Invited Review

Time-varying Photosynthetic Photon Flux Density and Relative Spectral Photon Flux Density Distribution to Improve Plant Growth and Morphology in Plant Factories with Artificial Lighting

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In contrast to fluorescent lamps and high-power sodium lamps, the use of light-emitting diode (LED) lamps enables the control of not only photosynthetic photon flux density (PPFD) at the plant level, but also the relative spectral photon flux density distribution (RSPD) of light because of the variety, even at different times of day, of producible light emitted by LEDs of different types. Effects of the spectral photon flux density on plant growth and morphology have been investigated using several types of LEDs and plant species. However, few studies on lighting methods with time-varying PPFD or RSPD have been published to date. In this paper, we summarize the effects of time-varying PPFD on the net photosynthetic rate ($P_n$) and those of time-varying RSPD on plant growth and morphology. Detailed modeling studies have been conducted on the reactions of the photosynthetic pathway under time-varying PPFD at a cycle of milliseconds to seconds. The results of these modeling studies and actual measurements of $P_n$ under pulsed light clearly indicate that pulsed light is not advantageous to improve $P_n$. Although the integrated PPFD of blue and red light was unchanged, the growth of leaf lettuce was promoted by asynchronous irradiation with blue light and red light compared with growth under simultaneous irradiation. We think that blue-light monochromatic irradiation promotes leaf elongation through leaf expansion as a primary factor in the enhancement of plant growth. In addition, changes in leaf photosynthetic capacity caused by blue-light monochromatic irradiation may be involved in plant growth promotion. An increasing number of studies have investigated the effects of time-varying RSPD on plants. However, the mechanisms underlying these effects remain to be elucidated.

Key Words: LED, photosynthesis, phytochrome, pulsed light.

Introduction

Light-emitting diodes (LEDs) are used as light sources for plants cultivated in plant factories with artificial lighting (PFALs) (Brown et al., 1995). Given that LEDs emit light in a narrow wavelength band, it is possible to create various spectral photon flux density distributions by using multiple types of LEDs and adjusting the photon flux of emitted light from each LED. The effects of photosynthetic photon flux density (PPFD) and relative spectral photon flux density distribution (RSPD) on the net photosynthetic rate ($P_n$) (McCree, 1972), morphology (Johkan et al., 2012), and growth of plants have been studied extensively. Methods to optimize plant growth and morphology using LED lighting are expected to improve the profitability of PFAL plant production by reducing lighting costs and improving the commercial value of the plant products (Jishi, 2020).

The PPFD–$P_n$ curve of leaves is affected by the cultivation environment (Sage et al., 1990), temperature (Rabinowitch, 1951), and CO$_2$ concentration (Ögren and Evans, 1993), and it generally produces a saturated-type curve (Blackman and Matthaei, 1905). On this basis, Fan et al. (2013) suggested that there is a PPFD that maximizes $P_n$ per energy consumption of lighting. The RSPD affects the light absorption rate and thus $P_n$ (McCree, 1972; Inada, 1976). The RSPD also influences morphogenesis, such as shade avoidance syn-
drome, via phytochromes (Smith and Whitelam, 1997), stomatal opening, phototropism, and chloroplast movements via blue-light receptors (Kozuka et al., 2005; Christie, 2007). On the basis of these findings, attention has been focused on the development of an appropriate and efficient method to improve plant growth and/or morphology by controlling the PPFD and/or RSPD in PFALs (Jishi, 2018, 2019).

The emission wavelength from an aluminum gallium indium phosphide-based LED, which has relatively high emission efficiency, ranges from 580 nm for yellow light to 650 nm for red light (Krames et al., 2007). This range covers the absorption peak of chlorophyll \( a \). This is the primary reason why many researchers have attempted to utilize red LED light for plant production in PFALs. However, the necessity of blue light to promote normal morphogenesis and growth of plants has been highlighted. Hoenecke et al. (1992) reported that the elongation of leaf lettuce stems under red light was suppressed by the addition of blue fluorescent light. Yorio et al. (2001) reported that the growth of radish, spinach, and lettuce plants was promoted under fluorescent light, and red LED light plus blue fluorescent light, compared with red LED light alone.

With the ready availability of blue LEDs, it has become easier to study the effects of blue and red light on plant morphology and growth. Matsuda et al. (2004) reported that the \( P_n \) of rice remained higher under irradiation with blue and red LED light compared with that under red LED light. Hogewoning et al. (2010) reported that the \( P_n \) under saturated light (\( A_{\text{max}} \)) and chlorophyll content were higher in leaves of cucumber plants cultivated under blue and red LED light compared with those cultivated under red LED light. Similarly, Liu et al. (2012) reported that the leaf \( P_n \) of tomato plants cultivated under blue and red LED light exceeded that of plants cultivated under red LED light. On the basis of these results, plant cultivation using blue and red LED light has been studied in greater detail. For example, a PPFD ratio of blue light to red light of 1:9 maximized the shoot fresh weight of cucumber (Hernández and Kubota, 2016) and the dry weight of tomato seedlings (Nanya et al., 2012). The addition of green light to blue and red light promotes the growth of leaf lettuce plants and makes it easier for growers to visually recognize plant color. Recently, phosphor-converted white LEDs, which emit broad-wavelength light, have been used in PFALs because of their improved luminous efficiency and lower cost (Cope and Bugbee, 2013).

In the majority of previous studies using LEDs, the PPFD and RSPD have remained constant during the light period. Few studies on lighting methods in which the PPFD or RSPD changes with time have been conducted. The LED lighting can change the PPFD with a delay of less than 1 \( \mu \)s, and even if LEDs blink repeatedly, their life is not shortened, unlike fluorescent lamps. Therefore, LEDs are a suitable light source for lighting in which PPFD is changed with time. Changing RSPD with time is possible by using several types of LEDs and independently changing the PPFD of light from each type of LED. Certain previous studies using time-varying PPFD or RSPD aimed to clarify the photosynthetic mechanism or photoreceptor reaction mechanism in plants (Borthwick et al., 1952; Sale and Vince, 1963). Few such studies have focused on morphological control or promotion of plant growth.

In this paper, we summarize the effects of time-varying PPFD on \( P_n \) and the effects of time-varying RSPD on plant growth and morphology.

**Time-varying PPFD (pulsed light)**

**Introduction**

In this article we refer to rectangular pulsed light with a frequency of 1 s or less simply as pulsed light (Fig. 1). Pulsed light has been used in photosynthesis studies to clarify the reaction rate constants of dark reactions (Emerson and Arnold, 1932; Weller and Franck, 1941) and the pool size of photosynthetic intermediates (PI) (Kok, 1956). In addition to basic research, many studies have investigated the application of pulsed light to plant cultivation.

**Photosynthesis mechanism under pulsed light**

The \( P_n \) measured under pulsed light is higher than the \( P_n \) calculated based on light use efficiency (or gross photosynthetic rate per PPFD; LUE) measured under continuous light. As an example, the \( P_n \) under pulsed light with an averaged PPFD of 100 \( \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} \) and a duty ratio of 25% has been calculated for the case illustrated in Figure 2. The PPFD is 400 \( \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} \) during the light period for 25% of one cycle and the remaining 75% is the dark period, and the \( P_n \) under continuous light with PPFD of 400 \( \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} \) and a dark respiration rate are 9.6 and 1.4 \( \mu\text{mol} \times \text{CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1} \), respectively. The \( P_n \) is calculated as \( 9.6 \times 0.25 + (−1.4) \times 0.75 = 1.35 \mu\text{mol} \times \text{CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1} \). However, the actual

![Figure 1](image-url)  

**Fig. 1.** Changes in photosynthetic photon flux density (PPFD) of pulsed light and pulsed light parameters. \( t_L \) and \( t_D \) are the duration of one light and one dark period, respectively.
measured $P_n$ is definitely higher than this value. This is due to the accumulation of PI. In photosynthesis, PI’s in the state used for the next reaction, such as NADPH and ATP, are synthesized using light energy and accumulate during the light reaction, and are then consumed in the dark reaction. Under continuous irradiation with a high PPFD, such as 400 μmol·m$^{-2}·$s$^{-1}$, the amount of stored PI stabilizes at a high concentration and a portion of the absorbed light energy is dissipated as heat without being used for PI synthesis. However, under pulsed light, accumulated PI is consumed during the dark period, and the amount of stored PI does not become saturated (i.e., does not reach a steady amount after being irradiated for a sufficient time) during the light period; absorbed light energy is used for PI synthesis with high efficiency (Tennesen et al., 1995; Jishi et al., 2015). When compared with equal average PPFD, using an equal supply of light energy, the $P_n$ is high and light energy is highly efficiently used for photosynthesis.

Emerson and Arnold (1932) observed the $P_n$ of green microalgae under pulsed light with several duty ratios, a constant light-period PPFD, and a constant frequency. They reported that the efficiency of $P_n$ per PPFD increased as the duty ratio decreased and the efficiency with a 17% duty ratio was a quarter of that with a 95% duty ratio. With a reduction in the duty ratio, that is, the longer the dark period, the greater the amount of PI consumed in the dark period, PI synthesis should have occurred with high efficiency in the following light period. Tennesen et al. (1995) observed the $P_n$ of tomato leaves under pulsed light of several frequencies with a constant light-period PPFD of 5,000 μmol·m$^{-2}·$s$^{-1}$ and duty ratio of 1%. They observed that the LUE increased with increases in the pulsed light frequency, and the LUE at frequencies of greater than 100 Hz was similar to that under continuous light with the same average PPFD of 50 μmol·m$^{-2}·$s$^{-1}$. The amount of stored PI should not approach saturation during short light periods at high frequencies, and PI synthesis cannot be performed with high efficiency. Similar results were obtained with lettuce leaves (Jishi et al., 2013).

Previous studies have demonstrated that the dark reaction is conducted in the dark period using the PI synthesized and accumulated in the light period. Kirschbaum and Pearcy (1988) measured temporal changes in the O₂ release and CO₂ absorption rates of leaves during and after irradiation. The CO₂ absorption rate increased gradually after the start of irradiation and decreased gradually over a few seconds after the end of irradiation, whereas the O₂ release rate increased immediately after the start of irradiation and stopped immediately after the end of irradiation. The process of CO₂ fixation utilizes PI; therefore, the CO₂ absorption rate gradually increased as the concentration of stored PI increased, and continued until the stored PI was consumed, even after irradiation had ceased.

These temporal changes in O₂ release and CO₂ absorption rates have been quantitatively explained by mathematical models. Gross et al. (1991) constructed a mechanistic model for the estimation of the temporal changes in amounts of ribulose 1,5-bisphosphate (RuBP) and intermediates in the glycolic acid cycle. Kirschbaum et al. (1998) developed a model incorporating the time course of Rubisco activity and the RuBP regeneration rate into the model of Gross et al. (1991). Empirical models to simulate $P_n$ under pulsed light have been proposed (Yoshimoto et al., 2005). These studies focused on the effects of light flecks on photosynthesis. Shade plants are suggested to have large amounts of poolable PI (pool size) to efficiently use the light energy of light flecks for photosynthesis (Sharkey et al., 1986). Applying the aforementioned models, a mechanistic model simulates the effect of average PPFD, pulse frequency, and duty ratio on $P_n$ under pulsed light (Jishi et al., 2015). Kirschbaum et al. (1998) suggested that triose phosphates are consumed and immediately reduced in the early dark period, but RuBP is still regenerated in the early dark period and eventually drives photosynthesis for a long time. In this way, multiple types of PI play roles as pools of energy, but the dynamics of individual PI are complicated and have not been elucidated.

**Pulsed light in plant cultivation**

Some researchers have misinterpreted that pulsed light enhances $P_n$ based on reports that LUE is higher under pulsed light in comparison with continuous light under the same light-period PPFD. With specific regards to the lighting method in PFALs, the $P_n$ should be compared at an identical PPFD averaged over the light and dark periods, involving almost identical electricity costs, rather than at an identical light-period PPFD.

Sager and Giger (1980) examined 20 published studies of $P_n$ measured under pulsed light. The authors concluded that no study reported that the $P_n$ under pulsed light was higher than that under continuous light at the same averaged PPFD, except for a study on cucumber (Klueter et al., 1980). Jishi et al. (2017) investigated the effects of average PPFD (averaged over the light and

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**Fig. 2.** Photosynthetic photon flux density (PPFD)–net photosynthetic rate ($P_n$) curve of cos lettuce leaves measured under continuous white LED light.
dark periods), pulse frequency, duty ratio, and their interactions on the $P_n$ of cos lettuce plants under pulsed light. It was observed that the $P_n$ under pulsed light with a frequency of more than 100 Hz was similar to the $P_n$ under continuous light, and that $P_n$ declined with decreases in pulse frequency and duty ratio. These reports are in general agreement with estimation of $P_n$ by a model that simulated PI accumulation (Jishi et al., 2015).

The majority of the aforementioned studies evaluated $P_n$ using leaves of plants grown under continuous light. Additional studies investigating the possibility that cultivation using pulsed light can promote plant growth by factors other than photosynthesis are needed. Nedbal et al. (1996) reported that microalgal growth was promoted under pulsed light with a frequency of 100 Hz, but the authors considered that the factor promoting growth was not an improvement in $P_n$. In addition, leaves of lettuce plants grown under pulsed light acclimated to attain a higher $P_n$ under pulsed light (Kanechi et al., 2016).

Pulsed light may be applied in PFALs as a result of pulse-width modulation (PWM) dimming, without the intention of increasing $P_n$. The PWM dimming method alters the average PPFD by adjusting the duty ratio of pulsed light with a constant light-period PPFD. PWM dimming is used for generic illumination because it facilitates the adjustment of the average PPFD linearly over a wide range. The frequency of PWM dimming is typically set to 100 Hz or greater so that humans do not recognize blinking. This frequency is sufficiently high enough that the application of PWM dimming to PFALs does not cause a decrease in $P_n$.

In this article, we focused on rectangular pulsed light, but the preceding discussion applies even in the case of non-rectangular pulsed light in which the PPFD changes periodically. That is, continuous light with a constant PPFD will maximize the $P_n$ when the average PPFD is identical (Jishi and Fujiwara, 2018). However, in a light environment in which PPFD changes in a cycle of 10 s or more, the effect of PI accumulation described herein must be small, and photosynthetic induction and circadian rhythms will be more important factors to control plant photosynthesis and growth. The abovementioned studies ignored many factors, such as changes in the xanthophyll cycle and NADPH pool size, as well as state transitions, because the units of time were seconds or less. Even when considering these factors, it is unlikely that plants will grow faster under pulsed light than under continuous light because plants cannot be instantly “optimized” to a fluctuating environment (Graham et al., 2017). These factors are being actively investigated (Kono and Terashima, 2014; Yamori, 2016), and new data may be applied to the lighting techniques used in PFALs.

### Time-varying RSPD

#### Introduction

Previous studies have observed plant reactions to changes in RSPD and revealed the mechanisms of plant responses to light changes. For example, when lettuce seeds are alternately irradiated with red light and far-red light, the germination frequency is affected by the latter (Mancinelli et al., 1966). This finding contributed to an elucidation of phytochrome properties.

Several studies focused on lighting-technology development reported that plant growth was promoted by time-varying RSPD depending on the time of day. Sung and Takano (1997) reported that blue light before sunrise promoted the growth of cucumber cultivated under sunlight compared with the effects of red light and non-irradiation. Hanyu and Shoji (2002) reported that blue light at the beginning of the light period promoted the growth of spinach cultivated under white fluorescent lamps compared with plants treated with red light and non-irradiation. Stomatal opening stimulated by blue light at the beginning of the light period and the immediate increase in $P_n$ after the start of the light period are considered to be growth-promoting mechanisms. Hanyu and Shoji (2002) also reported that red light at the end of the light period promoted spinach growth. Ohashi-Kaneko et al. (2010) reported that blue light at the beginning of the light period increased the spinach mesophyll cell number and that red light at the end of the light period increased the spinach mesophyll cell size.

The aforementioned studies were conducted in greenhouses under natural sunlight with supplemental lighting. In the remainder of this section, we discuss time-varying RSPD for plant production in PFALs.

#### Blue-light monochromatic irradiation

The growth of leafy vegetables is promoted by blue light at the beginning of the light period and red light at the end of the light period when irradiated with blue and red LED light. Compared with simultaneous irradiation with blue and red light, the growth of cos lettuce and leaf lettuce is promoted by delaying the timing of irradiation with red light; that is, applying a lighting regime in the order: blue light—blue and red light—red light. In these studies, as the shift in the timing of irradiation with blue and red light increased, the promotion of growth increased. Kuno et al. (2017) reported that leaf lettuce growth tends to be promoted as the shift in the timing of exposure increases, regardless of whether blue light or red light are applied first in the light period. Shimokawa et al. (2014) reported that the fresh and dry weights of leaf lettuce increased under alternate irradiation of blue and red light with a 24-h cycle compared with under simultaneous irradiation of blue and red light. These growth-promotive effects cannot be explained only by stomatal opening caused by light of a
specific wavelength band. Jishi et al. (2016) further investigated the morphology of cos lettuce plants cultivated under different LED lighting regimes and observed that monochromatic blue- or red-light irradiation resulted in the development of large, thin leaves. The increase in the amount of light intercepted by thin, large leaves was considered to be the primary reason for the growth promotion. Similarly, Chen et al. (2017) found that green oak leaves were lighter in color and elongated under alternate irradiation with blue and red light compared with simultaneous irradiation with blue and red light. The authors recently revealed that monochromatic blue-light irradiation caused narrow, thick leaf morphology (unpublished data). Consequently, the cultivation period can be shortened by promoting growth, and the electricity costs for lighting may be reduced by up to 66% (Ohtake et al., 2015).

The mechanism by which monochromatic blue-light irradiation affects plant morphology can be explained by the modes of action of phytochromes (Murakami et al., 2019). The percentage of activated phytochromes is termed the phytochrome photostationary state (PSS; Sager et al., 1988). The PSS assumes a low value under incident light containing a high proportion of far-red wavelengths, and the elongation of stems and expansion of broad, thin leaves occur as shade avoidance responses. The PSS value is approximately 0.7 under sunlight, approximately 0.55 under monochromatic blue-light irradiation, and approximately 0.9 under both monochromatic red-light and combined blue-light and red-light irradiation. The PSS value is relatively low under monochromatic blue light, so a low PSS value is considered to promote the development of large, thin leaves. The same mechanism has been used to explain the observation that monochromatic blue light promotes cucumber stem elongation compared with combined blue light and red light (Hernández and Kubota, 2016).

The effects of phytochromes may also be controllable by far-red light. However, blue light shows a lower transmittance through the leaves than far-red light, and each wavelength band should be used for different purposes. When a plant canopy is irradiated with light that includes far-red light, plants in the understory receive light with a high proportion of far-red light. Thus, the morphology of understory plants is greatly elongated compared with those in the upper vegetation layers. However, the difference is greatly reduced in the absence of far-red light (Shibuya et al., 2016).

Using time-varying RSPD for plant cultivation

Many reports on the utilization of time-varying RSPD suggest that it affects plant morphology, as in the case of blue-light irradiation, rather than directly affecting photosynthesis. However, Ohtake et al. (2018) reported that leaf lettuce growth was promoted under alternating irradiation with 12 h of blue light and 12 h of red light. Their growth analysis revealed that the proportion of growth could be attributed to a high $P_n$ per leaf area. However, the mechanism by which time-varying RSPD affects plant growth remains to be clarified.

Given that plant circadian rhythms follow a cycle of approximately 24 h, plants are unable to synchronize, and growth is inhibited under a light–dark cycle that differs substantially from a 24 h period (Dodd, 2005). Cryptochromes and phytochromes are photoreceptors that affect circadian rhythms (Kami et al., 2010). Thus, growth may be similarly inhibited under an irradiation cycle strongly divergent from 24 h.

Chang and Chang (2014) changed the RSPD according to the growth stage during cultivation to investigate the effects of lighting patterns on leaf lettuce growth and morphology. The authors reported that ultraviolet-A (UV-A) light at the seedling stage significantly increased the plant nitrate content compared with UV-A irradiation at the vegetative stage. Thus, the control of RSPD in accordance with the growth stage may be effective in regulating plant growth and morphology during cultivation. For example, to increase the growth rate of a plant canopy, RSPD with a low PSS may be effective for promoting leaf expansion to increase the amount of intercepted light when plants are small and do not shade each other. In contrast, when plants are large enough to shade each other, RSPD with a high transmittance to the leaves may be effective in increasing the canopy $P_n$ by penetrating into the understory.

LED light-source systems available for time-varying RSPD effect research

The most effective or appropriate light environments for plant cultivation can be determined through research conducted using LEDs as the light source. In turn, LEDs are anticipated to be used as a light source to realize such light environments during cultivation (Fujiwara, 2016). In the past decade, LED light-source systems consisting of five (Fujiwara et al., 2011; Yano and Fujiwara, 2012), six (Fujiwara and Yano, 2013), and 32 (Fujiwara and Sawada, 2006; Fujiwara and Yano, 2011; Fujiwara et al., 2013) wavelength LEDs have been developed for research purposes. Such LED light-source systems are ideal for conducting research on controlled light environments to improve plant production in PFALs (Fujiwara, 2019).

Conclusions

Time-varying PPFD and RSPD show great potential to improve the $P_n$, growth and morphology of plants, even if the daily PPFD integral is unchanged. However, the effects of time-varying PPFD and RSPD, and the development of appropriate and effective applications for plant production in PFALs are still under investigation. Further research on time-varying irradiation protocols may contribute to the popularization of PFALs in commercial crop production.
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