Upward LED Lighting from the Base Suppresses Senescence of Lower Leaves and Promotes Flowering in Indoor Rose Management

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Abstract. In indoor environments such as hotels, the light intensity is generally insufficient for managing plants, and flower buds often fail to open. Lamps placed above (downward lighting) take up space. We assessed the applicability of lighting from underneath (upward lighting) for the indoor management of roses. We grew plants indoors in dim light for 2 weeks under three conditions: 1) without supplemental lighting, 2) with downward light-emitting diode (LED) lighting, and 3) with LED lighting. We quantified photosynthetic components (chlorophyll and rubisco) and the maximum quantum yield of photosystem II (Fv/Fm, an indicator of plant health) to determine the effects of each treatment on the quality and photosynthetic abilities of the leaves. We determined the ratios of dead and opened flower buds to elucidate the effects of supplemental lighting on flower bud maturation. Management without supplemental lighting decreased the number of flowers and resulted in lower-leaf senescence. Downward LED lighting promoted blooming but also resulted in lower-leaf senescence. However, upward LED lighting promoted blooming and maintained the photosynthetic abilities of the leaves, including the lower leaves. This study shows a strong case for using upward LED lighting in appropriate settings for indoor plant management and LED-based horticulture.

In hotels, shops, and other buildings, plants are often used to add color, suggest luxury, and welcome customers. In hospitals, plants are often placed in receptions and wards. Several analyses of the effects of nature and plants on human health have suggested that greenery reduces physiological stress (Chang and Chen, 2005; Coleman and Mattson, 1995; Lohr et al., 1996; Park et al., 2008; Ulrich et al., 1991). Viewing nature or plants is considered a pleasant distraction that increases positive feelings, reduces anxiety, and helps recovery from stress (Miyazaki

et al., 2011; Park et al., 2004; Ulrich, 1992). Therefore, a comprehensive understanding of the mechanisms of flower opening and plant senescence would benefit commercial horticulture and plant science in general.

Many studies have focused on how to preserve cut flower quality because cut flowers are valued for their beauty. Therefore, most studies have focused on senescence to improve vase life (van Doorn and Woltering, 2008). Several agents, such as inhibitors of ethylene production or action (van Doorn and Woltering, 2008) and sugars (Ichimura et al., 2003; Paulin, 1979), have been developed to improve cut flower quality. In addition, the light level during cultivation affects the regulation of water loss, which is an important factor in long keeping quality (Fanourakis et al., 2013, 2019; Mortensen and Fjeld, 1998). It is also important to establish methods to control flower opening as well as senescence because the ornamental value of many plants lies in the process of blooming. Yet, there are few studies of the efficient maintenance of plants indoors, where the light intensity is low (Fanourakis et al., 2013). This highlights the need to study the effects of supplemental lighting on indoor plant management to delay senescence of leaves and promote flower opening.

Artificial lighting intensifies plant production, improves crop quality, and allows cultivation wherever natural light is not sufficient. Previously, the use of conventional light sources such as fluorescent lamps entails high electricity costs. The introduction of LEDs into

plant cultivation in the 2000s reduced the costs of both lighting and cooling because high-intensity LED lamps offer a long functional life, low energy consumption, small size, light weight, and low heat production (Hernández and Kubota, 2012; Zhang et al., 2011). In addition, the spectral distribution of LEDs can be easily controlled (Goto, 2012). Therefore, the use of LEDs as a supplemental light source enables fine control of the light environment.

Light conditions, including intensity, wavelength, and photoperiod, affect several aspects of plant physiology, including plant growth and flower opening (Currey and Lopez, 2013; Kaihara and Takimoto, 1980, 1981; Yamori et al., 2016a, 2016b; Yamori and Shikanai, 2016). Leaf senescence at low light intensity is accompanied by chlorophyll loss, degradation of photosynthetic proteins, decreased photosynthetic activity, and remobilization of nutrients to younger tissues (Brouwer et al., 2012; Gan and Amasino, 1997; Weaver and Amasino, 2001). Indoor environments with indirect lighting are generally inadequate for plant growth, and growth and flower bud maturation are generally suppressed (Corbesier et al., 1998; King et al., 2008; Sheldon et al., 2000). Therefore, the use of supplemental lighting is critical to enhancing both production and quality under low light environments. However, when plants are lit from above, the structure that supports the light source takes up space. Recent work has shown that supplemental upward lighting using LEDs could retard outer leaf senescence and increase the photosynthetic rate of lettuce, thus enhancing yield (Joshi et al., 2017; Zhang et al., 2015). With this method, the LED light source can be installed on the pot or the soil, requiring no special structure. Here, we investigated the effects of supplemental lighting from different directions on the indoor management of rose plants. We analyzed the contents of photosynthetic components and the maximum quantum yield of photosystem II (Fv/Fm) to determine the effects of each treatment on the photosynthetic characteristics of upper, middle, and lower leaves, and we determined the ratios of dead and flowering buds to elucidate the effects on flower bud maturation.

Materials and Methods

Plant materials, growth conditions, and supplemental light treatments. The 2-year-old plants of potted miniature rose (*Rosa hybrida* L.) grown in a mixture of peat and perlite (4:1 by volume) in 1-L pots were obtained from a commercial nursery (Rose Nakashima, Nagano, Japan) and grown until each plant had 50 to 60 flower buds. Then, the plants were moved indoors with 65% ± 5% relative humidity and 25 ± 1 °C. Light at 10 to 20 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at plant height was supplied for 12 h/day (0900–2100 HR) by fluorescent lamps located 20 cm above the plants to simulate the light conditions of hotel rooms and shops.

Three treatments were prepared: no supplemental lighting (control); downward lighting at 150 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$; and upward lighting at 150 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (E46 LED; MAXGTRS,

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Zhejiang, China). LEDs were positioned at plant height for the downward lighting and around the base for the upward lighting; they were lit for 12 h/day (0900–2100 HR) (Fig. 1). The wavelengths of light sources recorded with a spectrometer (SR9910-v7; Irradiant Ltd., Tranent, UK) were 300 to 800 nm. The temperature of directly lit leaves measured by an infrared thermometer was $<0.5^{\circ}\text{C}$ higher than the air temperature. The plants were fertilized every week with a commercial fertilizer (NPK 6:10:5 diluted 1/1000; Hyponex, Osaka, Japan). The treatments were established with a randomized block design of three blocks with four plants per block. Data were based on three replicate plants distributed over three blocks ($n = 3$). Plants grown for 2 weeks under each treatment condition were measured.

Measurements of chlorophyll fluorescence and gas exchange. Leaves were classified as lower, middle, or upper. In each layer, we measured the maximum potential photochemical efficiency (the ratio of variable to maximum fluorescence, F_v/F_m) using an Imaging-PAM fluorometer (Walz, Effeltrich, Germany) to evaluate the degree of senescence. Leaves were maintained in darkness for 30 min before measurements were performed (Zhang et al., 2015).

To evaluate the effects of each treatment on the leaf photosynthetic capacity, we measured net CO_2 assimilation rates and stomatal conductance (g_s) with a portable gas exchange system (LI-6400XT; LI-COR Inc., Lincoln, NE). After 30 min of illumination to obtain steady-state photosynthesis, gas exchange was measured as described previously (Yamori et al., 2009, 2010). We measured net CO_2 assimilation rates and g_s in upper leaves with $150\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ downward lighting and in lower leaves with $150\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ upward lighting from each treatment. The CO_2 concentration and leaf temperature in the chamber were $400\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and 25°C , respectively.

Determination of chlorophyll and rubisco contents. Immediately after the gas exchange measurements, 1.0-cm^2 leaf discs were taken from each layer, immersed in liquid nitrogen, and stored at -80°C until determination of chlorophyll and rubisco. Chlorophyll was extracted in N,N -dimethylformamide, and its content was determined by a spectrophotometer according to Porra et al. (1989). Rubisco content was quantified by SDS-PAGE as described by Yamori et al. (2005).

Flower bud maturation. We determined the effects of supplemental lighting on flower bud maturation in the same three treatments.

After 2 weeks of cultivation, we counted total buds, dead buds, and flowers by eye and calculated the ratios of dead buds, unopened buds, and flowers in each treatment.

Statistical analysis. Data are presented as means $\pm$ SE. An analysis of variance with a post hoc Tukey's test was performed using SPSS statistical software (SPSS, Chicago, IL). Differences were considered significant at $P < 0.05$.

Results

Effects of supplemental lighting on leaf senescence and photosynthetic characteristics. Without supplemental lighting, chlorophyll and rubisco contents were reduced in the middle leaves and were not measurable in the lower leaves, which had senesced (Fig. 2); no difference between treatments was detected in the upper leaves. Contents were significantly higher with upward lighting than with downward lighting in the lower leaves, but not in the middle or upper leaves. F_v/F_m without supplemental lighting was similar to that of other treatments in the upper leaves, decreased in the middle leaves, and not measurable in the lower leaves (Fig. 3). F_v/F_m with downward lighting was significantly lower than that with upward lighting in the lower leaves, but not in the middle or upper leaves. CO_2 assimilation rates and g_s in the upper leaves were not significantly different between downward and upward lighting, but they were significantly higher with downward lighting than without supplemental lighting (Fig. 4A and C). Because the upward lighting lit mainly the lower leaves, and because the control had no supplemental lighting, we measured the photosynthetic rates in the lower leaves. The CO_2 assimilation rate and g_s in the control were not detectable (Fig. 4B).

(A) Lighting conditions

Fig. 1. Schematic diagram of the experimental design of the present study. (A) Lighting conditions and (B) the relative spectral photon flux of supplemental lighting [white light-emitting diodes (LEDs)] and white fluorescent lamp. Miniature roses (*Rosa hybrida* L.) were grown in 1-L pots in a greenhouse for 2 years until flower buds appeared in March. Before they bloomed, the plants were moved to a laboratory under fluorescent lamps at 10 to $20\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for the following 2-week treatments: control (no supplemental lighting); downward lighting at $150\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$; and upward lighting at $150\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. The supplemental LEDs were set 5 to 10 cm away from the plants and lit for 12 h (0900–2100 HR).

Fig. 2. Effects of supplemental lighting on chlorophyll and rubisco contents in leaves. Plants had no supplemental lighting (control), downward lighting at $150\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, or upward lighting treatment at $150\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. The same letter above columns indicates no significant difference among treatments within a leaf layer ($P < 0.05$) according to the Tukey-Kramer test.

Fig. 3. Effects of supplemental lighting on Fv/Fm. Fv/Fm is the maximum potential photochemical efficiency in leaves. Plants experienced no supplemental lighting (control), downward lighting at $150 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, or upward lighting at $150 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. The same letter above columns indicates no significant difference among treatments within a leaf layer ($P < 0.05$) according to the Tukey-Kramer test.

Those in the lower leaves lit by upward lighting at $150 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ were higher with upward lighting treatment than with downward lighting treatment (Fig. 4B and D).

Effects of supplemental lighting on flower bud formation. Before the 2-week treatment, the number of buds per plant was 55.6 ± 1.2 , with no significant differences among plants.

After the 2-week treatment, without supplemental lighting, most buds turned yellow and died (Figs. 5 and 6). However, with both downward and upward lighting at $150 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, more than two-thirds of the buds bloomed and $<10\%$ of the buds were dead.

Discussion

Most studies have focused on senescence to improve the vase life of cut flowers (van Doorn and Woltering, 2008). Few studies have examined the effects of light on flower opening of indoor plants (Sabzalain et al., 2014). It is important to understand the flowering mechanism of ornamental plants and to establish methods to control flower opening and senescence because the value of such plants lies in their flowers. We examined the effects of supplemental lighting on leaf senescence and flower opening during the indoor management of roses. Dim light at 10 to $20 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ indoors was not sufficient for the roses to bloom or even maintain their leaves green. Chlorophyll and rubisco contents and Fv/Fm were similar in middle and upper leaves with downward and upward lighting, but they were significantly higher in lower leaves with upward lighting (Figs. 2 and 3), indicating that upward lighting can suppress the senescence of lower leaves. CO_2

assimilation rates and g_s in upper leaves with downward lighting were not significantly different in plants grown with downward and upward lighting treatments (Fig. 4A and C). Lower leaves that underwent the upward lighting treatment had a significantly higher CO_2 assimilation rate and g_s than those that underwent the downward lighting treatment (Fig. 4B and D), which is consistent with the high rubisco content in the lower leaves that underwent upward lighting treatment (Fig. 2). In summary, we showed that 1) without supplemental lighting, leaf senescence was promoted (Figs. 2 and 3) and flower buds browned and died (Fig. 5); 2) supplemental downward lighting promoted flower bud maturation and senescence of lower leaves; and 3) supplemental upward lighting promoted flower bud maturation and retarded senescence specifically in lower leaves. Although more flowers successfully opened with downward lighting than with upward lighting, upward lighting can be another option for indoor rose management because upward lighting does not require extra space for lighting equipment (Fig. 7).

Supplementary light is often applied to ornamental crops to promote the productivity and external quality of cut flowers and potted plants under protected cultivation (Fanourakis et al., 2013). During flower bud opening in roses in our experiment, the light requirement was absolute, and darkness totally inhibited flower bud burst. Light has been reported to have a considerable impact on sugar metabolism during bud burst (Girault et al., 2010). Sugars control the biosynthesis, transport, or signaling of certain hormones, including auxin and cytokinin (Kushwah and Laxmi, 2013; LeClere et al., 2010; Mishra et al., 2009; Sairanen et al., 2012; Stewart Lilley et al., 2012). In addition, sucrose has been identified recently as an early modulator of the key hormonal mechanisms controlling bud outgrowth in rose (Barbier et al., 2015). Because light is indispensable for mobilization of the carbohydrate reserves necessary for bud burst (Girault et al., 2010), the absence of burst of rose buds in darkness could, in part, be explained by the incapacity of the bud to mobilize its own carbohydrate reserves.

Plants respond to various combinations of light colors via their photosynthetic pigments (chlorophylls and carotenoids) and photoreceptor pigments (phytochromes, cryptochromes, and phototropins) (Fukuda et al., 2016). Light wavelength (as well as light intensity and the photoperiod) greatly affects plant growth (Inada, 1976; Lin et al., 2013; McCree, 1971–72). Therefore, understanding the response to light stimuli might lead to the development of new methods to control flower opening and water uptake in indoor plants. The light level during cultivation also affects the regulation of water loss, which is an important factor in postharvest quality (Fanourakis et al., 2019). Therefore, it is necessary to identify the optimal growth conditions for indoor plant management during periods of low light availability.

Fig. 4. Effects of supplemental lighting on the photosynthetic rate. Net CO_2 assimilation rates in plants grown with no supplemental lighting (control), downward lighting at $150 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, and upward lighting at $150 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ analyzed with a portable gas exchange system (LI-6400XT; LI-COR Inc., Lincoln, NE) are shown. (A) CO_2 assimilation rates and (C) stomatal conductance at $150 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ downward lighting in upper leaves that underwent each treatment. (B) CO_2 assimilation rates and (D) stomatal conductance at $150 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ upward lighting in lower leaves that underwent each treatment. The same letter above the columns indicates no significant difference among treatments ($P < 0.05$) according to the Tukey-Kramer test.

Fig. 5. Effects of supplemental lighting on flower bud maturation. Photographs of flower buds before (day 0) and after (day 14) 2-week treatments. Plants experienced no supplemental lighting, supplemental downward lighting at $150 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, or supplemental upward lighting at $150 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$.

Fig. 6. Effects of supplemental lighting on the fate of flower buds. Ratios of dead buds, unopened buds, and flowering buds of plants with no supplemental lighting, supplemental downward lighting at $150 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, and supplemental upward lighting at $150 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ are shown. After 2 weeks of treatment, the numbers of dead, unopened, and flowering buds were counted by eye, and the ratios were calculated for each treatment. Values are mean $\pm$ SE ($n = 3$).

Supplemental upward lighting can retard leaf senescence of the lower leaves while the photosynthesis rate increases. Because light has been shown to have an effect on pigment accumulation during development, darkness or

extremely low light (i.e., $<10\text{--}20 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) is known to induce senescence, which is accompanied by a rapid breakdown of chlorophyll concomitantly with chloroplast disassembly and a decrease in photosynthesis (Gepstein et al., 2003; Liebsch and Keech, 2016; Lim et al., 2007). The present work clearly showed that upward lighting can suppress the senescence of lower leaves (Fig. 2). This is supported by the recent work that showed that supplemental upward lighting using LEDs could retard outer leaf senescence and increase the photosynthetic rate of lettuce, thus enhancing yield (Joshi et al., 2017; Zhang et al., 2015), and that the postharvest senescence of green vegetables could be delayed by irradiation with low light intensities (such as $20\text{--}30 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) (Büchert et al., 2011; Costa et al., 2013; Favre et al., 2018; Gergoff-Grozeff et al., 2013).

The leaf senescence process is multifaceted; it involves a complex regulatory network that became apparent through studies demonstrating differential and global gene expression during natural and dark-induced senescence in *Arabidopsis thaliana* (Buchanan-Wollaston et al., 2005; Gepstein et al., 2003; Sobieszuk-Nowicka et al., 2018). Light is arguably the most significant environmental factor; it affects not only photosynthesis and photo-

Fig. 7. Supplemental upward lighting had positive effects on indoor rose management. (A) Without supplemental lighting, leaves senesced and flower buds died. (B) Supplemental downward lighting promoted flowering as well as lower leaf senescence. (C) Supplemental upward lighting promoted flowering and retarded lower leaf senescence.

assimilate availability but also phytochromes, which are photoreceptors that signal red and far-red light information. Recent studies have demonstrated that phytochromes are involved as mediators in light signaling-dependent retardation of senescence (Woo et al., 2019) because red light negatively regulates leaf senescence and far-red light positively regulates it (Lim et al., 2018). Moreover, phytochromes are regulators of the genes involved in chloroplast maintenance and chlorophyll catabolism (Liebsch and Keech, 2016). Although it cannot be ruled out that the metabolic status including the sugar level is involved in other signaling pathways for dark-induced or shade-induced senescence, it is highly possible that photoreceptor-mediated light signaling had an important role in retarding leaf senescence when supplemental upward lighting was applied.

Use of supplemental upward lighting during indoor rose management. In modern society, many people spend much of their time under stress and have no time for contact with nature outside their immediate surroundings. Flower arrangements offer a way of bringing nature into daily indoor life. The relaxing effects of fresh flowers such as roses are empirically known. Many studies of the psychological effects of exposure to blooming or green plants have shown that plants alleviate physiological stress and provide more positive feelings and higher satisfaction (Chang and Chen, 2005; Coleman and Mattson, 1995; Ikei et al., 2014; Lohr et al., 1996; Ulrich et al., 1991; Verderber and Reuman, 1987).

Studies have shown that introducing plants and flowers into hospital rooms during

the recovery period has a positive influence linked directly to health outcomes of surgery patients (Diette et al., 2003; Lohr and Pearson-Mims, 2000; Park et al., 2004; Park and Mattson, 2009; Ulrich, 1984, 1992). Therefore, blooming or green plants as well as colorful fresh cut flowers in a hospital environment could be a noninvasive, inexpensive, and effective complementary medicine for patients. When properly maintained, ornamental indoor plants can provide a great opportunity for patients denied outdoor scenery, and they can provide meaningful therapeutic contact for patients who spend much of their time indoors while recovering. Upward lighting can help keep plants green and promote flowering, thus improving one's mood.

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Supplemental Fig. 1. Chlorophyll and Rubisco contents before treatments Chlorophyll and Rubisco contents in lower, middle, and upper leaves were quantified before the 2-week supplemental lighting treatments.