Optimization of Light-Dark Cycles of *Lactuca sativa* L. in Plant Factory

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Several studies have reported that the circadian rhythm of leaf lettuce (*Lactuca sativa*) is approximately 24 h and that the fresh weight of Greenwave, a cultivar of leaf lettuce, is larger under the light-dark period of 22 h or 24 h. In this study, we investigated the optimal light-dark cycles for Greenwave and the deciding factors of optimal light-dark cycles by cultivation experiments under several light-dark conditions in plant factory. By optimization of light-dark cycles, we obtained the optimal light-dark conditions for the light/dark ratio (L/D) of L/D = 2 and the light-dark period of 15-22 h (T15-T22). In addition, the higher growth rate on T21 and T22 conditions was suggested to be related to the decrease in leaf starch concentration at night. The results in this study suggests that the cultivation of leaf lettuce under light-dark conditions reduce running costs in plant factory with artificial lighting (PFAL).

Keywords: circadian rhythm, leaf lettuce, light-dark cycle, light emitting diode, photoperiod, plant factory

INTRODUCTION

Plant factory produces high quality agricultural products stably year-round without pesticides. However, the reduction of high running and initial costs is one of the most crucial issues. In order to reduce running costs, several studies on the effects of light quality, photoperiod, or the patterns of exposure on mainly leafy vegetables have been studied with several types of light emitting diodes (LEDs; Hirai et al., 2006; Saito et al., 2013). However, little is known regarding the optimal light-dark cycles for such vegetables.

It has been reported that different plants have the endogenous circadian clock, which is an oscillation generator with a period of approximately 24 h (Michael and McClung, 2003; Harmer, 2009). In addition, previous studies revealed the phenomenon of circadian resonance; the matching of the circadian rhythm to diurnal environmental cycles affects the plant growth and yield (Highkin and Hanson, 1954; Dodd et al., 2005). Previous studies show that leaf lettuce (*Lactuca sativa* cv. Greenwave) has a circadian rhythm of approximately 22–24 h on the condition of 18–26°C under red LEDs (Higashi et al., 2014). Moreover, the value of fresh shoot weight of leaf lettuce (*Lactuca sativa* L. cv. Greenwave) under the light-dark period of 22 h or 24 h were significantly higher than those under the light-dark period of 18 h or 28 h with a fluorescence light for the former two weeks and with a red LED for the latter one week (Higashi et al., 2015).

In general, leaf lettuces in plant factory are cultivated for about four weeks after transplanting (Kozai, 2014), and the light-dark periods are, for example, 12–12 h (light-dark) at the early growth stage or 16–8 h (light-dark) at the late growth stage (private communication). Here, in consideration of such a general cultivation period and light-dark period of leaf lettuce in plant factory, we investigated the optimal light-dark cycles for leaf lettuce (*Lactuca sativa* L. cv. Greenwave) by satisfying the accumulated exposed time condition (16 h / d × 28 d = 448 h), and analyze the relationships between light-dark cycles and several physiological responses. Here, we examined the leaf photosynthetic capacity and the diurnal change of leaf starch concentration to find out mechanisms by which fresh shoot weight of leaf lettuces get higher on optimal light-dark cycles.

MATERIALS AND METHODS

Plant materials and conditions

Leaf lettuce (*Lactuca sativa* L. cv. Greenwave) seeds were sown on a water-soaked urethane sponge and grown under white LED (NEO2-000089(01), Shibasaki Inc., Chichibu, Saitama, Japan) on the condition of 14–11 h (light-dark) for one week. Here, we defined “light-dark period” as a sum of light period and dark period (shown as Fig. 1). After one week, the germinated seedlings were transplanted to a hydroponic system in plant factory (TAF-24A, Especmic Co., Osaka, Osaka, Japan). The light conditions were set at several PPFD conditions and light (L)-dark (D) cycles (shown as Table 1) using white panel LED (Especmic Co.) for six experiments (from Experiment A to Experiment F). For Experiment C, D, E, and F, all the leaf lettuces have been cultivated till the accumulated exposed time got to 440±20 h, thus the number of days till harvest differed from experimental plots or cultivation experi-

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ments, from 20.2 d under L/D=11 condition to 35.0 d under L/D=1 condition. In consideration of a general cultivation period (about 28 d after transplanting) and light-dark period (about 16 h / d) of leaf lettuce in plant factory, the accumulated exposed time condition (16 h / d × 28 d = 448 h) was satisfied among Experiment C, D, E, and F.

For Experiment A and B, whose aims were mainly the dark period (about 16 h / d) of leaf lettuce in plant factory, and the observed leaf temperature was 21.5°C, which was the set daytime air temperature of the plant factory, and the measured leaf temperature was 21.5 ±0.8°C for all the measurements. The relative humidity in the leaf chamber of LI-6400XT was kept at 20°C in all four experimental plots (Continuous light, T20, and T24 conditions).

The conceptual diagram of light-dark period (h).

Fig. 1 The conceptual diagram of light-dark period (h).

For all the experiments of cultivation, statistical significance for differences among three (Experiment A) or four (Experiment B, C, D, E, and F) light-dark cycles on each experiment was determined by a one-way ANOVA after conducting Bartlett’s test. All statistical analyses were done with JMP v.13.0.0 software (SAS Institute, Cary, North Carolina, USA). The optimal light-dark condition was estimated by a bubble chart and a contour plot with JMP v.13.0.0 software (SAS Institute), by using the data of fresh shoot weight and days after transplanting of Experiment C, D, E, and F. On optimization of light-dark cycles, the overlapping plot of T24 (L=16) indicates the average value.

Leaf photosynthetic rate

During the cultivation of Experiment A, net leaf photosynthetic rate (Pn) in the fully expanded leaves was measured for 75 h with a portable gas-exchange system (LI-6400XT; LI-COR). The accumulated exposed time of measuring samples were 394 ±10 h, and the measuring samples (one sample per plot) were all these lettuces of three plots (Continuous light, T20, and T24 conditions).

The days after transplanting till measurements of Pn were 16.8 d, 19.9 d, and 23.7 d, and the fresh weight including shoot and root just before those measurements were 34.6 g, 41.3 g, and 56.9 g on continuous light, T20, and T24 condition, respectively. The reference and sample CO2 in the leaf chamber was 900 ±3 and 895 ±7 μmol mol⁻¹ respectively for all measurements. The photosynthetic photon flux density (PPFD) was 200 ±20 μmol m⁻² s⁻¹ at the daytime. The block temperature of LI-6400XT was kept at 22°C, which was the set daytime air temperature of the plant factory, and the observed leaf temperature was 21.5 ±0.8°C for all the measurements. The relative humidity in the leaf chamber of LI-6400XT was ranged from 54.6 to 82.1%. After those measurements of Pn, the instantaneous values of Pn for 75 h were plotted on the same graph.

Measurement of Pn-C curve

On Experiment B, Pn was also measured at different values of intercellular concentration of CO2 (Ci) by changing the ambient CO2 concentration for six levels (50, 100, 300, 500, 700, and 900 μmol mol⁻¹) at two different growth stages (18 and 28 d after transplanting). The Pn-C curves were all measured during light period and almost at the same timing among four experimental plots (T24, T22, T12, and T6), from three to five samples per plot. The block temperature of LI-6400XT was kept at 20°C, which was the average air temperature of four experimental plots (T24, T22, T12, and T6) on Experiment B (Data not shown), and the observed leaf temperature was 20.5 ±0.3°C for all the measurements. Although the block temperature was kept at 22°C during measurement of leaf photosynthetic rate on Experiment A, the average air temperature of three experimental plots (Continuous light, T20, and T24 conditions) was about 20°C (Data not shown). On Experiment B, therefore, the block temperature was kept at 20°C in order to hold the measuring condition close to the environmental condition. The relative humidity in the leaf chamber was ranged from 71.0 to 86.4%. Potential rate of electron transport (Jmax) and maximum rate of Rubisco activity (Vcmax) were calculated with the measured Pn, Ci, and leaf temperature values by Barnacchi model (Barnacchi et al., 2001; McMurtrie et al., 1993), and a two-way analysis of variance (ANOVA) was conducted by JMP v.13.0.0 software (SAS Institute) to evaluate the effects of light-dark period (L), days after transplanting (D) and their interaction

<table>
<thead>
<tr>
<th>Table 1</th>
<th>Light-dark and PPFD conditions of each cultivation experiment.</th>
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<tbody>
<tr>
<td>PPFD (μmol m⁻² s⁻¹)</td>
<td>Light-dark period (T; h)</td>
</tr>
<tr>
<td>Experiment A</td>
<td>200 ± 20</td>
</tr>
<tr>
<td>Experiment B</td>
<td>200 ± 20</td>
</tr>
<tr>
<td>Experiment C</td>
<td>245 ± 20</td>
</tr>
<tr>
<td>Experiment D</td>
<td>245 ± 20</td>
</tr>
<tr>
<td>Experiment E</td>
<td>245 ± 20</td>
</tr>
<tr>
<td>Experiment F</td>
<td>245 ± 20</td>
</tr>
</tbody>
</table>

Values in each cell of light-dark period, light/dark ratio, light and dark period are corresponding to each value in order.
(L × D) on \( J_{\text{sat}} \) and \( V_{\text{sat}} \).

**Measurement of starch content**

On Experiment E, lettuce leaves of four experimental plots (T24, T23, T22, and T21 of L/D = 1 condition) were collected at the beginning of light period, the half past light period, the beginning of dark period and the half past dark period, and then oven-dried at 80°C for a minimum of 48 h and weighed to determine dry weight. By alcohol extraction, sugar was extracted from the dry matter. Starch content was quantified by using a phenol-sulfuric acid method (Hodge and Hofreiter, 1962).

**RESULTS AND DISCUSSION**

**Fundamental characteristics**

Table 2 shows the effect of light-dark cycle on several main characteristics of leaf lettuce (Lactuca sativa L. cv. Greenwave) on from Experiment A to Experiment F, and Experiment C, D, E, and F were all conducted by 440 ± 20 h of accumulated exposed time after transplanting under the same PPFD condition of 245 ± 20 μmol m⁻² s⁻¹. On the fixed condition of 16 h of light period (L = 16; Experiment A), the values of fresh shoot weight, dry shoot weight, maximum leaf length and stem length were highest on T24 and lowest on the continuous light condition (Table 2). In general, starch produced by photosynthesis is degraded into sucrose at nighttime, which is translocated from leaves to shoot apex or budlets (Yamaya, 2001). Under the continuous light, however, the available sucrose remains in leaves because of the decreased source capacity (Velez-Ramirez et al., 2011). Thus, the existence of night period seems to be an advantage for cultivation of leaf lettuce. On Experiment B (on the fixed condition of L/D = 2), the values of fresh shoot weight, dry shoot weight, and maximum leaf length were highest on the condition of T22 (Table 2). On the fixed condition of 24 h of light-dark period (T24; Experiment C), the values of fresh shoot weight, number of leaves and maximum leaf length were higher on L/D = 3 and L/D = 2 than on L/D = 1 (Table 2). The days until the accumulated exposed time get to 448 h on L/D = 11, L/D = 3 and L/D = 2 were 20.2, 25.5 and 28.0 d, respectively, and the incident of tipburn on L/D = 11 and L/D = 3 was triple of L/D = 2 (Data not shown). It is well-known that tipburn occurs mainly in inner developing leaves which have lower calcium concentrations (Goto and Takakura, 2003). Although the growth rate of butter lettuce (Lactuca sativa L.) grown under continuous light by light supplementation at night was higher than that without any light supplement, the incident of tipburn under continuous light was also much higher than that under contrast condition (Oda et al., 1989). Further, the turgor pressure of leaf lettuce under T24 (L/D = 7/5) condition began to increase logarithmically at dawn and reached to around 1 MPa in 9 h, then drastically declined into about 0.2 MPa at the beginning of nighttime. However, that of leaf lettuce under T3 (L/D = 7/5) condition was kept low (around 0.4 MPa), and started decreasing to around 0.2 MPa just after sunset (Goto and Takakura, 2003). Thus, on Experiment C, 2 h or 4 h of dark condition under T24 is suggested to be too short to translocate sucrose from leaves to sink adequately.

By comparing these four experiments (Experiment C, D, E, and F), the value of fresh shoot weight was highest on T21 under L/D = 1 condition (74.9 g), and the second highest value was 73.7 g on T22 under L/D = 1 condition (Table 2). The lowest value of fresh shoot weight was 33.9 g on the L/D = 11 condition (Table 2). On these conditions of T22 and T21 under L/D = 1, samples were cultivated for 35 d after transplanting, and on L/D = 11 condition, samples were cultivated for 18.7 d after transplanting (Data not shown). The value of dry shoot weight was highest on T21 conditions of Experiment E (4.70 g), and lowest on T12 under L/D = 2 condition (2.15 g; Table 2). The largest and second largest values of number of leaves were 17.3 and 17.0 on T21 and T22 under L/D = 1 condition, respectively (Table 2). The top-three highest values of maximum leaf length were 24.8, 23.7 and 23.6 cm on T21, T23 and T22 under L/D = 1 conditions, respectively (Table 2). The lowest value of maximum leaf length was 13.9 cm on L/D = 11 condition (Table 2). The stem length was longest on T21 (L/D = 1) condition (6.4 cm), and shortest on L/D = 5 (T24) condition (13.5 cm; Table 2). On cultivation of leaf lettuce (Lactuca sativa L. cv. Greenwave) under L/D = 1 condition using a fluorescent light for two weeks and a red LED for next one week, the values of fresh shoot weight of T22 and T24 photoperiod were higher than those of T18 or T28 (Higashi et al., 2015). In addition, the values of fresh shoot weight, dry shoot weight and number of leaves of leaf lettuce (Lactuca sativa L. cv. Okayama-saradana) were higher on T24 than that on T12 or T8 conditions under L/D = 0.5 using a high-pressure sodium lamp, and photosynthetic performance, circadian resonance, or the absorbance of nutrition were seemed to be related to the growth rate (Ishi et al., 1995b). The same cultivar of leaf lettuce “Okayamasaradana” grown under L = 12 (T24) with a high-pressure sodium lamp had higher values of fresh shoot weight, dry shoot weight and number of leaves than under L = 10 (T24) and L = 8 (T24) conditions (Ishii et al., 1995a). Summarizing the above, the growth rate of leaf lettuce is suggested to be higher on the light-dark period of T24-T15 under L/D = 1 or 2 conditions, and on the L/D ratio of L/D = 2-3 under T24 condition.

**Optimization of light-dark cycles**

By comparing the light-dark cycles of Experiment C, D, E, and F, all the plots above 60 g of mean fresh shoot weight fell within a range of T15-T22 and L/D = 1-2 (Fig. 2a; Table 2). By dividing the logarithmic value of average fresh shoot weight by days of cultivation, the average growth rate (r; d⁻¹) was calculated (Takatsuji, 2007; Fig. 2b). All the plots of r more than 0.15 fell within a range of L/D = 3-11 (Fig. 2b). The highest value was r = 0.174 on L/D = 11 (T24), and the lowest value was r = 0.107 on L/D = 1 (T23) condition (Fig. 2b). Similarly, Fig. 3 shows the contour plots of average fresh shoot weight (g; Fig. 3a) and average growth rate (d⁻¹; Fig. 3b). The domain of over 60 g of mean fresh shoot weight was shown within a range of L/D = 1-2 and T15-T22 (Fig. 3a), and the domain of r more than 0.14 was shown within a range of L/D = 2-11 and T15-T24 (Fig. 3b). By integrating these results, the
Effect of different light-dark cycles on leaf lettuce (*Lactuca sativa* L. cv. Greenwave) under PPF 245 µmol m⁻² s⁻¹. Using 18 klx of high-pressured sodium lamps and another cultivar of leaf lettuce (*Lactuca sativa* L.), however, the optimal light-dark conditions on the seedling stage and the vegetative growth stage were revealed to be L = 10 (T24) and continuous light conditions, respectively (Takatsuji et al., 1983). Thus, the more accurate optimization of light-dark cycles in response to the growth stages will be necessary.

### Photosynthetic capacity and continuous measurement of photosynthetic rate

In order to investigate the effect of light-dark cycle on leaf photosynthetic rate ($P_n$), the continuous $P_n$ values for
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75 h were measured under T24 (L = 16), T20 (L = 16), and continuous light conditions on Experiment A. Figure 4 shows the leaf photosynthetic rate ($P_n$) under T24 (L = 16), T20 (L = 16) and continuous light conditions for 75 h. On light period, $P_n$ was almost constant under every condition, on dark period as well (Fig. 4). Under L/D = 1 (T24) condition, $P_n$ on light period was also almost constant in wild-type Arabidopsis thaliana, so was constant on dark period (Dodd et al., 2005). The accumulated value of $P_n$ ranged from 0.89 mol m$^{-2}$ on the T24 (L = 16) condition to 1.56 mol m$^{-2}$ on the continuous light condition (Fig. 4; Table 3). The accumulated values of $P_n$ on T20 (L = 16) and T24 (L = 16) conditions were 2.5% and 42.7% smaller than that on the continuous light condition, respectively (Table 3).

The average of $P_n$ at daytime ranged from 5.13 μmol m$^{-2}$ s$^{-1}$ on T24 (L = 16) condition to 6.79 μmol m$^{-2}$ s$^{-1}$ on T20 (L = 16) condition (Fig. 4; Table 3). Those values of $P_n$ at daytime on T20 (L = 16) and T24 (L = 16) conditions were 17.5% greater and 11.3% smaller than that on the continuous light condition, respectively (Table 3).

In order to investigate the effect of light-dark period on leaf photosynthetic capacity, the $P_n$-Ci curves were measured under T24, T22, T12, and T6 (L/D = 2) conditions on Experiment B. Table 4 shows the effect of photoperiod, days after transplanting, and their interaction on maximum rate of Rubisco activity ($V_{cmax}$) and potential rate of electron transport ($J_{max}$), which are the important indexes of leaf photosynthetic capacity. Although the effect

| Table 3 | The accumulated values of $P_n$ for 75 h and the average $P_n$ in light period. |
|---------------------------------|---------------------------------|-----------------|-----------------|-----------------|
| Accumulated value of $P_n$ for 75 h (mol m$^{-2}$) | The ratio to under continuous light (%) | The average $P_n$ in light period (μmol m$^{-2}$ s$^{-1}$) | The ratio to under continuous light (%) |
| Continuous light | 1.56 | — | 5.78 | — |
| T20 (L = 16) | 1.52 | 97.5 | 6.79 | 117.5 |
| T24 (L = 16) | 0.89 | 57.3 | 5.13 | 88.7 |
of days after transplanting on the values of both \( V_{\text{max}} \) and \( J_{\text{max}} \) was significant \((P<0.01)\), the effects of photoperiod and their interactions on the values of \( V_{\text{max}} \) and \( J_{\text{max}} \) were not significant \((P<0.1)\; \text{Table 4})\). The values of \( V_{\text{max}} \) and \( J_{\text{max}} \) at 18 d after transplanting were 15% and 25% greater than those at 28 d after transplanting, respectively (Table 4). In Arabidopsis thaliana grown under L/D \(= \)1 (T24), the values of both \( V_{\text{max}} \) and \( J_{\text{max}} \) in young plants were significantly higher than those in old plants (Flexas et al., 2007). On Experiment A, the days after transplanting of measurement was used as a benchmark of sampling time on these four graphs.

### Table 4  Effect of different light-dark periods and days after transplanting on \( V_{\text{max}} \) and \( J_{\text{max}} \)

<table>
<thead>
<tr>
<th>Light-dark period (L)</th>
<th>Days after transplanting (D)</th>
<th>( J_{\text{max}} ) (μmol m(^{-2}) s(^{-1}))</th>
<th>( V_{\text{max}} ) (μmol m(^{-2}) s(^{-1}))</th>
</tr>
</thead>
<tbody>
<tr>
<td>T24</td>
<td>18 d after transplanting</td>
<td>10.7 ± 11.8</td>
<td>85.7 ± 37.7</td>
</tr>
<tr>
<td></td>
<td>28 d after transplanting</td>
<td>11.0 ± 11.8</td>
<td>82.7 ± 37.7</td>
</tr>
<tr>
<td>T22</td>
<td>18 d after transplanting</td>
<td>10.8 ± 12.4</td>
<td>76.7 ± 37.7</td>
</tr>
<tr>
<td></td>
<td>28 d after transplanting</td>
<td>11.3 ± 11.8</td>
<td>79.7 ± 37.7</td>
</tr>
<tr>
<td>T12</td>
<td>18 d after transplanting</td>
<td>9.9 ± 10.6</td>
<td>70.9 ± 16.5</td>
</tr>
<tr>
<td></td>
<td>28 d after transplanting</td>
<td>10.1 ± 10.6</td>
<td>73.9 ± 16.7</td>
</tr>
<tr>
<td>T6</td>
<td>18 d after transplanting</td>
<td>10.3 ± 11.8</td>
<td>63.9 ± 16.7</td>
</tr>
<tr>
<td></td>
<td>28 d after transplanting</td>
<td>10.5 ± 11.8</td>
<td>67.9 ± 16.7</td>
</tr>
</tbody>
</table>

Values are means ± SD for \( n=5 \) (T24, T22 and T12 of 18 d after transplanting), \( n=4 \) (T6 of 18 d after transplanting) or \( n=3 \) (28 d after transplanting). A two-way ANOVA was conducted to evaluate the effects of light-dark period (L), days after transplanting (D) and their interactions (L × D) on \( V_{\text{max}} \) and \( J_{\text{max}} \). ** Significant at \( P<0.01 \), and NS indicates non-significance.

Fig. 5  The comparison of diurnal change of leaf starch concentration (mg g\(^{-1}\) DW) on different photoperiod conditions. The vertical bars indicate the SD \((n=5 \text{ for T24, T23 and T21; } n=4 \text{ for T22})\). The sampling time after the beginning of light period were 00:00, 6:00, 12:00, 18:00, and 24:00 (T24), 00:00, 6:00, 12:00, 18:00 and 24:00 (T22), 00:00, 5:30, 11:00, 16:30, and 21:00 (T21). The beginning of dark period was used as a benchmark of sampling time on these four graphs.

Leaf starch concentration

To elucidate the relationship between fresh shoot weight and light-dark cycles, we continuously measured the leaf starch concentration for one light-dark cycle on the four experimental plots (T21, T22, T23, and T24) on Experiment E. Leaf starch concentration increased at daytime and decreased at nighttime monotonically for T21, T22, T23 and T24 conditions (Fig. 5). The starch concentration at the end of night \([(C_6H_{10}O_5)_n]_{\text{night}}\) was larger than that at the beginning of daytime \([(C_6H_{10}O_5)_n]_{\text{day}}\) on each photoperiod condition, and the differences \([(C_6H_{10}O_5)_n]_{\text{night}} - [(C_6H_{10}O_5)_n]_{\text{day}}\) of T21 and T22 were smaller than that of T23 and T24 (Fig. 5). The value of those differences under T24, T23, T22 and T21 condition was 92, 109, 70 and 11 mg g\(^{-1}\) DW, respectively (Data not shown). In cotton \((Gossypium arboreum L.)\) grown under L/D = 1 (T24) on the ambient CO\(_2\) concentration conditions of 350, 675 and 1,000 ppm, the starch concentration on leaves increased at daytime and decreased at nighttime monotonically, and the amplitude value varied with the ambient CO\(_2\) concentration (Delucia et al., 1985). In soybean \((Glycine max [L.] Merr.)\) grown under L/D = 1 (T24), the starch concentration on leaves, stems, petioles and roots increased at daytime and decreased at nighttime monotonically, and the maximum difference of leaf starch concentration was 200 mg g\(^{-1}\) DW (Kerr et al., 1985). In addition, the leaf starch content in A. thaliana under L/D = 1 (T24), L/D = 2 (T24), and L/D = 0.5 (T24) conditions rose at daytime and fell at night, and the value of starch content at the end of light period and dark period was highest under L/D = 2 (T24) and lowest under
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L/D = 0.5 (T24) condition, respectively (Scialdone et al., 2013). In our result, the fresh shoot weight under T21 and T22 conditions were larger than that under T23 and T24 (Table 2), and those samples were all harvested exactly at the end of dark period. Thus, the growth rate could be related to the enough decreasing of leaf starch concentration at night.

CONCLUSION

In general, most plant factories with artificial lighting, whose cultivation crops are leaf vegetables, have introduced 24 h of photoperiod for cultivation. In this study, we found that the growth rate of leaf lettuce was higher even under non-24 h photoperiod than 24 h photoperiod by using LEDs. To sum up the bubble charts of fresh shoot weight and growth rate, the optimal light-dark condition was within a range of L/D = 2 and T15-T22. The introduction of optimal light-dark conditions into the plant factory using artificial lighting, promotes efficient cultivation of leaf lettuce and the reduction of running costs.

REFERENCES


