# Original article



# Influence of light quality on flowering characteristics, potential for year-round fruit production and fruit quality of blueberry in a plant factory

H.Y. Cho<sup>1</sup>, M. Kadowaki<sup>2</sup>, J. Che<sup>3</sup>, S. Takahashi<sup>1</sup>, N. Horiuchi<sup>3</sup> and I. Ogiwara<sup>1,2,3,a</sup>

- <sup>1</sup> United Graduate School of Agricultural Science, Tokyo University of Agriculture and Technology, Fuchu 183-8509, Japan
- <sup>2</sup> Graduate School of Agriculture, Tokyo University of Agriculture and Technology, Fuchu 183-8509, Japan
- <sup>3</sup> Faculty of Agriculture, Tokyo University of Agriculture and Technology, Fuchu 183-8509, Japan

# Summary

Introduction - Blueberry harvest season is only from June to September in Japan. Developing new cultivation methods for year-round blueberry production is desired to reduce off-season blueberry imports at a high price. Consulting with previous studies about influences of environmental factors on plants, the current study was carried out to investigate flowering characteristics, plant morphology, and potential for year-round high quality blueberry production under different light quality in a plant factory. Materials and methods - Blueberry plants cvs. 'Misty' and 'Sharpblue' were grown in light emitting diodes (LED) chambers installed with LED of 100% blue (459 nm), 100% red (631 nm), a mixture of 1:1 = red:blue light (a mixture of LED lights). Fluorescent light was used as control. Results and discussion - Cumulative flower number was maximum in 'Misty' under blue LED light and in 'Sharpblue' under a mixture of LED lights. In 'Sharpblue', red LED light encouraged vegetative growth, and plants under blue light were delayed in growth with cessation of shoot elongation. However, a mixture of LED lights and fluorescent ones showed desirable vegetative growth and high potential for continuous flowering. In terms of fruit quality, higher soluble solid content (SSC) and less titratable acidity (TA) were found in fruits under blue LED light and a mixture of LED lights. Bigger fruits were found in plants under a mixture of LED lights and control but comparatively less SSC was found under control. Conclusion - Light quality has been shown to have a strong influence on flowering characteristics, plant morphology, and year-round high quality blueberry production in a plant factory.

#### Keywords

blueberry, *Vaccinium corymbosum*, flower development, light quality, plant growth, controlled environment

#### Introduction

Blueberry belongs to family *Ericaceae*, genus *Vaccinium* and it has approximately 400 species (Vander Kloet, 1988). Among fruits, blueberries are considered to be rich in phenolic compounds and aware due to its high antioxidant activity scores, flavor, color and nutritional properties (Diaconeasa

# Significance of this study

What is already known on this subject?

- Japanese farmers can extend blueberry harvest season using artificial heating system after dormancy in plastic houses, what enables harvest season from late March (generally it starts from June).
- It has been possible to harvest blueberry two times a year by accelerating plant life cycle under fluorescent light in TUAT plant factory.

What are the new findings?

- Light quality influenced plant morphology, flowering characteristics, fruit quality and potential for continuous flowering.
- Under a mixture of LED lights, plants flowered early, maximum, and high potential for year-round production, produced bigger fruits with higher soluble solid content and lower acidity compared to other lights.

What is the expected impact on horticulture?

• This morphological screening will contribute to further studies at molecular level for stable blueberry year-round production in plant factories.

et al., 2015; Giacalone et al., 2015; Zafra-Stone et al., 2007).

The origin of blueberry is the United States of America (Leisner et al., 2017) and blueberry was introduced into Japan in 1951 (Tamada, 2006). There are many benefits of blueberry for human health (Giacalone et al., 2015) and therefore, Japanese consumers' demand on blueberry has also increased year by year. In 1996, due to increased demand on blueberry, production area and local production increased but the amount of import also increased and it was over 50% of domestic production (Trade Statistics of Japan, 2015). Domestic production did not meet Japan market demand because the harvest season of blueberry fruit in Japan takes only for around 4 months (only from June to September) in the open-field production and Japan needs to import tons of fresh and frozen blueberry, especially during off-season, at a high price. Therefore, Japanese farmers tried to extend the blueberry harvest period using artificial heating systems in plastic houses, which enabled the blueberry harvest to start from late March (Higashide et al., 2006; Tokyo metropolitan wholesale market, 2018). However, year-round production of blueberry fruit, including the off-season (October to March), is still desired in Japan. Therefore, this current



<sup>&</sup>lt;sup>a</sup> Corresponding author: ogiwara@cc.tuat.ac.jp.

study was conducted to develop new cultivation methods for year-round blueberry production in Japan.

Plant factories have great potential for hyper-yield, superior product quality, off-season production, shorter production period and so on. Therefore, the current study was conducted in an environmental control room of a plant factory of Tokyo University of Agriculture and Technology (TUAT) using light emitting diodes (LED) equipped chambers. The TUAT plant factory has six environmental control rooms which simulate the four seasons of Japan, mainly focusing on blueberry year-round production (Ogiwara and Arie, 2010).

Previous studies discovered that light plays important roles in not only plant morphogenesis process, but also photosynthesis process (Long et al., 2015; Yamori, 2013; Yamori and Shikanai, 2016; Yamori et al., 2016; Zhu et al., 2010). Especially, plant factories mostly rely on artificial light for plant growth and development and fluorescent lamps have been used since long time ago. Nowadays, LED has become very popular in modern horticulture due to its abundant beneficial properties of energy saving, convenience of use, easy control of light spectrum - with narrow and specific wavebands - intensity and photoperiod, that all have direct influential effects on plant physiology, flowering characteristics and photomorphogenesis (Demotes-Mainard et al., 2016; Fan et al., 2013; Folta and Carvalho, 2015; Lin et al., 2013; Singh et al., 2015). For example, red spectrum decreased flower numbers and delayed flowering in 'Strawberry' (Takeda et al., 2008); or phytochromes (phy) encouraged vegetative growth in Indian mustard and other five cultivars of basil (Tarakanov et al., 2012; Endo et al., 2013). In contrast, some researchers mentioned the influence of blue light on reproductive phase: blue LED light promoted flowering in strawberry (Yoshida et al., 2012); in petunia in closed-type environment (Fukuda et al., 2011); controlled flowering and bud outgrowth (Huché-Thélier et al., 2016). Moreover, previous findings pointed that blue light inhibited stem extension in Brassicaceae (Kigel and Cosgrove, 1991; Liscum et al., 1992), produced smaller leaves in salvia 'vista red' than those under red light spectrum and other combinations of lights (Runkle, 2017), smallest stem diameter and least net photosynthetic rate in tomato seedlings (Yang et al., 2018). However, there is little information about a combination of blue and red light effects on flowering in blueberry under control environment.

Although information is limited about blueberry year-round production in plant factories from other parts of japan or other places, some information was obtained from previous experiments of TUAT plant factory. Horiuchi *et al.* (2013) and Ogiwara *et al.* (2012) reported that blueberry harvesting two times in one year is possible by accelerating plants' life cycle in controlled rooms with artificial lighting systems in TUAT plant factory. Furthermore, Thanda *et al.* (2014) has also pointed that blueberry plants grown under artificial light in the TUAT plant factory could produce high quality fruits which are bigger, with higher SSC and lower TA compared to plants under natural sunlight. However, it is still desired to develop new cultivation methods for blueberry year-round production using different light quality.

The previous studies mentioned above suggested that artificial light and other environmental factors had influential effects on plant morphology, flowering phenomenon and fruit quality in plants. Also, the previous TUAT plant factory experiments pointed that fluorescent light and temperature control influenced on flowering and plant life cycle, enabling to harvest twice a year with high quality in some blueberry cultivars. However, the influence of a specific light spectrum

on plant morphology, flowering phenomenon and its fruit quality in blueberry in the plant factory has not been well understood. Therefore, this current study was carried out based on the current need of Japan blueberry production and aim of this research was to investigate the flowering characteristics, plant morphology, fruit quality and potential for year-round production in response to different light quality by using LED and fluorescent light in TUAT plant factory.

# Materials and methods

#### Plant material

Two cultivars of 3-year-old blueberry plants were used in the experiments: 'Misty' and 'Sharpblue'. Both are southern highbush blueberry (*Vaccinium corymbosum*) commercial hybrids presenting very low chill requirements.

#### **Environmental conditions**

In this study, two experiments were carried out from 2014 to 2016. Experiment 1 was performed from 17.6.2014 to 10.10.2014. In Experiment 2, the first part was carried out from May 12th 2016 to July 6th 2016 for 55 days and the second part was carried out from July 7th to December 19th for 165 days. The light intensity was set  $380 \pm 10 \,\mu\text{mol m}^{-2}\,\text{s}^{-1}$ for Experiment 1 and 300 ± 10 μmol m<sup>-2</sup> s<sup>-1</sup> for Experiment 2 at the top of plant canopies in each treatment section (MIJ-14PAR Type 2; Environmental Measurement Japan Co. Ltd., Fukuoka, Japan). The mixture of peat moss and Kanuma soil was used as a soil medium and automated drip irrigation and nutrient fertigation system was applied (Otsuka AgriTechno Co. Ltd., Tokyo, Japan) directly to plants root zone about 250 mL per pot twice a day. pH range was adjusted between 4.0 and 4.5 with the help of pH reducing solution containing phosphate (P<sub>2</sub>O<sub>4</sub>-) (Otsuka Agri Techno Co. Ltd., Tokyo, Japan). Electric conductance (EC) was controlled from 0.8 to 1.0 dS m<sup>-1</sup>. For better pollination, black bumblebees were performed.

#### **Experiment 1**

In Experiment 1, 'Misty' 3-year-old plants were moved from open field to an environmental controlled room and grown in LED chambers with different light quality: 100% Red spectrum (631 nm); 100% Blue spectrum (459 nm); and fluorescent light (FHF 32 EX-N-H, Panasonic) as the control. The experimental room was set at 28 °C in daytime and 18 °C at night, 40 to 80% relative humidity and about 480 ppm  $CO_2$ . Key research parameters were flowering time and number of flowers in plants in response to different light wavelengths. The flowering time were examined and number of flowers were counted at 45, 60, 75, 90 and 110 days after treatment (DAT). When the flower petals were completely opened and before the color of petals changed from white into brown color, the number of flowers was counted. The counted flowers were marked with marker pen to avoid repeated data collection.

#### **Experiment 2**

Experiment 2 was divided into two steps. In the first step, the 3-year-old 'Sharpblue' plants were brought into plant factory and grown under blue LED light alone from  $12^{\rm th}$  May 2016 until flower bud differentiation. The experimental room was set with 14 hours photoperiod, 25 °C in daytime and 14 °C at night, 40 to 80% relative humidity and about 480 ppm  $\rm CO_2$ . When flower bud differentiation started at 55

DAT, the second step of Experiment 2 was continued under 10 hours photoperiod and 18–22 °C day/5–8 °C night provided room. The experimental pots with 5 replicates were placed in 3 chambers installed with LED lamps of 100% red LED light (631 nm), 100% blue LED light (459 nm), or a mixture of 50% red and 50% blue LED light (456 nm). Fluorescent lamps were applied as the control. Flowering time, flower numbers, plant morphology, potential for continuous flowering and fruit quality responses to different light quality were investigated. Flowering data were collected as in Experiment 1.

As part of fruit quality parameters, fruit weight, diameter, size and firmness, and soluble solid content (SSC) and titratable acidity (TA) of fresh fruit juice (in °Brix and in %, respectively) were analyzed. Fully ripe blueberry fruit, as judged by fully blue color at the pedicel end, were harvested randomly from each treatment and fruit weight (in g) and diameter (in mm) were measured. Fruit firmness was measured with a rheometer (RT-3005 D; Rheotech Co. Ltd., Tokyo, Japan). The fruits were placed perpendicularly on the table of the machine and the probe was applied to the fruits. The force to penetrate (with 2 mm  $\Phi$ ) the fruit was measured as fruit firmness in kilogram force (kgf). The juice was analyzed by titrating with 0.01 N NaOH. The TA was expressed in % as g citric acid 100 mL<sup>-1</sup> juice. For SSC analysis, five randomly harvested fully ripe fruits from each plant were ground and 1 g fruit pulp was diluted and homogenized with 3 mL distilled water. The diluted fruit juice was centrifuged at 13,000 rpm for 10 min and SSC was measured using a digital refractometer (model PR101; Atago Co. Ltd., Tokyo, Japan) standardized with distilled water. The Brix value was multiplied by 4 to the obtained value. Three replications were conducted for SSC, TA and SSC:TA ratio.

Plant morphology and continuous flowering were also examined at 165 DAT by checking new shoots, leaves, flowers, immature and mature fruits in 'Sharpblue' plants under different light wavelengths.

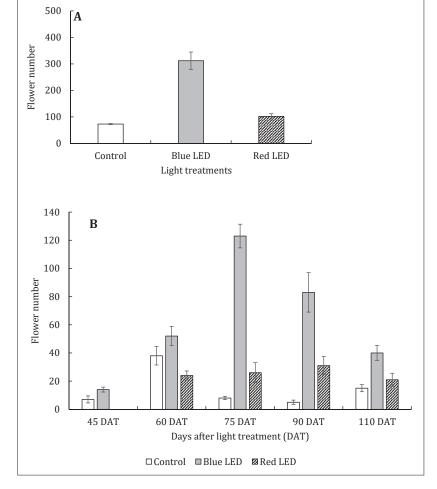
#### Statistical analysis

Plant morphological characteristics and fruit quality data in response to different light wavelengths were statistically analyzed by the Tukey Kramer's test at P=0.05 level after one-way ANOVA in Excel.

# Results and discussion

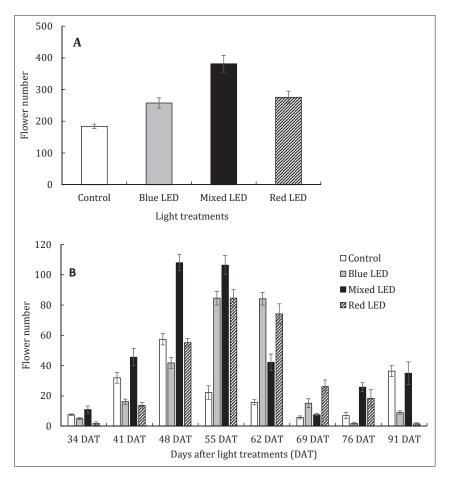
#### Flowering time and number of flowers

The flowering delayed most in plants grown under red LED light, starting from 60 DAT (Figure 1). In contrast, the flowering time was earliest in plants under blue LED light, showing the first flowering date started at 45 DAT and it was followed by that of the plants under control. Flowering period in three treatments was for 110 days. Similarly in Experiment 2, flowing in 'Sharpblue' delayed most under red LED light but plants flowered the earliest in plants under a mixture of LED lights and it was followed by that of the plants under control and blue LED light (Figure 2). Therefore, it can be assumed that red light delayed flowering in both 'Misty' and 'Sharpblue'. In addition, blue LED light encouraged early flowering most in 'Misty' (Experiment 1), and flowering time was promoted more when blue light combined with red light.



**FIGURE 1.** (A) Mean total number of flowers; (B) mean number of flowers with time in response to light treatments in the blueberry 'Misty' (*n*=3). The 3-year-old 'Misty' plants without flower bud differentiation were irradiated with different light wavelengths: 100% red spectrum (631 nm), 100% blue spectrum (459 nm), and fluorescent light (FHF 32 EX-N-H, Panasonic) as control. DAT: Days after treatment.





**FIGURE 2.** (A) Mean total number of flowers; (B) Mean number of flowers with time in response to light treatments at the same light intensity and photoperiod under controlled room (n=5). The 3-year-old blueberry 'Sharpblue' plants with flower bud differentiation after irradiation with blue light alone were grown under different lights: Fluorescent light (Control); 100% blue light; a mixture of 50% red and 50% blue LED lights; and 100% red light. DAT: Days after treatment.

Such synergic effect influenced flowering time, resulting in earliest among treatments in 'Sharpblue' (Experiment 2).

The total flower number of 'Misty' plants at 110 DAT was highest under blue light (almost 300 flowers), followed by the plants under red LED light (102 flowers) and the control (73 flowers) (Figure 1). The total flower number at 91 DAT was highest in 'Sharpblue' under a mixture of LED lights (382 flowers), followed by the plants under red LED light (276 flowers), blue LED light (259 flowers), and the control (184 flowers) (Figure 2).

Previous studies have reported that floral induction and flowering were late under red LED light across a range of species in both long-day (LD) and short-day (SD) plants because *phyB* inhibited in floral induction in both LD and SD plants (Childs *et al.*, 1997; Goto *et al.*, 1991; Lin, 2000; Mockler *et al.*, 1999; Takeda *et al.*, 2008; Tarakanov *et al.*, 2012; Weller and Reid, 1993). The current study agrees with these findings and shows delayed flowering time in both 'Misty' and 'Sharpblue', with a comparatively lower number of flowers under red LED light (Figures 1 and 2). A reason could be that the *phyB* inhibited flowering in both 'Misty' and 'Sharpblue' under red light.

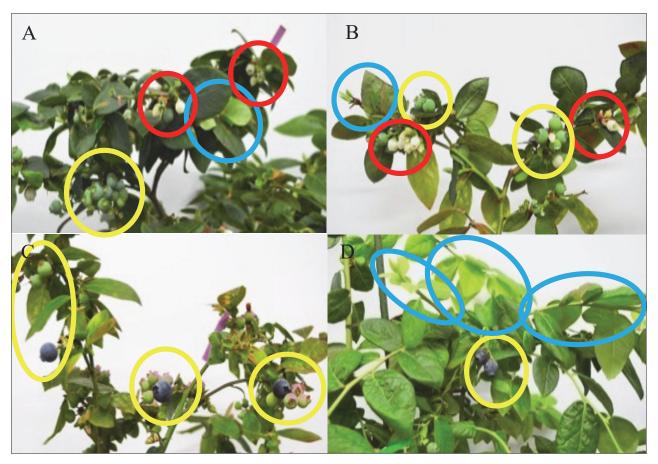
In contrast, flowering time was earlier and total flowers was highest under blue LED light in 'Misty' (Experiment 1). It has been reported that blue light promoted flowering in ever-bearing strawberry compared to that of the plants treated with red LED light (Yoshida *et al.*, 2012); in *Arabidopsis thaliana*, indicating that blue light inhibited *phyB* action and promoted flowering in *Arabidopsis* (Eskins, 1992; Guo *et al.*, 1998; Mockler *et al.*, 1999). It can also be assumed that the cryptochrome (*cry*) promoted flowering and encouraged early flowering in 'Misty' blueberry, like in strawberry and *Arabidopsis thaliana* from previous findings.

It is still unclear whether flowering was regulated by *cry1* or *cry2* in the present study, until further investigations are performed at molecular level for photoreceptor mechanisms under different light wavelengths.

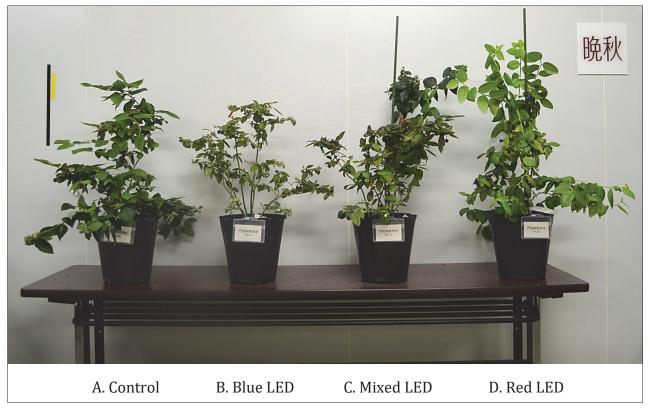
Blue light alone encouraged flowering and it was found that both flowering time and number of flowers in 'Sharpblue' were promoted more when red light combined with blue light and the greatest cumulative flower number was observed under a mixture of LED lights. It might be assumed that a mixture of LED lights provided positive synergic promotion effects on floral induction and flowering compared to irradiation with red LED light or blue LED light in this current study. The current study is in agreement with Stutte *et al.* (2009) and Yorio *et al.* (2001), who reported that a mixture of blue and red lights had more powerful effects on plant growth, biomass and development due to higher absorption of chlorophyll *a* and *b*.

# Plant growth and potential for continuous flowering in response to different light qualities

Plants under red LED light were observed with bigger leaves, greater number of leaves and overgrowth in vegetative parts but few fruits and flower (Figures 3 and 4). Similarly, Experiment 2 revealed that plant canopy was bigger under red LED light and it may be due to the fact that axillary buds differentiated into vegetative buds and *phy* encouraged vegetative phase. Tarakanov *et al.* (2012) and Endo *et al.* (2013) also provided similar proof that vegetative growth was promoted by red spectrum in Indian mustard and other five cultivars of basil, and the reason was that the *phy* encouraged vegetative phase. Yoshida *et al.* (2016) also reported that number of leaves under red light was greater than those under blue light and red to blue light. Yanagi *et al.* (1996) also report-



**FIGURE 3.** Plant morphological characteristics of blueberry 'Sharpblue' in response to different light treatments: A. Fluorescent light (control); B. Mixed LED lights (50% red + 50% blue); C. Blue LED light; D. Red LED light. Yellow circles represent immature and mature fruits; blue circles represent new shoots and young leaves; red circles represent flowers and immature fruit.



**FIGURE 4.** Blueberry 'Sharpblue' plant shape at 165 days after treatment (DAT) under different light treatments: A. Fluorescent light (control); B. Mixed LED lights (50% red + 50% blue); C. Blue LED light; D. Red LED light. Scale bar = 30 cm.



ed that lettuce plants grown under red LED alone had more leaves and longer stems than plants grown under blue LED.

In contrast, plant vigor was very weak under blue LED light, with very small leaves and new axillary buds not developed and undifferentiated. Past findings pointed that that blue light inhibited stem extension in Brassicaceae (Kigel and Cosgrove, 1991), and in red leaf lettuce (Johkan  $et\ al.$ , 2010). Runkle (2017) informed that plants under 100% blue light produced smaller leaves in salvia 'vista red' than those under red light spectrum and other combinations of lights. Yang  $et\ al.$  (2018) also provided the information about the effects of blue light on morphogenesis and photosynthetic pigment content in tomato seedlings, showing smallest stem diameter and least net-photosynthetic rate, less accumulation efficiency of chlorophyll a and b than those under red LED light and a mixture of red and blue LED.

Plants under a mixture of LED lights and control were observed with new shoots, healthy leaves, mature fruits, immature fruits, and flowers, which are positive results for continuous flowering year-round. Under mixed LED lights, the apical buds differentiated into flower buds because blue light enhances reproductive phase and desirable plant shapes were also observed because red LED light encouraged vegetative growth.

Finally, at 165 DAT, the potential for continuous flowering was examined and it was found that plants had high potential for continuous flowering under control and a mixture of LED lights (Figure 3) because plants had new shoots, young leaves, immature fruit, mature fruit and flowers. However, potential for continuous flowering was very low in plants under blue light which had no new shoot and flower, and under red LED light which had overgrowth and flowering almost stopped (Figures 2 and 3). Therefore, it can be assumed from this experiment that continuous irradiation with monochromatic light did not favor continuous flowering in 'Sharpblue' plants. However, flowers, new shoots, young leaves, immature and mature fruits were observed in plants under control (fluorescent light) and a mixture of LED lights, showing positive results for continuous flowering.

# Fruit quality responses to different light quality

Fruit size under a mixture of LED lights and control was significantly bigger than that of the plants under red LED light and blue LED light (Table 1). It might be due to the strong influence of a combination of LED light wavelengths on growth of crops than monochromatic wavelength, agreeing with past findings (Duong *et al.*, 2003; Stutte *et al.*, 2009; Yorio *et al.*, 2001). In addition, the total chlorophyll amount was greater under both red LED alone and a combination of

red and blue LED light whereas blue light had comparatively less efficiency to accumulate chlorophylls. Thus, fruit yield was lowest. This study was conducted by Choi *et al.* (2015). Yang *et al.* (2018) also provided the message that fruit size was smallest and yield was lowest under blue LED among treatments and control. This current study agreed with Choi *et al.* (2015) and Yang *et al.* (2018), although the total yield was not investigated.

Fruit firmness value was higher in plants under blue LED light and control compared to that of the plants under a mixture of LEDs and red LED light, respectively. Fruits in plants under blue LED light and a mixture of LED lights had significantly higher SSC than that of the fruits under control and red LED light: highest SSC in fruits under a mixture of LED lights and lowest under red LED light. Fruits under red LED light had the highest TA and it was followed by that of the fruits under a mixture of LED lights, blue LED light and control, respectively. The sugar acid ratio was the highest in the control group, followed by a mixture of LED lights group, the blue light group, and red light group, respectively.

Previous findings indicated that blue LED light increased the total sugar content in strawberry (Xu *et al.*, 2014) and sugar and starch in *in vitro* growth of grape "Teleki 5BB' (Heo *et al.*, 2006), their results were in agreement with our current study, indicating that blue light increased SSC in blueberry. However, the information about the influence of red LED light and a mixture of LED lights on acidity in fruits was limited. In this experiment, a mixture of LED lights increased SSC although red LED light decreased SSC most. According to Beaudry (1992), high-quality blueberry fruit should have SSC > 10 °Brix and TA between 0.3 and 1.3%. In this study, SSC was higher than 12 °Brix and TA was less than 1.3%, meaning that fruit tasted sweet and fruit quality was high under all treatments, including the control.

### Conclusion

Plants irradiated with a mixture of LED lights produced larger size fruits with higher SSC, lower TA and the balance of the sugar: acid ratio in fruit was good whereas small fruits with low SSC and high TA were observed in plants under red LED light. The plants under blue LED light produced the smallest size fruits among treatments although sugar content in fruit was high. However, fruits under control had lowest SSC and TA, resulting in flat taste fruit although the fruit size was big. This study provides some important information to develop stable blueberry year-round fruit production methods and high-quality blueberry production in Japan using LED technology in TUAT plant factory.

**TABLE 1.** Fruit characteristics of 'Sharpblue' blueberry in response to different light treatments in TUAT closed-type plant factory. Data are mean values (n = 3). FL: Fluorescent light; LED: Light emitting diodes; SSC: Soluble solid content; TA: Titratable acidity.

	Fruit quality traits					
Treatments	Weight	Size	Fruit firmness	SSC	TA	Sugar:acid
	(g)	(mm)	(kgf)	(° Brix)	(%)	ratio
Control (FL)	2.2 a <sup>z</sup>	11.0 a	0.1670 a	12.7 b	0.30 b	42.3
Blue LED	1.6 b	9.7 b	0.1686 a	14.1 a	0.56 ab	25.2
Mixed LED light	2.1 a	11.2 a	0.1593 b	14.2 a	0.44 ab	32.3
Red LED	1.8 b	10.5 a	0.1537 b	12.8 b	0.65 a	19.7

<sup>&</sup>lt;sup>z</sup> Values within the same column followed by different letters are significantly different at *P*=0.05 level using Tukey Kramer's test after one-way ANOVA in Excel.

Experiments 1 and 2 revealed that it is possible to accelerate plant life cycle in 'Misty' and 'Sharpblue' blueberries under different light quality in an environmental controlled room. Although blue LED light encouraged reproductive phase in both 'Misty' and 'Sharpblue', it did not encourage plant growth after about seven months constant blue light irradiation. In contrast, red LED light delayed flowering in both cultivars and reduced flower number but overgrowth in 'Misty'. However, it is assumed that adding blue light to red light could be more effective for early flowering, great flower number, big fruit with high SSC and low TA, desired plant growth and potential for continuous flowering.

Finally, this study confirmed that it is possible to produce high quality blueberry year-round under a mixture of LED lights in facilities like TUAT plant factory. Further studies are recommended to investigate at molecular level photoreceptors and plant interactions under different light wavelengths.

## References

Beaudry, R. (1992). Blueberry quality characteristics and how they can be optimized. In Annual Report of the Michigan State Horticultural Society (122<sup>nd</sup>) (Morrice, MI, USA: Michigan State Horticultural Society), p. 140–145.

Childs, K.L., Miller, F.R., Cordonnier-Pratt, M.M., Pratt, L.H., Morgan, P.W., and Mullet, J.E. (1997). The sorghum photoperiod sensitivity gene, *Ma3*, encodes a phytochrome B. Plant Physiol. *113*, 611–619. https://doi.org/10.1104/pp.113.2.611.

Choi, H.G., Moon, B.Y., and Kang, N.J. (2015). Effects of LED light on the production of strawberry during cultivation in a plastic greenhouse and in a growth chamber. Sci. Hortic. *189*, 22–31. https://doi.org/10.1016/j.scienta.2015.03.022.

Demotes-Mainard, S., Péron, T., Corot, A., Bertheloot, J., Le Gourrierec, J., Pelleschi-Travier, S., Crespel, L., Morel, P., Huché-Thélier, L., Boumaza, R., Vian, A., Guérin, V., Leduc, N., and Sakr, S. (2016). Plant responses to red and far-red lights, applications in horticulture. Environ. Exp. Bot. 121, 4–21. https://doi.org/10.1016/j.envexpbot.2015.05.010.

Diaconeasa, Z., Leopold, L., Rugină, D., Ayvaz, H., and Socaciu, C. (2015). Antiproliferative and antioxidant properties of anthocyanin rich extracts from blueberry and blackcurrant juice. Int. J. Mol. Sci. 16, 2352–2365. https://doi.org/10.3390/ijms16022352.

Duong, T.N., Takamura, T., Watanabe, H., Okamoto, K., and Tanaka, M. (2003). Responses of strawberry plantlets cultured in vitro under super bright red and blue light-emitting diodes (LEDs). Plant Cell Tissue Organ Cult. *73*, 43–52. https://doi.org/10.1023/A:1022638508007.

Endo, M., Tanigawa, Y., Murakami, T., Araki, T., and Nagatani, A. (2013). Phytochrome-dependent late-flowering accelerates flowering through physical interactions with phytochrome B and CONSTANS. Proc Natl. Acad. Sci. USA *110*(44), 18017–18022. https://doi.org/10.1073/pnas.1310631110.

Eskins, K. (1992). Light-quality effects on *Arabidopsis* development. Red, blue and far-red regulation of flowering and morphology. Physiol Plant 86, 439-444. https://doi.org/10.1111/j.1399-3054.1992. tb01341.x.

Fan, X.-X., Xu, Z.-G., Liu, X.-Y., Tang, C.-M., Wang, L.-W., and Han, X. (2013). Effects of light intensity on the growth and leaf development of young tomato plants grown under a combination of red and blue light. Sci. Hortic. *153*, 50–55. https://doi.org/10.1016/j.scienta.2013.01.017.

Folta, K.M., and Carvalho, S.D. (2015). Photoreceptors and control of horticultural plant traits. HortScience *50*, 1274–1280.

Fukuda, N., Ishii, Y., Ezura, H., and Olsen, J.E. (2011). Effect of light quality under red and blue light emitting diodes on growth and expression of FBP28 in petunia. Acta Hortic. *907*, 361–366. https://doi.org/10.17660/ActaHortic.2011.907.59.

Giacalone, M., di Sacco, F., Traupe, I., Pagnucci, N., Forfori, F., and Giunta, F. (2015). Blueberry polyphenols and neuroprotection. In Bioactive Nutraceuticals and Dietary Supplements in Neurological and Brain Disease, R.R.W.R. Preedy, ed. (San Diego, CA, USA: Academic Press), p. 17–28. https://doi.org/10.1016/B978-0-12-411462-3.00002-3.

Goto, N., Kumagai, T., and Koornneef, M. (1991). Flowering responses to light-breaks in photomorphogenic mutants of *Arabidopsis thaliana*, a long-day plant. Physiol. Plant. *83*, 209–215. https://doi.org/10.1111/j.1399-3054.1991.tb02144.x.

Guo, H., Yang, H., Mockler, T.C., and Lin, C. (1998). Regulation of flowering time by *Arabidopsis* photoreceptors. Science *279*(5355), 1360–1363. https://doi.org/10.1126/science.279.5355.1360.

Heo, S.J., Cha, S.H., Lee, K.W., and Jeon, Y.J. (2006). Antioxidant activities of red algae from Jeju Island. Korean Soc. Phycol. *21*, 149–156. https://doi.org/10.4490/ALGAE.2006.21.1.149.

Higashide, T., Aoki, N., Kinoshita, T., Ibuki, T., and Kasahara, Y. (2006). Forcing culture of blueberry grown in a container using a hydroponics system suitable for use in hilly and mountainous areas. Hort. Res. (Japan) *5*(3), 303–308. https://doi.org/10.2503/hri.5.303.

Horiuchi, N., Sya, K., Thanda Aung, Mayumi, Y., and Ogiwara, I. (2013). Flowering and shoot growth responses of blueberry grown under different day-lengths and temperatures after harvest. J. Hortic. Sci. 12(1), 43.

Huché-Thélier, L., Crespel, L., Le Gourrierec, J., Morel, P., Sakr, S., and Leduc, N. (2016). Light signaling and plant responses to blue and UV radiations – Perspectives for applications in horticulture. Environ. Exp. Bot. 121, 22–38. https://doi.org/10.1016/j.envexpbot.2015.06.009.

Johkan, M., Shoji, K., Goto, F., Hashida, S., and Yoshihara, T. (2010). Blue light-emitting diode light irradiation of seedlings improves seedling quality and growth after transplanting in red leaf lettuce. HortScience 45, 1809–1814.

Kigel, J., and Cosgrove, D.J. (1991). Photo inhibition of stem elongation by blue and red light. Plant Physiol. *95*, 1049–1056. https://doi.org/10.1104/pp.95.4.1049.

Leisner, C.P., Kamileen, M.O., Conway, M.E., O'Connor, S.E., and Buell, C.R. (2017). Differential iridoid production as revealed by a diversity panel of 84 cultivated and wild blueberry species. PLoS ONE *12*(6), e0179417. https://doi.org/10.1371/journal.pone.0179417.

Lin, C. (2000). Photoreceptors and regulation of flowering time. Plant Physiol. 123, 39–50. https://doi.org/10.1016/j.scienta.2012.10.002.

Lin, K.H., Huang, M.Y., Huang, W.D., Hsu, M.H., Yang, Z.W., and Yang, C.M. (2013). The effects of red, blue, and white light-emitting diodes on the growth, development, and edible quality of hydroponically grown lettuce (*Lactuca sativa* L. var. *capitata*). Sci. Hortic. *150*, 86–91. DOI: 10.1016/j.scienta.2012.10.002.

Liscum, E., Young, J.C., Poff, K.L., and Hangarter, R.P. (1992). Genetic separation of phototropism and blue light inhibition of stem elongation. Plant Physiol. *100*, 267–271. https://doi.org/10.1104/pp.100.1.267.

Long, S.P., Marshall-Colon, A., and Zhu, X.G. (2015). Meeting the global food demand of the future by engineering crop photosynthesis and yield potential. Cell *161*, 56–66. https://doi.org/10.1016/j. cell.2015.03.019.



Mockler, T.C., Guo, H., Yang, H., Duong, H., and Lin, C. (1999). Antagonistic actions of *Arabidopsis* cryptochromes and phytochrome B in the regulation of floral induction. Development *126*, 2073–2082.

Ogiwara, I., and Arie, T. (2010). Development on year-round production method of Blueberry fruits in plant factory with artificial four seasons. In Plant Factory Encyclopedia (in Japanese), B.P. Nikkei Cleantech Institute, and Nikkei Monozukuri, eds. (Tokyo: Nikkei Business Publications, Inc.), p. 40-46.

Ogiwara, I., Horiuchi, N., and Che, J. (2012). Method for producing blueberry fruits, and continuously flowering blueberry plant obtained thereby. WO20121-61351 A1.

Runkle, E. (2017). Effects of blue light on plants (USA: Michigan State University). http://www.flor.hrt.msu.edu/assets/Uploads/Bluelight.pdf.

Singh, D., Basu, C., Meinhardt-Wollweber, M., and Roth, B. (2015). LEDs for energy efficient greenhouse lighting. Renew. Sust. Energ. Rev. 49, 139–147. https://doi.org/10.1016/j.rser.2015.04.117.

Stutte, G.W., Edney, S., and Skerritt, T. (2009). Photoregulation of bioprotectant content of red leaf lettuce with light-emitting diodes. HortScience 44, 79–82.

Takeda, F., Glenn, D.M., and Stutte, G.W. (2008). Red light affects flowering under long days in a short-day strawberry cultivar. HortScience 43, 2245–2247.

Tamada, T. (2006). Blueberries in Japan. In Blueberries for Growers, Gardeners and Promoters, N.F. Childers, and P.M. Lynere, eds. (Gainesville, Florida: Dr. Norman F. Childers Publications), p. 255–256.

Tarakanov, I., Yakovleva, O., Konovalova, I., Paliutina, G., and Anisimov, A. (2012). Light-emitting diodes: on the way to combinatorial lighting technologies for basic research and crop production. Acta Hortic. 956, 171–178. https://doi.org/10.17660/ActaHortic.2012.956.17.

Thanda, A., Muramatsu, Y., Horiuchi, N., Che, J., Mochizuki, Y., and Ogiwara, I. (2014). Plant growth and fruit quality of blueberry in a controlled room under artificial light. J. Japan. Soc. Hort. Sci. *83*, 273–281. https://doi.org/10.2503/jjshs1.CH-110.

Tokyo Metropolitan Wholesale Market, Japan (2018). Tokyo Metropolitan Central Wholesale Market – Statistics Information. Search results/handling results by origin (blueberry). www.shijoutokei.metro.tokyo.jp.

Trade Statistics of Japan (2015). Ministry of Finance, Japan. http://www.customs.go.jp/toukei/.

Vander Kloet, S.P. (1988). The genus *Vaccinium* in North America (Agriculture Canada Research Branch), Publ. 1828.

Weller, J.L., and Reid, J.B. (1993). Photoperiodism and photocontrol of stem elongation in two photomorphogenic mutants of *Pisum sativum* L. Planta *189*, 15–23. https://doi.org/10.1007/BF00201338.

Xu, F., Shi, L., Chen, W., Cao, S., Su, X., and Yang, Z. (2014). Effect of blue light treatment on fruit quality, antioxidant enzymes and radical-scavenging activity in strawberry fruit. Sci. Hortic. *175*, 181–186. https://doi.org/10.1016/j.scienta.2014.06.012.

Yamori, W. (2013). Improving photosynthesis to increase food and fuel production by biotechnological strategies in crops. J. Plant Biochem. Physiol. *1*, 113–115.

Yamori, W., and Shikanai, T. (2016). Physiological functions of cyclic electron transport around photosystem I in sustaining photosynthesis and plant growth. Annu. Rev. Plant Biol. *67*, 81–106. https://doi.org/10.1146/annurev-arplant-043015-112002.

Yamori, W., Makino, A., and Shikanai, T. (2016). A physiological role of cyclic electron transport around photosystem I in sustaining photosynthesis under fluctuating light in rice. Sci. Rep. *6*, 20147. https://doi.org/10.1038/srep20147.

Yanagi, T., Okamoto, K., and Takita, S. (1996). Effects of blue and blue/red lights of two different PPF levels on growth and morphogenesis of lettuce plants. Acta Hortic. 440, 117–122. https://doi.org/10.17660/ActaHortic.1996.440.21.

Yang, X., Xu, H., Shao, L., Li, T., Wang, Y., and Wang, R. (2018). Response of photosynthetic capacity of tomato leaves to different LED light wavelength. Environm. and Experim. Bot. *150*, 161–171. https://doi.org/10.1016/j.envexpbot.2018.03.013.

Yorio, N.C., Goins, G.D., Kagie, H.R., Wheeler, R.M., and Sager, J.C. (2001). Improving spinach, radish, and lettuce growth under red light-emitting diodes (LEDs) with blue light supplementation. Hort. Sci. *36*, 380–383.

Yoshida, H., Hikosaka, S., Goto, E., Tanaka, H., and Kudou, T. (2012). Effects of light quality and light period on flowering of ever bearing strawberry in a closed plant production system. Acta Hortic. *956*, 107–112. https://doi.org/10.17660/ActaHortic.2012.956.9.

Yoshida, H., Mizuta, D., Fukuda, N., Hikosaka, S., and Goto, E. (2016). Effects of varying light quality from single-peak blue and red light-emitting diodes during nursery period on flowering, photosynthesis, growth, and fruit yield of ever bearing strawberry. Plant Biotechnol. 33(4), 267–276. https://doi.org/10.5511/plantbiotechnology.16.0216a.

Zafra-Stone, S., Yasmin, T., Bagchi, M., Chatterjee, A., Vinson, J.A., and Bagchi, D. (2007). Berry anthocyanins as novel antioxidants in human health and disease prevention. Mol. Nutr. Food Res. *51*, 675–683. https://doi.org/10.1002/mnfr.200700002.

Zhu, X.G., Long, S.P., and Ort, D.R. (2010). Improving photosynthetic efficiency for greater yield. Annu. Rev. Plant Biol. *61*, 235–261. https://doi.org/10.1146/annurev-arplant-042809-112206.

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