

# Differences in plant growth and leaf sesamin content of the lignan-rich sesame variety ‘Gomazou’ under continuous light of different wavelengths

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**Abstract** Sesamin is a major lignan constituent of sesame seeds and beneficial to human health. We previously reported that sesamin is contained in leaves as well as seeds of sesame and proposed that sesame leaves could be a new sesamin source. Growth and constituents of plants are affected by light wavelength. In this study, growth and leaf sesamin content of sesame variety ‘Gomazou’ were investigated in plants grown under continuous white fluorescent and monochromatic red or blue light emitting diode (LED) light. Under red LED light, plants developed pale-green, epinastic leaves. Compared with white fluorescent light, red LED light promoted stem elongation 1–3 weeks after sowing but retarded it 3–5 weeks after sowing. Under blue LED light, plants exhibited interveinal necrosis in the leaf blades and excessive stem elongation occurred irrespective of plant age. Leaf yields were lower in plants grown under red and blue LED lights relative to those under white fluorescent light. Blue LED light increased leaf sesamin content by 2.0 and 4.5 times compared with white fluorescent and red LED lights, respectively. From these results, we concluded that blue (LED) light may be effective at producing sesamin-rich leaves if the unfavorable morphological changes and reduction in growth can be prevented.

**Key words:** Blue LED, closed-type plant factory, leaf production, sesame lignan, stem elongation.

Sesame (*Sesamum indicum*) is an important oil seed crop due to its high nutritional value and health benefits. It is cultivated widely in tropical, subtropical, and southern temperate regions, particularly in India, China, South America, and Africa (Anilakumar et al. 2010). Sesamin is a major lignan constituent of sesame seed and one of the key contributors to the beneficial health effects of sesame (Jeng and Hou 2005). We previously reported that sesame leaves also contained sesamin. Therefore they could be used as a new source of sesamin (Hata et al. 2010). Furthermore, continuous light (24-h photoperiod) increased the sesamin content in leaves to 1/200 of that in seeds, while the sesamin content in normally-grown leaves was 1/5,000 or less of seed levels (Hata et al. 2012).

A closed-type plant factory may offer a viable means of sesamin-rich leaf production, because high temperatures and continuous light required for fast growth and increasing sesamin contents, respectively, can be applied all year round. A multi-shelf cultivation system is usually used in closed-type plant factories to enable mass production in a small space. When plants

are grown in a multi-shelf cultivation system equipped with low-intensity illumination, such as fluorescent or light emitting diode (LED) lights, photoperiod must be increased to increase the daily light integral. As long as plants are not negatively affected, continuous light can accelerate plant growth by providing a high daily light integral (Hata et al. 2011a, 2011b, 2011c; Sysoeva et al. 2010). We previously showed that vegetative growth of sesame ‘Gomazou’ was maximized by continuous white fluorescent light without injuries to newly expanding leaves (Hata et al. 2012).

Light wavelengths in the blue, red, and far-red regions affect plant growth through plant photoreceptors, including red and far-red light-absorbing phytochromes and UV-A/blue light-absorbing cryptochromes and phototropins (Chen et al. 2004). In a closed-type plant factory system, light wavelength can be controlled through selection of light sources. Because wavelength also affects plant constituents, many studies have aimed to produce high value-added crops in closed-type plant factories by controlling the light wavelengths (Afreen

Abbreviations: fresh weight, FW; light emitting diode, LED; photosynthetic photon flux density, PPF; specific leaf area, SLA.

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et al. 2005; Brechner et al. 2011; Lefsrud et al. 2008; Matsumoto et al. 2010; Nishimura et al. 2007, 2009; Ohashi-Kaneko et al. 2007). However, plant responses to wavelengths differ among species and cultivars (Goto 2003; Hamamoto et al. 2003), suggesting that the effects of specific wavelengths on crop quality and quantity must be studied for each target species or cultivar. There are few reports on the effects of wavelengths on the growth and/or constituents of sesame, except for studies on elongation (Drumm-Herrel and Mohr 1984) and phototropism (Woitzik and Mohr 1988a, 1988b) of seedling hypocotyls soon after germination.

In this study, we investigated the applicability of controlling light wavelength in production of sesamin-rich leaves in a closed-type plant factory. We compared the growth characteristics and leaf sesamin contents of sesame 'Gomazou' grown under continuous white fluorescent light with those grown under continuous monochromatic light produced by red or blue LEDs. To our knowledge, this is the first report that lignan contents are affected by specific wavelengths of light in intact plants.

## Materials and methods

### *Plant material and light sources*

Seeds of Japanese sesame variety 'Gomazou' were purchased from Ota Seed (Shiga, Japan). This variety was chosen because of its high sesamin content in both leaves and seeds (Hata et al. 2010). Plants were grown in a growth chamber (LHM-2000NC; Nippon Medical and Chemical Instruments, Osaka, Japan) at 28°C. The growth chamber was equipped with both an array of white-light fluorescent tubes (FL40SN; Toshiba, Tokyo, Japan) and LED light panels (300×300 mm) containing blue (470 nm), red (660 nm), and far-red (735 nm) LEDs in a 1:3:1 proportion (IS series; CCS Inc., Kyoto, Japan). Therefore, white fluorescent light, monochromatic and multichromatic LED lights could be used as light sources. Spectral distributions in relative energy of the white fluorescent, red, and blue LED lights are shown in Figure 1. The maximum intensity of monochromatic blue LED light was  $80 \mu\text{mol m}^{-2} \text{s}^{-1}$  photosynthetic photon flux density (PPFD), which was defined to be a standard light intensity in this study.

### *Effects of irradiation of cotyledon-stage seedlings on subsequent shoot growth*

Germinated seeds with emerged radicles which had been incubated on moistened paper towels in the dark for 1 day were sown into 72-cell plug trays filled with Metro-Mix-350 (Sun Gro Horticulture Canada, Vancouver, BC, Canada). The trays were placed under continuous white fluorescent light with  $300 \mu\text{mol m}^{-2} \text{s}^{-1}$  PPFD for a week. Then, cotyledon-stage seedlings in the cell plug trays were grown under continuous white fluorescent, red, and blue LED lights (ca.  $80 \mu\text{mol m}^{-2} \text{s}^{-1}$  PPFD). Light intensity at the plant canopy was maintained by

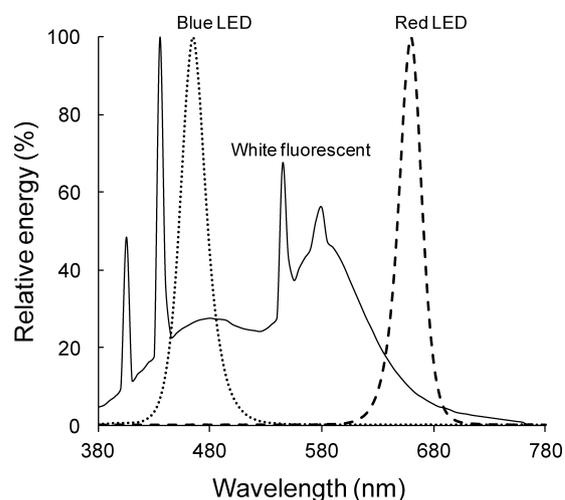


Figure 1. Spectral distributions in relative energy of white fluorescent, red, and blue LED lights.

controlling the height of the light sources during the growing period. The plug trays were subirrigated by immersion in a tray containing half-strength complete nutrient solution (Ohtsuka A-Solution; Ohtsuka Chemical, Osaka, Japan) beginning 1 week after sowing. After light treatment for 2 weeks, 12 uniform seedlings were measured for number of unfolded leaves on the main stem, length of the main stem, fresh weight (FW) of the main stem and whole leaves, and size of the largest leaf (fourth true leaf) as evaluated by leaf blade length and width and petiole length.

### *Effects of irradiation of young plants on subsequent shoot growth and leaf sesamin content*

Plants were grown for 3 weeks after sowing under continuous white fluorescent light ( $300 \mu\text{mol m}^{-2} \text{s}^{-1}$  PPFD) as described above, except where noted. After 3 weeks, 12 uniform seedlings at the eight true-leaf stage were transplanted into plastic pots (9 cm diameter) and divided into three groups of four plants each. Each group was grown under one of the three types of continuous light as described above. The positions of the pots in the chambers were rotated every day to ensure uniform growth.

After light treatment for 2 weeks, numbers of unfolded leaves on the main stem and lengths and fresh weights of the main stems were measured. For all plants, one of the each pair of leaf blades at every nodal position was sampled; fresh weights were measured, and the leaves were frozen in liquid nitrogen and kept at  $-80^\circ\text{C}$  until sesamin analysis. The remaining leaf blades were weighed and used to measure leaf blade area (multiplied by two to obtain total leaf-blade area) using a flatbed scanner and Scion Image software (Scion, Frederick, MD, USA). Individual stem and the leaf samples were then dried completely in an oven at  $60^\circ\text{C}$  to measure dry weight and calculate specific leaf area (SLA).

Analysis of sesamin content in the leaves was conducted as described previously (Hata et al. 2010, 2012). A freeze-dried sample (ca. 50 mg) in a 2-ml Eppendorf tube was

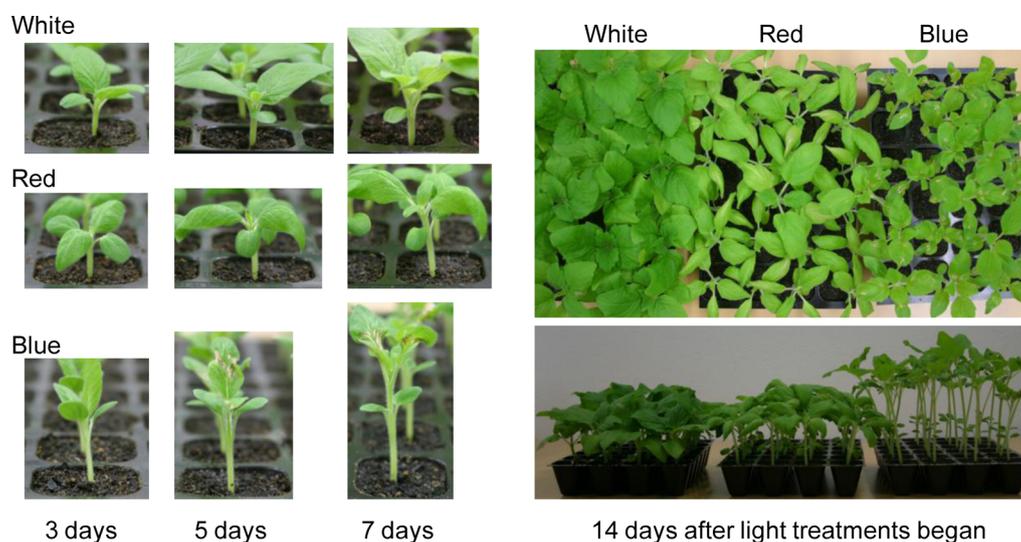


Figure 2. Differences in the growth of sesame seedlings exposed to continuous illumination at different wavelengths from 1–3 weeks after sowing. After sowing, plants were grown for 1 week under continuous white fluorescent light ( $300 \mu\text{mol m}^{-2} \text{s}^{-1}$  PPFD) before light treatments ( $80 \mu\text{mol m}^{-2} \text{s}^{-1}$  PPFD) began.

ground to a fine powder with a vibratory ball mill (MM300; Retsch, Haan, Germany), at a vibration velocity of  $20 \text{ s}^{-1}$  for 1 min, using a zirconia ball (5 mm diameter). Samples were vigorously vortexed for 1 min with 1.2 ml of 100% ethanol, and centrifuged at  $16,100 \times g$  for 5 min. The supernatant was pooled and the residue was re-extracted with 1 ml of 100% ethanol as described. After centrifugation, the combined extracts were filtered through a  $0.2\text{-}\mu\text{m}$  pore-size membrane filter (Advantec Toyo Kaisha, Tokyo, Japan), and 1.5 ml of the solution was evaporated for 4 h using a centrifugal vacuum concentrator (VC-36S; TAITEC, Saitama, Japan).

The residue was dissolved in 0.2 ml of 80% ethanol and analyzed with the ACQUITY UPLC system (Waters, Milford, MA, USA), using a Waters ACQUITY UPLC HSS T3 Column ( $100 \text{ mm} \times 2.1 \text{ mm}$ ,  $1.8 \mu\text{m}$ ). Detection was performed using a Waters 470 Scanning Fluorescence Detector set at an excitation wavelength of 280 nm and an emission wavelength of 340 nm. The mobile phase was distilled water (solvent A) and 100% methanol (solvent B). The gradient elution program, with a mixture of solvents A and B, was as follows: 60–90% B for 0–14.0 min (Waters convex curve No. 5), 90–95% B for 14.0–14.5 min (Waters linear curve No. 6), 95% B for 14.5–16.0 min, 95–60% B for 16.0–16.5 min (Waters convex curve No. 5), and 60% B for 16.5–18.0 min. The flow rate was  $0.25 \text{ ml min}^{-1}$ . The column oven was set at  $40^\circ\text{C}$ , and  $3 \mu\text{l}$  of the sample was loaded. The amount of sesamin was quantified from the peak area of the authentic standard compound ((+)-sesamin (purity  $\geq 95\%$ ) purchased from Cayman Chemical, Ann Arbor, MI, USA) using the external standard method. The resulting chromatograms were analyzed with the Waters Empower 2 software.

## Results

### *Effects of lighting on shoot growth 1 to 3 weeks after sowing*

In a preliminary experiment, aberrant hypocotyl elongation patterns were observed when emerging plants were exposed to red LED light immediately after sowing (Figure S1). In contrast, red LED light did not cause hypocotyl curvature when seedlings were grown to the cotyledon stage under white fluorescent light then transferred to red LED light 1 week after sowing (Figure S2). Therefore, seedlings were grown under white fluorescent light to the cotyledon stage before use in our experiments to ensure normal stem elongation.

Stems of plants grown under red LED light elongated more than those under white fluorescent light (Table 1; Figure 2). Although there was no significant difference between treatments in stem FW, stem length was significantly (1.2 times) longer under the red LED light than that under the white fluorescent light. Leaf epinasty, characterized by the downward curling of laminae near the margin, was observed under red LED light within 3 days from the start of light treatment, and these seedlings developed pale green leaves. The number of unfolded leaves was around six in both treatments, but leaf FW was significantly (1.6 times) higher when the plants were grown under white fluorescent light than those under red LED light. The largest leaf was also significantly larger in the white fluorescent treatment than that in the red LED treatment.

Excessive stem elongation was observed in seedlings grown under blue LED light with significant differences between blue LED and other light treatments (Table 1; Figure 2). Stem lengths in blue LED treatment were 2.5 and 2.0 times longer than those in the white fluorescent

Table 1. Growth of stems and leaves of sesame seedlings grown under continuous illumination at different wavelengths from 1–3 weeks after sowing.

Light source	Main stem		No. of unfolded leaves	Fresh weight of total leaves (g)	Largest leaf (cm)		
	Length (cm)	Fresh weight (g)			Petiole length	Blade length	Blade width
White fluorescent	4.9±0.1 c*	0.5±0.0 b	6.2±0.1 a	1.7±0.0 a	2.3±0.1 a	6.6±0.1 a	4.9±0.1 a
Red LED	6.0±0.1 b	0.5±0.0 b	6.0±0.0 b	1.0±0.0 b	2.0±0.1 b	5.8±0.1 b	2.8±0.2 b
Blue LED	12.1±0.2 a	0.6±0.0 a	6.0±0.0 b	0.5±0.0 c	1.4±0.1 c	4.2±0.1 c	2.7±0.1 c

Newly-sown seeds were grown for 1 week under continuous white fluorescent light ( $300\mu\text{mol m}^{-2}\text{s}^{-1}$  PPFD), then illuminated for 2 weeks at  $80\mu\text{mol m}^{-2}\text{s}^{-1}$  PPFD as indicated. Values are means±standard errors ( $n=12$ ). \*Different letters within a column indicate significant differences among treatments (Tukey's multiple range test,  $p<0.05$ ).

and the red LED treatments, respectively, whereas there was little difference in stem FW among the three treatments. When newly-sown seedlings were grown for 1 week under continuous white fluorescent light at  $80\mu\text{mol m}^{-2}\text{s}^{-1}$  PPFD instead of  $300\mu\text{mol m}^{-2}\text{s}^{-1}$  PPFD before the beginning of the treatments, a similar tendency was observed (Figure S3A). Like the white fluorescent and red LED treatments, the number of unfolded leaves was around six under blue LED light 3 weeks after sowing (Table 1). However, leaf biomass production was significantly suppressed under the blue LED light; the plants exposed to blue LED light produced 74% and 56% less leaf mass compared with those exposed to white fluorescent and red LED light, respectively. The largest leaf under blue LED light was also significantly smaller than those in the other two treatments.

Intervinal necrosis occurred in leaf blades of plants grown under blue LED light 4–5 days after the beginning of treatment (Figure 2). The leaf necrosis was not caused by the stress of transferring the plants from white fluorescent light to blue LED light, because the necrotic lesions occurred even when plants were exposed to blue LED light from the beginning of cultivation (data not shown).

#### Effects of lighting on shoot growth and leaf sesamin content 3–5 weeks after sowing

The effects of specific light exposure on plant growth patterns were mostly independent of the plant ages within the investigation period. Older plants (exposed from 3–5 weeks after sowing) grown under each light treatment grew similarly to plants exposed to the same type of light from 1–3 weeks after sowing. Plants grown under red LED light developed pale-green, epinastic leaves (Figure 3). Under blue LED light, stems elongated excessively, and intervinal necrosis in the leaf blades expanded. Hata et al. (2012) previously reported that sesame plants grown under a long photoperiod of white fluorescent light grew trilobate rather than normally-shaped leaves towards their upper nodal positions. In this experiment, trilobate leaves occurred under both red and blue LED light as well as white fluorescent light.

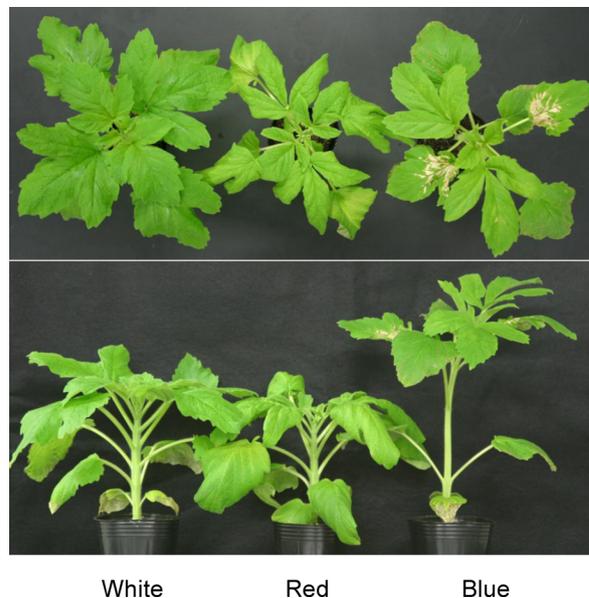


Figure 3. Difference in the growth of sesame plants exposed to continuous illumination at different wavelengths from 3–5 weeks after sowing. After sowing, plants were grown for 3 weeks under continuous white fluorescent light ( $300\mu\text{mol m}^{-2}\text{s}^{-1}$  PPFD) before light treatments ( $80\mu\text{mol m}^{-2}\text{s}^{-1}$  PPFD) began.

There was, however, an age-dependent effect of red LED light on stem growth. When seedlings at the eight true-leaf stage were irradiated by red LED light, stem length was significantly shorter than that under white fluorescent light (Table 2; Figure 3). Stem FW and dry matter ratio under red LED light were also significantly lower than those under white fluorescent light.

Plants under red LED light produced about one leaf fewer than those under white fluorescent light with significant differences between two light treatments. Red LED light also reduced FW, dry matter ratio, and area of leaf blades relative to white fluorescent light significantly. Plants developed thinner leaves under red LED light, as indicated by their higher SLA relative to those of plants grown under white fluorescent light.

Excessive stem elongation under blue LED light resulted in the stems being 1.7 and 2.0 times longer than those under white fluorescent and red LED light, respectively. When seedlings were grown for

Table 2. Growth of stems and leaves of sesame plants grown under continuous illumination at different wavelengths from 3–5 weeks after sowing.

Light source	Main stem			No. of unfolded leaves	Leaf blades			
	Length (cm)	Fresh weight (g)	Dry matter ratio		Fresh weight (g)	Dry matter ratio (%)	Area (cm <sup>2</sup> )	Specific leaf area (cm <sup>2</sup> g <sup>-1</sup> )
White fluorescent	11.7±0.1 b*	4.3±0.1 b	5.8±0.2 a	15.1±0.3 a	13.4±0.4 a	10.5±0.4 a	767±18 a	551±21 b
Red LED	10.0±0.1 c	2.9±0.1 c	4.8±0.2 b	14.1±0.0 b	9.4±0.7 b	8.9±0.1 b	529±16 b	645±8 a
Blue LED	19.6±0.2 a	5.8±0.0 a	4.0±0.1 c	14.1±0.0 b	6.4±0.3 c	11.4±0.2 a	422±20 c	566±10 b

Newly-sown seeds were grown for 3 weeks under continuous white fluorescent light ( $300\mu\text{mol m}^{-2}\text{s}^{-1}$  PPFD), then illuminated for 2 weeks at  $80\mu\text{mol m}^{-2}\text{s}^{-1}$  PPFD as indicated. Values are means±standard errors ( $n=4$ ). \*Different letters within a column indicate significant differences among treatments (Tukey's multiple range test,  $p<0.05$ ).

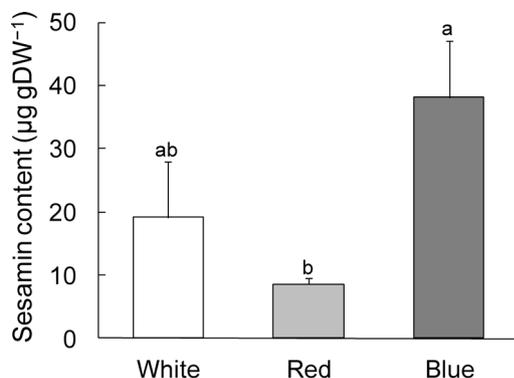


Figure 4. Difference in sesamin content in sesame plants grown under continuous illumination at different wavelengths from 3–5 weeks after sowing. Vertical bars indicate SE ( $n=4$ ). After sowing, plants were grown for 3 weeks under continuous white fluorescent light ( $300\mu\text{mol m}^{-2}\text{s}^{-1}$  PPFD) before light treatments ( $80\mu\text{mol m}^{-2}\text{s}^{-1}$  PPFD) began. Different letters above the bars indicate significant differences among treatments (Tukey's multiple range test,  $p<0.05$ ).

3 weeks under continuous white fluorescent light of  $80\mu\text{mol m}^{-2}\text{s}^{-1}$  PPFD before beginning of the light treatments to determine the effects of varying the light intensity, a similar tendency was observed (Figure S3B). Under blue LED light, stem FW was also the highest, whereas stem dry matter ratio was the lowest, among the treatments (Table 2). These measurements were significantly different between blue LED and other light treatments.

Although the difference in numbers of unfolded leaves was relatively small among the three light treatments, plants exposed to blue LED light produced 52% and 33% less leaf mass compared with those exposed to white fluorescent and red LED light with significant differences. A similar trend was also seen in the leaf blade area with significant differences among the treatments. In contrast, the leaf dry matter ratio and SLA were not significantly different between the white fluorescent and blue LED treatments.

Leaf sesamin content was the highest under blue LED light and the lowest under red LED light (Figure 4). Leaves exposed to blue LED light contained 2.0 and 4.5 times more sesamin than leaves exposed to white fluorescent and red LED light, respectively. Sesamin

content of the leaves grown under blue LED light reached 1/400 of that in seeds ( $15\text{ mg gDW}^{-1}$ , Hata et al. 2010). The difference in leaf sesamin contents was statistically significant between the red and blue LED light treatments using Tukey's multiple range test ( $p<0.05$ ), whereas there was no significant difference between white fluorescent light and each LED light treatment. On the other hand, sesamin content per plant under blue LED light ( $27.5\text{ mg plant}^{-1}$ ) was also higher than that under red LED light ( $7.1\text{ mg plant}^{-1}$ ), but was not different with that under white fluorescent light ( $27.4\text{ mg plant}^{-1}$ ).

## Discussion

We examined the effects of white fluorescent, red LED, and blue LED lights on the growth and sesamin production of sesame seedlings. Red LED light enhanced stem elongation from 1–3 weeks after sowing, but retarded it from 3–5 weeks after sowing (Tables 1, 2, Figures 2, 3, S3). Red LED light appeared to specifically promote stem elongation during early developmental stage (1–3 weeks after sowing), because there was no difference in stem FW under red LED light, although leaf biomass production was poor. However, later in seedling growth (3–5 weeks after sowing), stem FW was significantly lower under red LED light than those under other lights, suggesting that stem elongation was retarded by the poor biomass production, even though red LED light itself had promoting effect of stem elongation. Thus, the contrasting responses of stem elongation to red LED light according to age may have been due to decreased biomass production.

Hirai et al. (2006) reported that blue LED light promoted stem elongation of eggplant and sunflower, whereas it suppressed that of leaf lettuce. In this study, excessive stem elongation under blue LED light was observed regardless of the growing stage (Tables 1, 2, Figures 2, 3, S3). Because stems elongated rapidly even though leaf growth was suppressed, blue LED light probably had a very strong stimulating effect on stem growth in sesame 'Gomazou'. On the contrary, the longitudinal growth rate of sesame 'cf. S.35' hypocotyls

was strongly inhibited by continuous blue light ( $7 \text{ W m}^{-2}$ ) (Drumm-Herrel and Mohr 1984), indicating differences in responses to blue light among cultivars. Hamamoto et al. (2003) similarly found that cultivars of spinach responded differently to far-red LED light in night break treatments. Thus, the optimal wavelengths of light for efficient plant production in a closed-type plant factory should be investigated for each target cultivar or variety.

When the sesame 'Gomazou' plants were grown under a photoperiod longer than 16 h, they continued vegetative growth without floral induction and leaves at the upper nodes changed shape from normal to trilobate (Hata et al. 2012). In this study, trilobate leaves were observed not only under white fluorescent light, but also under red and blue LED lights (Figure 3). Whether leaf heteromorphism was regulated by only photoperiod regardless of a specific wavelength of light is unclear, because the leaf primordia that produced trilobate leaves had probably formed under white fluorescent light before the light treatments from 3 weeks after sowing. However, at least, neither the red nor blue LED light seemed to inhibit the development of trilobate leaves.

Previous studies have shown that continuous light induces injury symptoms characterized by leaf chlorosis and necrosis in some species (Hata et al. 2011a, 2011b; Sysoeva et al. 2010). However, it is still unclear whether a specific wavelength of light is involved in continuous-light-induced injury (Hata et al. 2011c). Sesame 'Gomazou' was previously reported to grow under continuous white fluorescent light without injury to newly-expanding leaves (Hata et al. 2012), and continuous white fluorescent and red LED light treatments did not induce leaf injury in this study (Figures 2, 3). However, interveinal necrosis was observed under continuous blue LED light, suggesting that blue light causes leaf injury and/or that other wavelength(s) present in white fluorescent light prevents leaf injury. Our study may provide the first data that specific wavelength(s) of light are involved in continuous-light injury to plants.

Dry weights of some plants, such as *Glycyrrhiza uralensis* (Afreen et al. 2005), spinach, Japanese mustard spinach (Ohashi-Kaneko et al. 2007), and St. John's wort (Nishimura et al. 2007), were higher under red fluorescent light than under white fluorescent light. In contrast, dry-weight accumulation was significantly lower when the plants were grown under red LED light than under white fluorescent light in wheat (Goins et al. 1997), radish, spinach, and lettuce (Yorio et al. 2001). Our study also demonstrated growth reduction under red LED light compared with white fluorescent light (Tables 1, 2). In various plant species, blue-light supplementation to red LED light has been reported to enhance the growth and/or photosynthetic rates of plants compared with those grown under red LED light alone

(Goins et al. 1997; Hogewoning et al. 2010; Matsuda et al. 2004, 2007; Ohashi-Kaneko et al. 2006; Yorio et al. 2001). Sesame plants also seemed to require blue-light supplementation to red LED light for normal growth.

It should be noted that effects of monochromatic red and blue LED lights might be distinguished with those of multichromatic red and blue fluorescent lights. Red fluorescent light greatly enhanced dry biomass compared with blue fluorescent light in many species including bell pepper (Masuda et al. 2004), *Glycyrrhiza uralensis* (Afreen et al. 2005), leaf lettuce, spinach, Japanese mustard spinach (Ohashi-Kaneko et al. 2007), red perilla (Nishimura et al. 2009), and St. John's wort (Nishimura et al. 2007). However, LED lights had the opposite effects on dry weights of eggplant, leaf lettuce, and sunflower, which tended to be higher under blue than red LED light (Hirai et al. 2006). Furthermore, the growth rates of leaf lettuce under red and blue LED lights were reported to be similar (Matsumoto et al. 2010; Mori and Takatsuji 1999). In our study, the growth of sesame was quite different under red and blue LED lights (Tables 1, 2, Figures 2, 3, S3), but the total dry weight of shoots (stem+petiole+leaf blade) did not differ between the two treatments (data not shown) because of the high dry-matter ratio of leaf blades under blue LED light (Table 2). Therefore, dry matter production did not seem to be inhibited by blue LED light relative to red LED light, in contrast with previous reports comparing the effect of red versus blue fluorescent lights.

The effects of specific wavelengths of light on lignan production in tissue culture experiments appear to differ depending on compounds and/or species studied. The podophyllotoxin content in *Podophyllum peltatum* callus increased compared with a dark control when they were cultured under orange or red fluorescent lights but not when they were cultured under blue or green fluorescent lights (Kadkade 1982). Similarly, contents of eleutheroside E (syringaresinol-4,4'-*O*- $\beta$ -*D*-diglucoside) and eleutheroside E<sub>1</sub> (syringaresinol-4-*O*- $\beta$ -*D*-glucoside) in *Eleutherococcus senticosus* somatic embryos increased under white fluorescent and red LED lights, but blue LED light did not increase the contents of those lignan glucosides compared with the dark condition (Shohael et al. 2006). These results imply that red light induces the production of some lignans, but blue light does not. However, Morimoto et al. (2011) recently reported that both red and blue LED light similarly increased the contents of pionesinol glucosides in cell cultures derived from *Forsythia koreana* as compared with the dark control, although the effects of the LED lights were less than that of white fluorescent light. In this study, sesame leaves exposed to blue LED light contained substantially more sesamin than leaves exposed to either white fluorescent or red LED light (Figure 4). These results suggest that both red and blue

light induce production of some lignans, and blue light may enhance lignan production more than red light, at least with respect to sesamin. The effects of different ratios of red to blue LED light on leaf sesamin content need to be investigated further, because sesamin content ( $\text{mg plant}^{-1}$ ) cannot be increased under blue LED light alone due to poor plant growth even if sesamin content ( $\text{mg DW}^{-1}$ ) is increased.

There have been many reports that abiotic and biotic stresses altered the biosynthesis of phenylpropanoid compounds including lignin (Dixon and Paiva 1995; Moura et al. 2010). If the biosynthesis of sesamin, one of phenylpropanoid compounds, is also affected by stress exposure, blue LED light might increase leaf sesamin content as some kind of stress inducer represented by occurrence of leaf injury (Figure 3). As shown that the contents of medicinal substances in many plants are increased by ultraviolet radiation (Zhang and Björn 2009), application of ultraviolet light is also expected for increasing the sesamin content via stress response.

In conclusion, monochromatic red and blue LED lights are not adequate for cultivation of sesame 'Gomazou' plants, because they induce unfavorable morphological changes and reduce growth relative to white fluorescent light. However, blue LED light increased leaf sesamin content and may prove useful for producing sesamin-rich leaves if the negative effects can be mitigated.

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White (control)

Red

Figure S1. Aberrant hypocotyl elongation observed in 3-day-old sesame seedlings grown under continuous illumination with white fluorescent (left) versus red LED (right) light.



Figure S2. Normal hypocotyl elongation under red LED light. Seedlings were grown under continuous white fluorescent light for 7 days after sowing then exposed to continuous red LED light for 5 days.

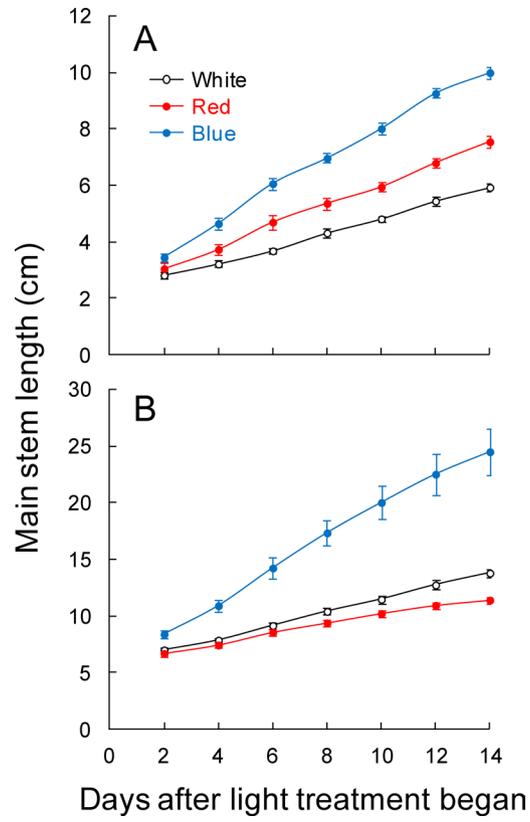


Figure S3. Differences in stem elongation of sesame grown under continuous illumination at different wavelengths for 2 weeks. Vertical bars indicate SE ( $n=6$ ). Plants were grown for 1 week (A) and 3 weeks (B) after sowing under continuous white fluorescent light ( $80 \mu\text{mol m}^{-2} \text{s}^{-1}$  PPFD) before light treatments ( $80 \mu\text{mol m}^{-2} \text{s}^{-1}$  PPFD) began.