Effects of Temperature Variations during Light Period on Growth and Tipburn Incidence of Hydroponic Leaf Lettuce Grown under Artificial Lighting

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This study identified the effects of temperature variations during the light period on the growth of hydroponic leaf lettuce grown under artificial lighting. The temperature during 16-h light period and 8-h dark period was set at 23°C and 18°C, respectively, as a control. In experiment 1, the temperature was quickly risen (QR) at the start of the light period (SL), kept at 23°C during the first half of light period, and then slowly decreased during the second half of light period, as QRS treatment. In experiment 2, the temperature was increased gradually during the first half of light period, kept at 23°C during the second half of light period, and then quickly dropped (QD) at the end of the light period (EL), as QDEL treatment. The temperature during the dark period was set to 18°C in both treatments. Both treatments increased fresh and dry weights of shoot. The QRSL treatment increased the growth rate and decreased the tipburn incidence. Meanwhile, the QDEL treatment decreased the growth rate because of the tipburn occurrence before harvesting. It was possible that these effects of temperature variations include the effects of vapor pressure deficit fluctuations since humidity varied with temperature.

Keywords: plant factory, relative growth rate, shoot/root ratio, vapor pressure deficit

INTRODUCTION

Closed facilities, such as plant factories and growth chambers, can precisely control environmental factors influencing plant growth (Kozai et al., 2019; Ahmed et al., 2020). The controllable environmental factors that influence plant growth in these facilities are light, temperature, humidity, air velocity, and CO₂ concentration (Yabuki and Miyagawa, 1970; Mortensen, 1986; Kitaya et al., 1998; Shibuya and Kozai, 1998; Goto, 2003; Park et al., 2012; Becker and Kläring, 2016). Temperature is a major environmental factor influencing plant growth and development (Tollenaar et al., 1979; Cao and Moss, 1989; Karlsson and Werner, 2001). Particularly, temperature influences the growth rate of lettuce (Gent, 2016) and the occurrence of tipburned leaves in lettuce (Choi and Lee, 2003). Tipburn in lettuce, which usually occurs at inner and newly developed leaf margins, is a serious problem in vegetable production under controlled environments (Cox et al., 1976), such as closed plant production systems with artificial light (Son and Takakura, 1989). Therefore, optimizing the temperature control is critical for lettuce production in plant factories and in greenhouses.

In greenhouses, there is a method that controls temperature by setting different temperatures depending on the time of day. This method of temperature control enhances photosynthesis, promotes the translocation of photosynthates, and reduces consumption due to dark respiration, resulting in increased productivity (Kawashima, 2008). In tomato and cucumber, optimum temperatures for the translocation and inhibition of respiratory consumption at night have been identified, and both growth and yield have been demonstrated to be enhanced by temperature management at night (Suzuki et al., 1983; Toki, 1995). The control of nighttime temperature in cut-roses (Mito et al., 1980) and short-term heating treatment at the end of day in spray-type chrysanthemums have also been reported (Douzono, 2012; Kawanishi et al., 2012). In addition to temperature management at night, Ehara et al. (2017) reported that fruit growth was accelerated by maintaining higher air temperatures in the afternoon than in the morning and quickly dropping them in the early evening in greenhouse cucumbers. However, previous studies conducted in plant factories and growth chambers investigated the influence of temperature on the growth of lettuce by controlling air temperature at a constant temperature during the light and dark periods (Choi and Lee, 2003; Gent, 2016; Lee et al., 2019). There have been few reports that examine the influence of time-dependent temperature control on the growth of leaf lettuce grown under controlled environment with artificial lighting.

This study aims to identify the benefits of a temperature control that varies air temperature, depending on the time of day on the growth of leaf lettuce grown in a controlled environment with artificial lighting. In this study, a 16-h light period was divided into the first and second halves, and air temperature in a growth chamber was controlled by varying the temperatures with time. The effects of temperature variations during the light period on the growth and tipburn incidence of leaf lettuce grown in the growth chamber with artificial lighting were investigated.
MATERIALS AND METHODS

Plant material and growth conditions
Leaf lettuce (Lactuca sativa L. var. crispa) cultivar, ‘Frill-ice’ (Snow Brand Seed Co., Ltd., Japan) was used in experiments 1 and 2. Seeds were sown into polyurethane foam in plastic tray (580×280×28 mm) on March 24, 2020 in experiment 1 and September 24, 2019 in experiment 2. They were supplied with water for 7 days after sowing. Afterward, the seedlings were supplied with a nutrient solution and grown in a hydroponic culture system with the nutrient film technique for 7 days. OAT House A-prescription nutrient solution (OAT Agrio Co., Ltd., Japan: 260 (mg L⁻¹) N, 120 P₂O₅, 230 K₂O, 1.5 MnO, 1.5 B₂O₃, 2.7 Fe, 0.03 Cu, 0.09 Zn, 0.03 Mo), which was adjusted to an electrical conductivity of 1.2–1.3 dS m⁻¹ and pH of 6.5–6.6, was used as the hydroponic nutrient solution for all experiments. The seedlings were illuminated with 12-h photoperiod using neutral white fluorescent lamps (FPR96EX-N/A; Panasonic Corp., Japan). The photosynthetic photon flux density (PPFD) at the surface of polyurethane foam was 280 μmol m⁻² s⁻¹. The air temperature in the nursery area was set to 23 °C for 24 h. The seedlings were transplanted at 14 days after sowing and cultivated for 28 days in two walk-in environment-controlled growth chambers (2.7×2.7×2.2 m). These growth chambers consisted of walls and ceilings of insulated panels (Genesta MR; Nikkei Panel System Co., Ltd., Japan), and each of them was equipped with an air conditioner (PKZ-RP50SKB; Mitsubishi Electric Corp., Japan) with a 4.5-kW rated cooling capacity and a CO₂ supply system to control air temperature and CO₂ concentration, respectively (Fig. 1). The seedlings were transplanted into 16-hole floating panels (440×310×230 mm), which were installed in a black plastic container (459×331×155 mm) containing 15 L of the nutrient solution. The solution was aerated using an air pump (S-100, Japan Pet Design Co., Ltd., Japan) connected to an air stone. The nutrient solution was replaced at 14 and 21 days after transplanting (DAT) to refresh the solution to the initial nutrient concentration. At 14 DAT, the plants were thinned to 8 plants per floating panel to increase the spacing between plants. Afterward, the plants were grown at 8 plants per floating panel until 28 DAT at harvest time. The transplanted plants were illuminated with 16-h photoperiod using three sets of light-emitting diode (LED) bar-type light (Agrimate AGR900-PP12EP; Otomo Co., Ltd., Japan) with a 38-W of rated power consumption. Spectral photon flux distribution of the LED light measured using a spectroradiometer (MS-720; Eko Instruments Co., Ltd., Japan) is shown in Fig. 2. The PPFD at the surface of floating panel was 195 μmol m⁻² s⁻¹. The air temperature in the growth chambers was controlled as shown in the next section, “Temperature treatments.” In all experiments, the humidity was not controlled, and the CO₂ concentration was controlled at 500–600 μmol mol⁻¹. The air temperature, relative humidity, and CO₂ concentration in the growth chambers were monitored at 2-minute intervals using CO₂ logger (TR-76Ui; T and D Corp., Japan) during the experiments. The vapor pressure deficit (VPD) was calculated using the data of temperature and relative humidity data (Buck, 1981).

Temperature treatments
The air temperature in the growth chamber was set at 23°C and 18°C during the light (06:00–21:59) and dark periods (22:00–05:59), respectively, as a control for experiments 1 and 2. In experiment 1, the air temperature in the

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**Fig. 1** Plane figure (A) and vertical view (B) of the walk-in environment-controlled growth chamber. Gray bars in the plane figure are LED bar-type lights.

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growth chamber was increased quickly (QR: quick rise) from 18°C to 23°C at the start of light period (SL: start of light period). The air temperature was set to 23°C during the first half of light period (06:00–13:59). Afterward, the temperature was dropped by 1°C per 2 h, as follows: 22°C from 14:00 to 15:59, 21°C from 16:00 to 17:59, 20°C from 18:00 to 19:59, and 19°C from 20:00 to 21:59. This method of temperature control was named QRSL treatment. In experiment 2, the air temperature was increased by 1°C per 2 h from the start of the light period, as follows: 19°C from 06:00 to 07:59, 20°C from 08:00 to 09:59, 21°C from 10:00 to 11:59, and 22°C from 12:00 to 13:59. The temperature during the second half of light period (14:00–21:59) was set to 23°C. The air temperature was decreased quickly (QD: quick drop) from 23°C to 18°C at the end of light period (EL: end of light period). This method of temperature control was named QDEL treatment. The air temperature during the dark period was set at 18°C in both experiments.

Measurement of growth parameters and statistical analysis

The shoot length was measured and the numbers of leaves and tipburned leaves per plant were counted every 7 days from transplanting to harvesting (28 DAT). All leaves having more than 10-mm length were counted. For each four plants thinned at 14 DAT and those harvested at 28 DAT, the shoot was cut just below the cotyledon node, and the fresh weight of shoot was measured immediately. The shoot and root were dried at 70°C for 72 h, and dry weights of shoot and root were measured. To determine the plant growth rate, the relative growth rate (RGR) between 14 and 28 DAT was calculated for each plant using the following equations:

\[ \text{RGR} (\text{g g}^{-1} \text{day}^{-1}) = \frac{(\ln W_{28\text{DAT}} - \ln W_{14\text{DAT}})}{14} \]

where \( \ln W_{14\text{DAT}} \) (g) and \( \ln W_{28\text{DAT}} \) (g) are natural logarithms of the dry weight of a whole plant at 14 and 28 DAT, respectively, and the number 14 (days) is the period between sampling for \( W_{14\text{DAT}} \) and \( W_{28\text{DAT}} \).

Four plants were measured for each temperature treatment. All experiments were conducted two times. The data represented the means for four plants of two replicate experiment. Statistical analysis was subjected to analysis of variance, followed by t-test at \( P < 0.05 \) or \( P < 0.01 \).

RESULTS

Experiment 1: Effects of QRSL treatment

In the control and QRSL treatments, the air temperature measured in the growth chambers was maintained almost the same as the set temperature (Fig. 3A). The mean temperatures during the light, dark, and 24-h periods in the control were 22.3°C, 18.4°C, and 21.0°C, respectively. Those in the QRSL treatment were 21.6°C, 18.6°C, and 20.6°C, respectively. The difference in mean temperatures during the light, dark, and 24-h periods between the control and treatment was lower than 1°C. The relative humidity measured in the growth chambers varied from 63.9% to 100% in the control and varied from 69.6% to 97.8% in the QRSL treatment during the experiment period. The VPD in the growth chambers in both treatments varied greatly when the temperature setting changed (Fig. 3B). The VPD ranged from 0 to 0.62 kPa in the control, and from 0.05 to 0.64 kPa in the QRSL treatment. The mean VPD in the control was almost 0.20 kPa through the light and dark periods during the experiments. In the QRSL treatment, the averaged VPDs during the light, dark, and 24-h periods were 0.31, 0.09, and 0.23 kPa, respectively. During the light period, the VPD in the QRSL treatment was higher than that in the control, while during the dark period, the VPD in the QRSL treatment was lower than that in the control.
In the control and QRSL treatments, the shoot elongated rapidly from 7 to 28 DAT (Fig. 4). The shoot length was almost the same in both treatments in the experiment.

The number of leaves increased similarly in both treatments during the first 14 DAT (Fig. 5A). The number of leaves in the QRSL treatment was smaller than that in the control after 21 DAT. In both treatments, the tipburned leaves occurred from 21 DAT (Fig. 5B, C). The number and incidence of tipburned leaves in the QRSL treatment were smaller than those in the control.

At 14 DAT, the differences in the fresh weight of shoot, dry weight of shoot and root and shoot/root ratio between the control and QRSL treatments were insignificant (Table 1). On the other hand, at 28 DAT, the fresh and dry weights of shoot and shoot/root ratio in the QRSL treatment were greater than those in the control. The dry weight of root was similar in both treatments, whereas the dry weight of shoot was greater in the QRSL treatment than in the control. As a result, the total dry weight was also greater in the QRSL treatment. The relative growth rate in

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**Table 1**

| Days after transplanting | Fresh weight of shoot (g) | Dry weight (g) | Shoot/root ratio | Relative growth rate (g g⁻¹ day⁻¹) |
|--------------------------|--------------------------|----------------|-----------------|-----------------------------------|
|                          |                          | Shoot | Root | Total |                          |                                  |
| Control                  | 14                       | 11.7  | 0.59 | 0.12  | 0.71                      | 5.28                             |
| QRSL                     | 14                       | 11.1  | 0.56 | 0.13  | 0.69                      | 4.33                             |
|                          | NS                       | NS    | NS   | NS    | NS                       | NS                               |
| Control                  | 28                       | 108.9 | 3.84 | 0.44  | 4.28                      | 8.79                            | 0.129                           |
| QRSL                     | 28                       | 130.7 | 4.70 | 0.48  | 5.18                      | 9.71                            | 0.144                           |

The data are the means of eight replicates.

*, **: Differences are statistically significant by t-test at P < 0.05 and P < 0.01, respectively.

NS indicates no statistically significant difference.
Experiment 2: Effects of QDEL treatment

In the control and QDEL treatments, the air temperature measured in the growth chambers was maintained almost the same as the set temperature (Fig. 6A). The mean temperatures during the light, dark, and 24-h periods in the control were 22.2°C, 18.5°C, and 21.0°C, respectively. Those in the QDEL treatment were 21.3°C, 19.2°C, and 20.6°C, respectively. The difference in the mean temperatures during the light, dark, and 24-h periods between the control and treatment was lower than 1°C.

The relative humidity measured in the growth chambers varied from 44.2% to 97.7% in the control and varied from 47.9% to 95.1% in the QDEL treatment during the experiments. The VPD in the growth chambers in both treatments varied greatly when the temperature setting changed (Fig. 6B). The VPD ranged from 0.03 to 1.20 kPa in the control, and from 0.08 to 0.99 kPa in the QDEL treatment during the experiments. The mean VPDs during the light, dark, and 24-h periods in the control were 0.52, 0.58, and 0.54 kPa, respectively. Those in the QDEL treatment were 0.23 kPa, 0.30 kPa and 0.32 kPa, respectively. During the first 2 h of the light period, the VPD in the QDEL treatment was higher than that in the control, whereas from 4 h after the start to the end of light period, the VPD in the QDEL treatment was lower than that in the control. The difference in the VPD during the dark period between both treatments was smaller than that during the light period.

In the control and QDEL treatments, the shoot rapidly elongated from 7 to 28 DAT (Fig. 7). The shoot length in the QDEL treatment was shorter than that in the control from 7 to 21 DAT. At 28 DAT, the shoot length was almost the same in both treatments. The number of leaves increased similarly in both treatments until 21 DAT, whereas at 28 DAT, the number of leaves in the QDEL treatment was larger than that in the control (Fig. 8A). In both treatments, the tipburned leaves occurred from 21 DAT, and their number rapidly increased from 21 to 28 DAT (Fig. 8B, C). The number and incidence of tipburned leaves at 28 DAT tended to be higher in the QDEL treatment than in the control, although the difference was not statistically significant.

At 14 DAT, the fresh weight of shoot, dry weight of shoot and root, and shoot/root ratio in the QDEL treatment were larger than those in the control (Table 2). At 28 DAT, the fresh weight of shoot and dry weight of shoot and root in the QDEL treatment were also larger than those in the control. However, the shoot/root ratio in the QDEL treatment was smaller than that in the control. The relative growth rate in the QDEL treatment was also smaller than that in the control.

DISCUSSION

In butterhead lettuce grown under continuous lighting, a periodic temperature variation has been known to increase the relative growth rate as well as the fresh and dry weight compared with the constant temperature (Inada and Yabumoto, 1989). The present study also showed that both the QRSL and QDEL treatments increased the fresh and dry weights of shoot at harvesting (28 DAT) compared with the control (Tables 1, 2). In addition, it was demonstrated that the QRSL treatment decreased the incidence of tipburned leaves at harvesting (Fig. 5C), whereas the QDEL treatment tended to increase that (Fig. 8C). The QRSL treatment increased the relative growth rate in the late growth stage from thinning (14 DAT) to harvesting compared with the control (Table 1). However, the fresh
and dry weights of shoot at thinning were the same in the QRSL treatment and control (Table 1), suggesting that the QRSL treatment hardly affected the shoot growth in the early growth stage. These results indicated that the QRSL treatment was effective to accelerate the shoot growth in the late growth stage due to a reduction in the incidence of tipburned leaves.

On the other hand, the QDEL treatment decreased the relative growth rate in the late growth stage (Table 2). However, the QDEL treatment promoted the shoot elongation before harvesting (Fig. 7), which increased the fresh weight of shoot and dry weight of shoot and root at both thinning and harvesting (Table 2). In the QDEL treatment, the number of tipburned leaves rapidly increased from 21 to 28 DAT (Fig. 8B). Thus, it appeared that the QDEL treatment promoted the growth, even in the early growth stage, but it reduced the growth rate in the late growth stage due to a rapid increase in the occurrence of tipburned leaves. The decrease in the shoot/root ratio at harvesting was observed only in the QDEL treatment (Table 2). Ehara et al. (2017) have reported that a rapid decrease in the temperature in the early evening promoted the growth of fruit, which is a sink organ, in greenhouse cucumber. This promotion of fruit growth has been considered to result from increasing the translocation of photosynthates from leaves to fruits by maintaining a higher temperature of fruits than leaves after sunset (Yoshioka et al., 1986; Kitano et al., 1998; Ehara et al., 2017). In plant species with separate vegetative and reproductive growth stages, such as leaf lettuce, roots and young leaves are major sink organs during the vegetative growth stages. In the QDEL treatment in this study, wherein air temperature decreases rapidly at the end of light period, the temperature of the root zone was probably higher than that of the shoot after the end of light period because the temperature of the nutrient solution (root zone) decreased later than the air temperature. This difference in the temperature between the shoot and root zones seemed to promote the translocation of photosynthetic assimilates from leaves to roots, resulting in the increase in the root growth in the QDEL treatment.

Previous temperature managements in plant factories control the temperature during the light and dark periods at a constant level (Choi and Lee, 2003; Kang et al., 2016; Lee et al., 2019), such as the temperature management in the control in this study. By contrast, the QRSL treatment is a temperature control that rapidly increases the tempera-

![Fig. 8 Changes in the leaf number (A), the number of tipburned leaves (B), and the incidence of tipburned leaves (C) of leaf lettuce grown under different temperature variations during the light period (Experiment 2). Vertical bars represent the standard errors (n = 8). Double-asterisk (**) indicates statistically significant differences by t-test at P < 0.01. NS indicates no statistically significant difference.](image)

### Table 2

| Days after transplanting | Fresh weight of shoot (g) | Dry weight (g) | Shoot/root ratio | Relative growth rate (g dry g⁻¹ day⁻¹) |
|--------------------------|---------------------------|---------------|------------------|---------------------------------------|
|                          |                           | Shoot         | Root             | Total                                 |
| Control 14               | 10.0                      | 0.54          | 0.15             | 0.69                                  | 3.72 | |
| QDEL 14                  | 14.4                      | 0.96          | 0.21             | 1.17                                  | 4.44 | |
| *                        | **                       | **            | **               | **                                    |
| Control 28               | 119.0                     | 4.49          | 0.52             | 5.01                                  | 8.76 | 0.140 |
| QDEL 28                  | 136.9                     | 5.94          | 0.75             | 6.69                                  | 7.93 | 0.126 |
| *                        | **                       | **            | **               | *                                     |

The data are the means of eight replicates.

*, **: Differences are statistically significant by t-test at P < 0.05 and P < 0.01, respectively.
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ture at the start of the light period and then gradually decreases it at the latter half of the light period (Fig. 3). The QDEL treatment is a temperature control that gradually increases the temperature from the start of the light period and then rapidly decreases it at the end of the light period (Fig. 6). Most previous studies have discussed the effects of air temperatures maintained at a constant during the light and dark periods or averaged temperature on plant growth. Choi and Lee (2003) reported that the optimum temperature for leaf lettuce in the light period was 22°C to 26°C in the early and middle growth stages and 20°C to 24°C in the late growth stage, whereas the optimum temperature in the dark period was 15°C to 20°C. The mean temperatures during light and dark periods in this study were 22°C and 18.5°C in the control, 21.4°C and 18.6°C in the QRSRL treatment, and 21.2°C and 19.1°C in the QDEL treatment, respectively. These temperatures were approximately within the range of the optimum temperatures reported by Choi and Lee (2003). The difference in the mean temperature for 24 h between the control and treatments was slight (<1°C). It seemed difficult to explain the differences in the growth and tipburn occurrence between the control and treatment observed in experiments 1 and 2 according to the mean temperature during the light and dark periods and 24 h.

Although humidity was not controlled in this study, the relative humidity varied with the change in temperature, and thus the VPD, which depends on air temperature and relative humidity, also varied (Figs. 3, 6). Therefore, the effect of VPD should not be disregarded when the effects of temperature variations during the light period are evaluated. The VPDs between 0.2 and 1.0 kPa have been considered to have little effect on the physiology and development of horticultural crops (Grange and Hand, 1987). It has been reported that in butterhead lettuce, the growth rate at 0.35 kPa of VPD was greater than that at 1.16 kPa of VPD, and the leaf number, leaf size, and dry weight were also greater at the low VPD (Tibbett and Bottenberg, 1976). In romaine lettuce, Collier and Tibbett (1984) reported that an increase in VPD from 0.87 to 1.65 kPa during the light period reduced the dry weight of shoot and the leaf size and delayed the occurrence of tipburn, whereas an increase in VPD from 0.07 to 0.14 kPa during the dark period also reduced the dry weight of shoot and the leaf size but accelerated the incidence of tipburn. In this study, the VPD associated with the chambers varied greatly with the change in the temperature setting, so that the periods with large VPD fluctuations were shorter in the control than in the QRSRL and QDEL treatments (Figs. 3, 6). However, the dry weight of the shoot was smaller in the control than in the QRSRL and QDEL treatments (Tables 1, 2). In the experiments of Inoue et al. (2021), the VPD was fluctuated in a short cycle (around 10 min) throughout 24 h. This difference in VPD fluctuation conditions seemed to affect the growth of lettuce plants. Therefore, it was considered that the effects of temperature treatments on the lettuce growth and tipburn development shown in this study included the effects of VPD fluctuations on them as well. Further research would be needed to optimize the control of environments for plant cultivation in a plant factory, considering both the temperature variations and VPD fluctuations.

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Inoue et al. (2021) have reported that the VPD fluctuations affected stomatal conductance and photosynthesis, as well as plant growth, in romaine lettuce. According to Inoue et al. (2021), minimizing VPD fluctuations maintains a higher stomatal conductance and photosynthesis, resulting in an increase in shoot dry weight and leaf area. In this study, the VPDs between 0.2 and 1.0 kPa were expected to be different between the two experiments, which was probably one of the reasons for the differences in the VPD fluctuations in the control between experiments 1 and 2.

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