period. After that, seedlings were transplanted to a nursing panel (90 holes, 600 mm×600 mm) and grown under white LEDs for a one week nursing period. Finally, they were transplanted to a cultivation panel (15 holes, 600 mm×600 mm) and grown under light conditions of R and B LEDs (UL0009#01-0R, wavelength R=660 nm, B=450 nm, SHOWA DENKO K.K., Tokyo, Japan) described in the next section as the cultivation period. The temperature was set to 23°C by the air conditioner and relative humidity was set to 65% using a humidifier and dehumidifier (MCZ70T-W, DAIKIN INDUSTRIES, LTD., Osaka, Japan). Nutrient water was used in germination, nursing and cultivation (OAT house; A prescription or SA prescription used, OAT Agrio, Tokyo, Japan).

**Light conditions and measurement items**

**Experiment 1 Determining the optimum time ratio of red/blue irradiation**

Light conditions in experiment 1 are shown in Fig. 1. They include treatments with short period irradiation of B light, as well as ones with short period irradiation of R light, as well as ones with short period irradiation of B light.

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### Table 1 Environmental conditions in each growth stage.

| Growth stage | Date (d) | Hydroponic system | Air temperature (°C) | Humidity (%) | Light source | PPFD* (μmol m⁻² s⁻¹) | Photoperiod (h) | Light/dark | Solution condition pH / EC (mS m⁻¹) | CO₂ concentration (μmol/mol) |
|--------------|----------|--------------------|----------------------|--------------|--------------|----------------------|----------------|------------|-----------------------------------|-----------------------------|
| Sowing       | R⁺       | Passivew           | 7                    | Not controlled | Nothing      | 0                   | 0/24          | 7.1/0.2    | Not controlled                    |                             |
|              | D⁻       | Passivew           | 23                   | 65           | Nothing      | 0                   | 0/24          | 7.1/0.2    | Not controlled                    |                             |
| Germination  | 2-9      | Passive            | 23                   | 65           | White LED    | 185                 | 16/8          | 6.3/1.5    | Not controlled                    |                             |
| Nursing      | 9-16     | DFT                | 23                   | 65           | White LED    | 185                 | 16/8          | 6.7/2.0    | Not controlled                    |                             |
| Except for   | RB12⁺    | DFT                | 23                   | 65           | Red and blue LED | 100             | 24/0          | 6.7/2.0    | Not controlled                    |                             |
| Cultivation  | 16-30    | DFT                | 23                   | 65           | Red and blue LED | 200             | 12/12         | 6.7/2.0    | Not controlled                    |                             |

* R: in the Refrigerator
+ D: in the Dark place
⁻ RB12: Simultaneous irradiation of red and blue lights (L/D=12 h/12 h). For all the other light conditions, see Fig. 1.
w There was no flow in water.
⁺ PPFD: Photosynthetic Photon Flux Density
w Tap water without adding anything
⁻ EC was set as the target value, and pH was taken as the measured value at that time.

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**Fig. 1** Illustration of light conditions in experiment 1. The character strings shown on the left were names of treatments. R0B24 and R24B0 were continuous monochromatic irradiation treatments. R3B21, R6B18, R9B15, R12B12, R15B9, R18B6 and R21B3 were alternating irradiation treatments by using red (R) and blue (B) LEDs. RB12, which had a 12 hours dark period and RB24 were set to be simultaneous irradiation treatments of R and B LEDs as control treatments.
light. R0B24 and R24B0 were monochromatic irradiation, R3B21, R6B18, R9B15, R12B12, R15B9, R18B6 and R21B3 were alternating irradiation (R/B), and RB12 (12 hours light/12 hours dark) and RB24 (continuous) were simultaneous irradiation (control treatments). All treatments had the same DLI (Daily Light Integral). Two weeks after cultivation began under these light conditions (Fig. 1), shoot fresh weight, shoot dry weight, dry matter ratio, number of leaves, leaf area (LA) and LMA (Leaf Mass per Area) were measured (n=10). Shoot dry weight was measured after the shoot was dried in a drying machine (DO-450FA, AS ONE Co., Osaka, Japan) at 103°C for 24 hours, then dry matter ratio [%] was calculated as shoot dry weight divided by shoot fresh weight multiplied by 100. Each shoot of lettuce was broken down into leaves and some force was added with my hands so as leaves would be as flat as possible. A 30 cm ruler was placed next to leaves, and images of leaves and the ruler was captured in one photo using the iphone8 (Apple Inc., California, USA) camera. After that, the resolution for each picture was calculated from the ruler, and the leaf area was determined using that value by ImageJ software (1.48v; https://imagej.nih.gov/ij/). PC that executed ImageJ has Intel(R) Core(TM) i3-3220 CPU @ 3.30GHz (OS; 64bit, Memory size; 4.00 GB, Hard disk size; 4.64 GB). However, the captured picture possibly underestimated leaf area because leaves have curves and waves on a flat plane. LMA was calculated as shoot dry weight divided by leaf area.

**Experiment 2 Photosynthetic rate per area**

In order to compare photosynthetic ability among leaf lettuce grown under different light conditions, seedlings were cultivated under RB24, R21B3 and R12B12 light treatments. In this study, we defined photosynthetic rate per area at the same level of shoot fresh weight as PAW (Photosynthetic rate per Area at the same Weight) to compare photosynthetic ability at the same growth stage. After the cultivation period, PAW was measured under the same light conditions (RB; simultaneous irradiation of R and B lights, R 50 µmol m⁻² s⁻¹, B 50 µmol m⁻² s⁻¹) using LI-6400xt (LI-COR Inc., Lincoln, USA). The biggest leaf of a lettuce was selected and the measurement point was just one point; the middle part of the tip. The measurement was carried out using a small chamber (2×2 cm), and temperature was set to 20°C, relative humidity was not controlled and CO₂ concentration was set to 400 µmol/mol. Photosynthetic rate was measured after the photosynthetic rate was sufficiently stabilized. Since the possibility of taking a large value instantaneously was considered, the mean value obtained three times at intervals of several seconds was taken as the measured value.

**Experiment 3 Measurement of morphological index over time**

Twenty replicates of leaf lettuce were transplanted after a nursing period and grown under RB24, R21B3 and R12B12 treatments for two weeks. Every two or three days, four replicates were harvested and shoot fresh weight and PA/LA (Projected Area divided by Leaf Area) were measured. The PA (Projected Area) is the area when observing lettuce from above as shown in Fig. 2 and LA is same as explained in experiment 1, while PA/LA indicates leaf angle and overlapping. If the value is large, that means leaf angle is small or overlapping is small (Furuyama et al., 2017). Overlapping, or efficiency of light interception, was evaluated by comparing PA/LA at the same shoot fresh weight for each plant.

**Statistical analysis**

Data were analyzed with one way ANOVA through Microsoft Excel 2016, and then Ryan’s multiple comparison test was performed using ANOVA4 software (https://www.hju.ac.jp/~kiriki/anova4/index.js.html) at P<0.05.

**RESULTS**

**Experiment 1 Determining the optimum time ratio of R/B irradiation**

Results of experiment 1 are shown in Table 2. Shoot fresh weight under R21B3 conditions was significantly higher than that in the other experimental treatments and was twice as high as the control treatments (RB12 and RB24). Furthermore, there was a tendency of increased shoot fresh weight with increased length of exposure to R light irradiation. This tendency was observed in shoot dry weight, the number of leaves and total leaf area as well. On the other hand, the opposite trend was observed with respect to dry matter ratio and the value was decreasing with the increased length of exposure to R light irradiation. Moreover, LMA in the R6B18 treatment was the highest, and a tendency to decrease with the increase or decrease

![Fig. 2](image-url) Photos taken from above the leaf lettuce plants at the time of the last harvest of those grown under RB24, R21B3 and R12B12 conditions. RB24 was a simultaneous irradiation treatment without a dark period. R21B3 and R12B12 treatments were alternating irradiation treatments with red (R) and blue (B) light periods.
exposure length to R light irradiation was observed. In addition, LMA in the R24B0 treatment was less than 2.0 mg cm$^{-2}$ and smallest of all the treatments.

**Experiment 2 Photosynthetic rate per unit area at the same weight (PAW)**

Results of experiment 2 are shown in Fig. 3. While shoot fresh weight was almost the same among the leaf lettuce in all three treatments, photosynthetic ability in the RB24 treatment was significantly lower. The irradiation method of the R21B3 treatment was greatly different from that of R12B12, but no difference in PAW was observed between these two treatment groups.

**Experiment 3 Measurement of morphological index over time**

Results of experiment 3 are shown in Fig. 4. The difference of shoot fresh weight between leaf lettuce grown under alternating irradiation and those grown under simultaneous irradiation got bigger and bigger as the days passed. Finally, shoot fresh weight was about two times higher at 30 DAS for those under alternating irradiation treatments. The polygonal line of projected area was very similar to that of shoot fresh weight in each light condition. Overall, PA/LA decreased with the increase of DAS. This may be because leaf lettuce has an increased number of leaves as it grew and matures, and an increased number of leaves increases the amount of overlapping due to the typical growth pattern of the lettuce.

**DISCUSSION**

**Effect of alternating irradiation time of R and B lights on plant growth**

R21B3 was considered to be the optimum light treatment for 'Greenwave' in all the light conditions, due to a significant difference in shoot fresh weight (Fig. 1, Table 2). Generally, shoot fresh weight is the main quantitative measurement of lettuce in plant factories, so from a production viewpoint, it is one of the most important indicators of the alternate irradiation success. It was determined that one of the reasons why the treatment with a much longer time of R radiation, such as R21B3, was optimum was that RQE (Relative Quantum Yield) of R light is larger than that of B light (McCree, 1972). Therefore, shoot fresh weight and dry weight increased with an increasing time of R irradiation overall, in the results of experiment 1 (Table 2). However, compared to R21B3, shoot fresh weight of R24B0 was significantly smaller in spite of longer time of

**Table 2** Plant growth parameters in experiment 1.

| Treatments | Shoot Fresh Weight (g) | Shoot Dry Weight (g) | Dry Matter Ratio (%) | Number of Leaves $^x$ | Leaf Area (cm$^2$) | LMA (mg cm$^{-2}$) |
|------------|------------------------|---------------------|---------------------|-----------------------|-------------------|--------------------|
| R0B24      | 25.84 f                | 1.55 e              | 6.0 a               | 9.8 d                 | 666.5 e           | 2.34 ab            |
| R3B21      | 31.76 ef               | 1.79 e              | 5.6 ab              | 10.0 cd               | 749.7 e           | 2.39 ab            |
| R6B18      | 37.29 de               | 2.06 de             | 5.5 b               | 10.5 cd               | 827.5 de          | 2.48 a             |
| R9B15      | 48.56 c                | 2.40 cd             | 4.9 c               | 11.2 bc               | 990.4 cd          | 2.41 ab            |
| R12B12     | 67.22 b                | 3.05 ab             | 4.5 cde             | 12.0 ab               | 1,384.8 b         | 2.21 ab            |
| R15B9      | 66.55 b                | 2.91 abc            | 4.4 de              | 12.0 ab               | 1,395.7 b         | 2.09 bc            |
| R18B6      | 71.35 b                | 3.19 a              | 4.5 de              | 12.6 a                | 1,471.4 ab        | 2.18 ab            |
| R21B3      | 82.00 a                | 3.48 a              | 4.2 e               | 12.9 a                | 1,661.8 a         | 2.09 bc            |
| R24B0      | 70.16 b                | 2.93 abc            | 4.2 e               | 12.8 a                | 1,573.6 ab        | 1.87 c             |
| RB12       | 37.44 cde              | 1.77 e              | 4.7 cd              | 11.0 bc               | 753.6 e           | 2.36 ab            |
| RB24       | 45.60 cd               | 2.61 bc             | 5.7 ab              | 11.1 bc               | 1,049.1 c         | 2.50 a             |

ANOVA$^y$ **** **** **** ****

$^x$ R0B24 and R24B0 were monochromatic irradiation treatments. R3B21, R6B18, R9B15, R12B12, R15B9, R18B6 and R21B3 were alternating irradiation treatments. RB12 and RB24 were simultaneous irradiation treatments.

$^y$ Leaves counted were at least 3 cm in length or longer.

$^z$ **** Significant at $P<0.001$. The same letters indicate no significant differences at $P<0.05$ (Ryan’s multiple comparison test, $n=10$).
This was thought to be due to the lack of B light within that treatment. In general, it is known that blue light is involved in plant morphology, and that it plays a part in the function of some molecules within plants, such as phototropin and cryptochrome. Dougher and Bugbee (2001) reported that stem elongation of lettuce was remarkably suppressed by irradiating B light. Moreover, Oshima et al. (2015) suggested that it was possible B light didn’t so much extend leaf area as thicken leaves because leaf area in red leaf lettuce under monochromatic B light was greatly decreased and LMA under B light was increased. In addition, one study reported that plants under monochromatic R light without any B light such as R24B0 treatment couldn’t grow normally (Yorio, 2001). Thus, R21B3 treatment, which doesn’t have a little time of B irradiation, was considered to be optimum in this study.

Mechanism of growth acceleration by alternating irradiation

When we consider just RQE of photosynthesis, monochromatic R radiation will promote plant growth. However, it is understandable that growth analysis is not this simple, as mentioned above. Moreover, the results of a study of cucumber cultivation under R light, B light, CWF (Cool White Fluorescent), and simultaneous irradiation with R and B, indicated that shoot fresh weight and dry weight were minimum under R light (Hernández, 2013). Furthermore, Hirai et al. (2006) reported that dry mass production of eggplant, leaf lettuce and sunflower were largest under B light compared to R light, G (green) light, and B-G light with the same photosynthetic photon flux density (PPFD). As the previous studies revealed, R light was most effective for photosynthesis, but this did not lead to an increase in plant biomass directly. It has been suggested that not only photosynthetic ability but also plant shape must be taken account when evaluating plant growth (Ohashi et al., 2006). Indeed, in ‘St. John’s Wort’ (Hypericum perforatum L.) cultivation, conducted by Nishimura et al. (2006), the reason why the dry weight of plant grown under an R fluorescent lamp was larger than that of those grown under an B fluorescent lamp was investigated for both photosynthetic ability and morphology. The results of that study indicated that morphology greatly contributed to the increase of biomass.

In the present study, we investigated how alternating irradiation accelerates the growth of leaf lettuce by evaluating both PAW and morphology. First, PAW was measured in experiment 2 and the result showed that the value was greater in alternation. In a report of Kuno et al. (2017), SPAD value in leaf lettuce was not significantly different between plants grown under RB24 and R12B12 conditions. Consequently, the chlorophyll concentration was thought not to have an effect on the difference of PAW between plants grown under alternating irradiation and simultaneous irradiation. In addition, LMA, which was proportional to leaf thickness was greater than that under alternating irradiation, as shown in Table 2. The thicker leaves were, the longer distance photons traveled in a leaf. This means chlorophyll captures these photons with higher probability. Therefore, photosynthetic rate per unit area of leaf lettuce under simultaneous irradiation could be greater than that under alternating irradiation, but in fact, somehow the opposite result was obtained. This fact suggested that the outer characteristics (SPAD, LMA, and etc.) didn’t cause the difference of PAW. One possibility is that the activity of photosynthesis has been enhanced in their body for some reason, and for now how PAW in plants grown under alternating irradiation got higher remains an unknown. However, Ohtake et al. (2018) suggested photosynthetic ability under alternating irradiation was higher because of high NAR (Net Assimilation Rate) and LMA in the early growth stage. Next, the relationship between shoot fresh weight and PA/LA was shown in Fig. 5 to compare morphology of plants exposed to different irradiation treatments that were the same shoot weight. Plotting points with each light quality were fitted by exponential approximation. An exponential curve of RB24 is located in the leftmost portion of Fig. 5, followed by curves illustrating values for plants irradiated under R21B3 and R12B12 treatments.
treatments. This indicated that the further the curves were to the right, the larger PA/LA was at the same shoot fresh weight and the greater leaf overlapping was occurring. Hence, leaf lettuce grown in alternating irradiation conditions had a posture more effective at intercepting light with less leaf overlapping. Hirai et al. (2006) reported that monochromatic B light caused plants to have a posture more effective at intercepting light. In this study, leaf area of leaf lettuce, eggplant and sunflower grown under monochromatic B light were the same or less compared to those grown under monochromatic R light, G light and B-G light, but dry weight of those grown under B light was greater. However, there was a study reporting that the addition of B light to the other lights led to dwarving in leaf lettuce (Saito et al., 2012). In this study, as shown in Fig. 2, leaf lettuce was dwarfed under RB24, which was to irradiate B light added to R light. Therefore, we can consider that since alternating irradiation has time of monochromatic B irradiation and simultaneous irradiation was to irradiate B light added to R light, the results of Fig. 5 were obtained.

From experiment 2 and 3, both PAW and morphology very likely attributed to growth acceleration by alternating irradiation.

CONCLUSION

We obtained two new findings. The first was the optimum time ratio of R/B irradiation is R21B3 in the treatments which I investigated. Longer time of R light irradiation was effective, but a small amount of B light irradiation was absolutely necessary. The second finding was the growth acceleration by alternating irradiation with R and B lights was probably caused by high photosynthetic ability and morphological superiority.

In the future, based on the above results, we believe that not only obtaining more yield but also increasing excellent ingredients in crops from the viewpoint of light quality strongly contributes to the profitability problem of the plant factory.

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