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# Variety Comparison of Effect of Supplemental Lighting with LED on Growth and Yield in Forcing Culture of Strawberry

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The effect of supplemental lighting with high irradiance LED on growth and fruit yield of various cultivars was examined in forcing culture of strawberry. Four cultivars of strawberry plants, having the different flowering timing and the flower number per inflorescence were illuminated 12 h daily from October to May. Supplemental lighting significantly accelerated leaf photosynthesis in all cultivars, which supported the translocation of additional carbohydrate to fruits, and improved fruit quality compared with non-lighting treatments. The flower opening of 2nd inflorescences in 'Sagahonoka' and 'Benihoppe' were accelerated by supplemental lighting, and this brought a remarkable increase in fruit yield. In 'Akihime', flower number per inflorescence was remarkably increased through an acceleration of leaf photosynthesis resulting in a significant increase in fruit yield. In 'Ookimi', supplemental lighting inhibited flower bud differentiation, and the positive effect of supplemental lighting was not observed on fruit yield. An acceleration of anthesis and an increase in flower number under supplemental lighting varied in each cultivar. These results suggest that supplemental lighting provided based on the hereditary characteristics (e.g., flowering timing, flower number) of each cultivar is appropriate for high-yield production based on the stabilizing effect of supplemental lighting in forcing culture of strawberry.

Keywords : cultivar, flower bud differentiation, flower number, photosynthesis

## INTRODUCTION

Production areas and levels are continuously declining for Japanese strawberry production. Solving these problems, there is an increasing trend towards strawberry productions in large-scale industrial facilities. Techniques to obtain consistently high yield are required in large-scale greenhouse. This requires the development of environment control techniques (e.g., light, air temperature, $CO_2$ concentration, humidity, wind velocity) to allow plants to realize their full photosynthetic potential. Miyoshi et al. (2013) provides an example of environment control in forcing culture of strawberry, reporting on an energy-saving control of ambient air temperature using a constant soil temperature layer. Furthermore, Hidaka et al. (2012) reported that controlling the light environment directly influences leaf photosynthesis and fruit yield; this is required because variable light environments that are dependent on factors such as cropping season and cultivation location frequently lead to inadequate light levels for leaf photosynthesis, plant growth and fruit yield, resulting in declining productivity in greenhouse production. Consequently, the development of a supplementary lighting technique, independent of cropping season or cultivation location, is needed for consistently high strawberry production.

Hidaka et al. (2013) examined the effects of 12 h of supplemental lighting (6:00–18:00) from two different commercial light sources, high-irradiance LEDs and fluorescent lamps. In that study, we found high-irradiance LEDs significantly enhanced leaf photosynthesis compared with fluorescent lamps. This led to improved fruit quality and a significant increase in marketable yield of strawberries in forcing culture. Hidaka et al. (2014) further examined the optimum photoperiod of supplemental lighting with LEDs to the June bearing strawberry (*Fragaria* × *ananassa* Duch. cv. Fukuoka S6). The best fruit yield in this cultivar was found under 12-h illumination when four different photoperiods (12-h, 14-h, 16-h and 24-h illumination) were compared.

Darrow (1966) classified June bearing strawberry (*Fragaria* × *ananassa* Duch.) as a facultative short day plant. Ito and Saito (1962) and Taylor (2002) clarified that each cultivar has a respective critical day-length that is needed to induce flower bud differentiation. Photoperiods exceeding a critical day-length may inhibit flower bud differentiation, and subsequently bring decreasing in yield. Therefore, a sufficient effect of supplemental lighting with 12-h photoperiods, which was seen when using the cultivar known as 'Fukuoka S6' (Hidaka et al., 2014), may not always be obtained using any other cultivars. Understanding the varietal differences in the supplemental lighting effect is required for developing a technique of supplemental lighting that can be broadly and successfully applied. The mechanism that produces an increase in yield based on supplemental lighting may also vary with each cultivar having

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the different characteristics such as flowering timing and flower number per inflorescence.

To understand the effects of supplemental lighting on different cultivars of strawberry grown in forcing culture, four different cultivars, having the different characteristics in the timing of flowering (early or late flowering) and the number of flower per inflorescence (many, medium or few flowers) were compared with the effects of supplemental lighting using high-irradiance LEDs on the growth and yield of these cultivars. The study included analyses of photosynthesis and dry matter partitioning of plants.

## MATERIALS AND METHODS

*Plant materials and growth conditions*

Four cultivars of June bearing strawberries (*Fragaria* × *ananassa* Duch. cvs. Sagahonoka, Ookimi, Akihime and Benihoppe) were grown by bench culture in a section (37 m long × 9 m wide) of a large-scale greenhouse (37 m long × 27 m wide × 4.5 m high) at the NARO Kyushu Okinawa Agricultural Research Center, Japan (33°18.4′N, 130°32.8′E). Each cultivar of 'Sagahonoka', 'Ookimi', 'Akihime' and 'Benihoppe' has different characteristics of the flowering timing and the flower number per inflorescence as follows, the early flowering and the medium flower number in 'Sagahonoka' (Itou and Matsuzawa, 2008), the late flowering and the few flower number in 'Ookimi' (Sone et al., 2008), the early flowering and the many flower number in 'Akihime' (Nishimori et al., 2010) and the early flowering and the medium flower number in 'Benihoppe' (Nishimori et al., 2010). In early June 2012, 45 nursery plants respectively selected from mother stocks of different four cultivars were transplanted into plastic pots (6 cm diameter; 0.2 L volume) remaining the connection to the mother stocks thorough the runners. Pots were filled with a mixed substrate (peat moss: coconut shells: charcoal 3:5:2 [v/v/v]) and placed on the nursery bench. Only water was supplied to the nursery plants before rooting. After the rooting, nursery plants were cut off the runners from the mother stocks in late June, and thereafter grown with supplying a nutrient solution. Nutrient solution (OK-F-1, OAT Agrio Co., Ltd., Tokyo, Japan) with an electrical conductivity of 0.6 dS $m^{-1}$ was supplied at a rate of 300 mL $d^{-1}$ per plant at 9:00, 11:00, 13:00, 15:00 and 17:00 daily. From August 21 to September 17, nutrient supplementation was halted to induce anthesis, with only water supplied. On September 18, 2012, nursery plants, which were not confirmed previously the flower bud differentiation of the first inflorescence, were transplanted into substrate-filled cultivation beds (30 m long × 30 cm wide × 80 cm high), with plants spaced 20 cm apart and with 15 cm between rows. The plants were then grown with nutrient solution supplementation until May 31, 2013. Substrates and nutrient solutions were the same as those used to cultivate nursery plants, with approximately 3 L substrate per plant. During the growing period, the ventilation starting temperature was set at 26°C, and an air temperature was kept above 6°C with heating in a greenhouse by a fuel burning heater (HK2027TEV, NEPON Inc., Tokyo, Japan). Flower pollination was performed by bees. Fruit thinning was not conducted.

*Supplemental lighting system and lighting conditions*

The supplemental lighting employed the same LED lighting system described previously (Hidaka et al., 2013; 2014). This system consisted of an LED lamp unit (LLM0312A, Stanley Electric Co., Ltd., Tokyo, Japan) coupled to an exclusive power supply (LLP0019A, Stanley Electric Co., Ltd.). Three LED lighting systems were placed 30 cm apart at 50 cm directly above each cultivation bed and the base of the plants. This 30 cm apart between LED lamps was determined to be approximately equal the horizontal distribution of the photosynthetic photon flux densities (*PPFD*) at plant bases. Each LED lighting system consumed 26 W. The LED lighting system featured peak light intensity at 450 and 550 nm, and the *PPFD* at heights of 10, 20 and 30 cm (normal leaf heights) from plant bases were 400, 690 and 1200 μmol $m^{-2}$ $s^{-1}$, respectively, as reported previously (Hidaka et al., 2013).

The LED supplemental lighting was supplied for 12 h per day from 6:00 to 18:00 (lighting), and controls used no supplemental lighting (non-lighting). Timer switches (TB22101, Panasonic Corp., Osaka, Japan) controlled the photoperiods. The experiments were conducted from October 1, 2012 to May 31, 2013.

*Measurements of leaf photosynthesis*

In May 28, 2013, we measured leaf photosynthesis under lighting or non-lighting treatment in different four cultivars using a portable photosynthesis and fluorescence system (LI-6400XT, LI-COR, Lincoln, NE, USA). Photosynthetic rates of leaves were measured using the chamber head with a natural light window. Leaves were set into the chamber head positioned horizontally at 10 cm above the base of the plants. Measurement controlled conditions were: 25°C air temperature, 50% relative humidity and 400 μmol $mol^{-1}$ $CO_2$. Measurement was conducted on cloudy daytime from 10:00 to 16:00 using the fully expanded third leaflets of greenhouse-grown strawberry plants. We analyzed four plants per cultivar and treatment. The *PPFD*, leaf temperature and photosynthetic rate in the leaf chamber were recorded simultaneously.

*Analyses of flowering characteristics, yield, and fruit quality*

To analyze the effect of supplemental lighting on flowering of four cultivars, we recorded the flowering dates of the first and second inflorescences, and the number of flowers in each inflorescence. We analyzed five plants per cultivar and treatment.

To determine the effects of supplemental lighting on yield, marketable fruits (fruit fresh weight ≥6 g) were harvested from five plants in each cultivar and treatment. In the fruits harvested from the first inflorescence, the following fruit quality parameters were analyzed: soluble solids content (*SSC*), titratable acidity (*TA*) and flesh firmness (*FF*). The *SSC* and *TA* of fruit juice and the *FF* of fruit were measured using a digital refractometer (PAL-1, Atago Co., Ltd., Tokyo, Japan), a coulometric acidity meter (CAM-500, Kyoto Electronics Manufacturing Co., Ltd., Kyoto, Japan) and a penetrometer (RX-2, Aikoh

Engineering Co., Ltd., Osaka, Japan), respectively. For fruit quality analysis, eight fruits per cultivar and treatment were used.

*Growth analysis*

To analyze the long-term responses of leaf photosynthesis and the partition of photosynthates to the plant organs, growth analysis was conducted. Plant growth was divided into two stages, 1) before fruit set and 2) after fruit set, and then the growth characteristics in these two stages were analyzed. Five plants of each cultivar and treatment were harvested on September 26 (8 days after the transplanting) in 2012, November 27 (during fruit set) in 2012 and February 26 (after fruit set) in 2013 for growth analysis. The leaf area of each cultivar was calculated from the length ($L_L$) and width ($W_L$) of leaflets using each cultivar's equation obtained with the method described previously by Hidaka et al. (2013) as follows:

Leaf area ('Sagahonoka') $=1.717\times(L_L\times W_L)+5.232$

Leaf area ('Ookimi') $=1.746\times(L_L\times W_L)+2.128$

Leaf area ('Akihime') $=1.808\times(L_L\times W_L)-4.181$

Leaf area ('Benihoppe') $=1.658\times(L_L\times W_L)+2.495$

The harvested plants were separated into leaf, crown, peduncle, fruit and root. Each part was dried for 48 h at 80°C in a circulation drier, cooled to room temperature, and then weighed. We calculated growth characteristic parameters of specific leaf weight (*SLW*: an index of leaf thickness), crop growth rate (*CGR*: the dry matter production rate per unit ground area), leaf area index (*LAI*: the leaf area per ground area), net assimilation rate (*NAR*: the dry matter production rate per unit leaf area), shoot growth rate ($GR_S$: the dry matter partition rate to shoot per unit ground area), root growth rate ($GR_R$: the dry matter partition rate to root per unit ground area) and fruit growth rate ($GR_F$: the dry matter partition rate to fruit per unit ground area) as follows:

$SLW$ = leaf dry weight per plant / leaf area per plant

$CGR=(W_{T2}-W_{T1})\times PD\ /\ (t_2-t_1)$

$LAI$ = leaf area per plant $\times PD$

$NAR=CGR\ /\ LAI$

$GR_S=(W_{S2}-W_{S1})\times PD\ /\ (t_2-t_1)$

$GR_R=(W_{R2}-W_{R1})\times PD\ /\ (t_2-t_1)$

$GR_F=(W_{F2}-W_{F1})\times PD\ /\ (t_2-t_1)$

where $W_{T1}$ and $W_{T2}$, $W_{S1}$ and $W_{S2}$, $W_{R1}$ and $W_{R2}$, and $W_{F1}$ and $W_{F2}$ indicate total dry weight (leaf, crown, peduncle, fruit and root), shoot dry weight (leaf, crown, peduncle), root dry weight and fruit dry weight at plant harvest dates of $t_1$ and $t_2$, respectively. *PD* indicates the planting density (plant number per unit area). The *LAI* data used the average value of two dates ($t_1$ and $t_2$).

*Statistical analysis*

The significance of differences among means was tested using the Tukey-Kramer test. The time course data of dry shoot and root weights were tested by a *t*-test. These statistical analyses were performed using statistical software (SAS Ver 9.2, SAS Institute Inc., Cary, NC, USA).

## RESULTS AND DISCUSSION

Figure 1 shows the photosynthetic rate of fully expanded third leaflets of four cultivars under the supplemental lighting on a cloudy day. With supplemental lighting on cloudy daytime, fully expanded third leaflets were exposed to increased *PPFD* (about 400 μmol $m^{-2}$ $s^{-1}$) as compared with that in non-lighting (about 100 μmol $m^{-2}$ $s^{-1}$) at the leaf heights of 10 cm above plant bases. Supplemental lighting resulted in an increased photosynthetic rate of more than 2-fold higher than in non-lighting plants for all tested cultivars. Acceleration of leaf photosynthesis with supplemental lighting was highest in 'Akihime' when compared with those in the other three cultivars.

Table 1 shows the effect of supplemental lighting on flowering characteristics of the four cultivars. In the first inflorescence, supplemental lighting did not affect to the flower opening. Varietal differences and supplemental lighting also affected flower number. 'Akihime' produced the largest number of flowers, while 'Ookimi' produced the fewest. Flower number of 'Akihime' approximately doubled with supplemental lighting, but significant increases with supplemental lighting were not observed in 'Sagahonoka', 'Ookimi' and 'Benihoppe'. In the second inflorescence, flowering date were affected by supplemental lighting treatment. With supplemental lighting, flowering dates in 'Sagahonoka' and 'Benihoppe' were earlier than those under non-lighting. In 'Ookimi', flower bud differentiation was inhibited by supplemental lighting, and flower opening was not observed at all. The effect of supplemental lighting on flower number in the second inflorescence in each cultivar followed almost the same pattern as that observed in the first inflorescence. When the flower numbers of the 1st and 2nd inflorescence were compared, the flower number in 'Sagahonoka' increased in the second inflorescence, but decreased in the other three cultivars.

The reaction of flowering characteristics to the supplemental lighting varied among cultivars. In 'Sagahonoka' and 'Benihoppe', supplemental lighting resulted in accelerated flower opening of the 2nd inflorescence. Hidaka et al. (2014) previously reported that the higher photosynthetic activity of plants illuminated with LED resulted in a short-

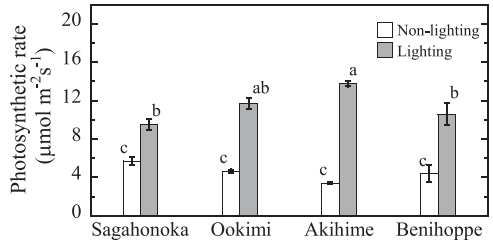


**Fig. 1** Photosynthetic rate of fully expanded third leaflet under the supplemental lighting treatments among different four cultivars. Data are mean ±S.E. ($n=4$). Different letters indicate significant differences by Tukey-Kramer test among treatments in different cultivars ($P<0.05$). Photosynthetic rate was measured at the controlled environment of air temperature 25°C, relative humidity 50% and $CO_2$ concentration 400 μmol $mol^{-1}$ with a portable photosynthesis and fluorescence system (LI-6400XT, LI-COR) on cloudy daytime (10:00–16:00) in May 28, 2013.

ened period from flower bud differentiation to anthesis thorough an acceleration of plant growth. The acceleration of flower opening in 'Sagahonoka' and 'Benihoppe' under supplemental lighting is believed to be caused by an acceleration of plant growth through increasing in leaf photosynthesis. Anthesis was not observed in the 2nd inflorescence of 'Ookimi'. Presence of non-anthesis in 'Ookimi' under supplemental lighting would be caused by the inhibition of flower bud differentiation with 12-h illumination by high irradiance LED.

The increase in the number of flowers produced with supplemental lighting also varied by cultivars. The flower number of 'Akihime' increased significantly with supplemental lighting, but not in 'Sagahonoka', 'Benihoppe' and 'Ookimi'. Peng and Iwahori (1994) reported that flower bud differentiation and development require high levels of carbohydrates, while Sung and Chen (1991) reported an acceleration of leaf photosynthesis increased fruit set per plant. Therefore, an increase in flower number in the 1st and 2nd inflorescence under the supplemental lighting should be induced by a higher allocation of carbohydrates, which were produced abundantly with accelerated leaf photosynthesis, to bud primordia. Especially in 'Akihime', leaf photosynthetic activity may directly affect the number of flowers produced. In 'Ookimi', the upper limit of flower number is a definite hereditary trait, which may not appear to clearly affect flower numbers under the supplemental lighting. Therefore, these varietal differences in the reactions of flowering characteristics, flower bud differentiation and flower numbers, to supplemental lighting are believed to be attributable the genetics of each cultivar.

Figure 2 shows time courses of shoot and root dry weights among the four cultivars studied here. In the stage before fruit set (Sep. 26–Nov. 27), supplemental lighting resulted in increased shoot dry weights in 'Sagahonoka' and 'Ookimi', but not in 'Akihime' and 'Benihoppe'. Supplemental lighting significantly increased root dry weights among all cultivars, and a remarkable increase occurred in 'Akihime'. In the stage after fruit set (Nov. 27–Feb. 26), shoot dry weights increased significantly in 'Sagahonoka', 'Ookimi' and 'Akihime', but not in 'Benihoppe'. Supplemental lighting resulted in a greater increase in shoot dry weight in 'Sagahonoka' and 'Ookimi' (1.7 times that of non-lighting) than in 'Akihime' (1.3 times that of non-lighting). Supplemental lighting resulted in significantly increased root dry weights in 'Sagahonoka' and 'Akihime', but not in 'Ookimi' and 'Benihoppe'. Supplemental lighting treatment also resulted in increase in root dry weight in 'Sagahonoka' and 'Akihime' in both stages, before and after fruit set. However, supplemental lighting increased the root dry weight in 'Ookimi' and 'Benihoppe' only before fruit set, and was not observed after fruit set.

Table 2 lists *SSC*, *TA* and *FF* of harvested fruits under the supplemental lighting treatment among the four cultivars. Supplemental lighting resulted in increased *SSC* values among all cultivars. Within cultivars, *SSC* was highest in 'Ookimi' and lowest in 'Sagahonoka'. With supplemental lighting, an increase tendency in *TA* was observed in 'Ookimi' and 'Benihoppe'. Within cultivars, *TA* was highest in 'Benihoppe' and lower in 'Sagahonoka' and 'Akihime'. *FF* was unaffected by supplemental lighting, but was affected by cultivar. *FF* in 'Ookimi' was remarkably higher than that in the three other cultivars. The observed increases in *SSC*, which is related to fruit sweetness, may also be caused by the higher accumulation of photosynthate to fruits through an acceleration of leaf photosynthesis under LED lighting; this finding confirmed our previous studies (Hidaka et al., 2013; 2014). Supplemental lighting was also found to result in an increase of *TA* in some cultivars. Several researchers have verified that citric and malic acid are the main organic acids in strawberry fruit (Montero et al., 1996; Roussos et al., 2009). These organic acids are synthesized from precursor sugars such as sucrose, glucose and fructose through cellular respiration including the glycolytic pathway and TCA cycle (Taiz and Zeiger, 2002). Therefore, supplemental lighting is believed to result in an increase in *TA* that was caused by the higher sugar accumulation to fruits as shown in the *SSC* data (Table 2). In 'Akihime' and 'Sagahonoka', remarkable increase in *TA* was not observed under supplemental lighting. It is known that *TA* in 'Akihime' and 'Sagahonoka' are lower than those of 'Ookimi' and 'Benihoppe' (Itou and Matsuzawa, 2008; Sone et al., 2008; Nishimori et al., 2010). Therefore in 'Akihime' and 'Sagahonoka', *TA* increase with supplemental lighting may have been limited hereditarily as compared with those in 'Ookimi' and 'Benihoppe'.

Figure 3 shows average fruit weight, number of fruits and marketable yield under supplemental lighting treatment for all four cultivars. Supplemental lighting treatment resulted in remarkably increased average fresh weight per

**Table 1** Effect of supplemental lighting treatments on flowering characteristics among different four cultivars.

| Cultivar | Treatment | First inflorescence | | Second inflorescence | |
|---|---|---|---|---|---|
| | | Flowering date | Flower number | Flowering date | Flower number |
| Sagahonoka | Non-lighting | 2012. Nov. 13 | 7.2±0.9 cde | 2013. Jan. 9 | 11.2±1.1 bc |
| | Lighting | 2012. Nov. 7 | 10.6±1.3 cde | 2012. Dec. 17 | 15.8±1.8 b |
| Ookimi | Non-lighting | 2013. Feb. 19 | 5.4±0.7 de | 2013. Apr. 5 | 3.6±0.5 d |
| | Lighting | 2013. Feb. 18 | 5.2±0.8 e | — | — |
| Akihime | Non-lighting | 2012. Nov.12 | 19.6±1.7 b | 2013. Jan. 14 | 15.4±1.9 b |
| | Lighting | 2012. Nov. 7 | 39.0±2.7 a | 2013. Jan. 17 | 26.8±2.3 a |
| Benihoppe | Non-lighting | 2012. Nov. 13 | 11.4±1.3 cd | 2013. Jan. 15 | 8.0±0.5 cd |
| | Lighting | 2012. Nov. 10 | 13.0±0.7 c | 2013. Jan. 4 | 11.8±1.1 bc |

Data are mean ±S.E. ($n=5$). Different letters indicate significant differences by Tukey-Kramer test among treatments in different cultivars ($P<0.05$)

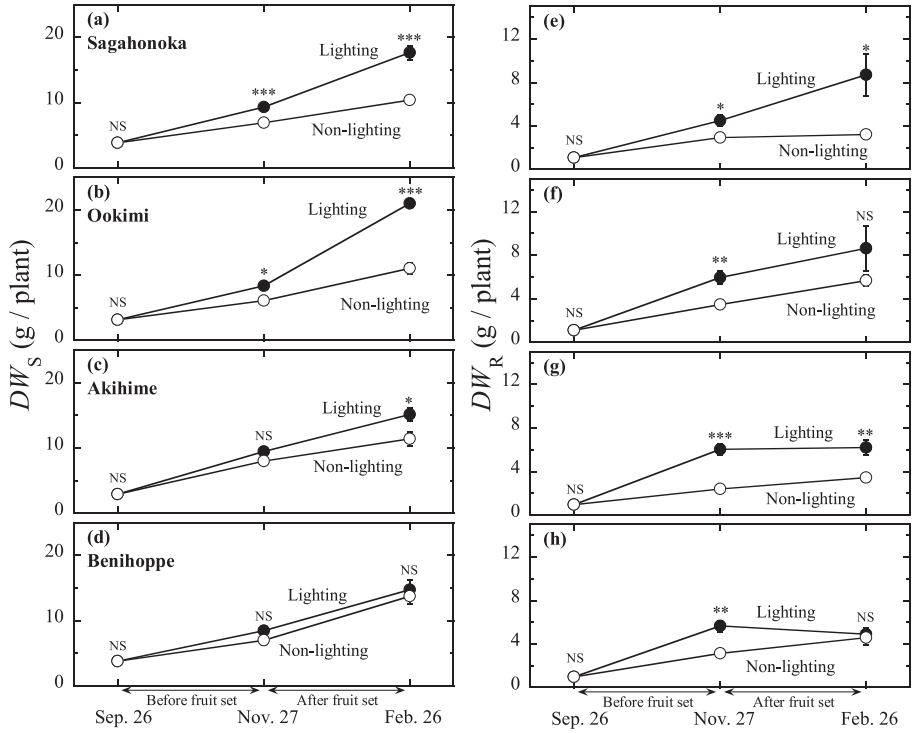


**Fig. 2** Time courses of shoot dry weight ($DW_S$) and root dry weight ($DW_R$) under the supplemental lighting treatments among different four cultivars of 'Sagahonoka' (a, e), 'Ookimi' (b, f), 'Akihime' (c, g) and 'Benihoppe' (d, h). Data are mean ±S.E. ($n=5$). *, **, *** indicate significant differences at $P<0.05$, $P<0.01$, $P<0.001$ by *t*-test among treatments at each sampling time. NS: not significant ($P\geq0.05$).

**Table 2** Effect of supplemental lighting treatments on fruit quality among different four cultivars.

| Cultivar | Treatment | *SSC* (°Brix) | *TA* (%) | *FF* (N) |
|---|---|---|---|---|
| Sagahonoka | Non-lighting | 8.19±0.28d | 0.35±0.02 d | 1.50±0.06 b |
| | Lighting | 10.03±0.25 abc | 0.40±0.02 d | 1.45±0.07 b |
| Ookimi | Non-lighting | 9.90±0.36 abc | 0.42±0.02 cd | 2.16±0.10 a |
| | Lighting | 10.85±0.40 a | 0.53±0.04 bc | 2.29±0.16 a |
| Akihime | Non-lighting | 9.58±0.28 bc | 0.38±0.01 d | 1.32±0.04 b |
| | Lighting | 10.76±0.15 ab | 0.39±0.03 d | 1.48±0.10 b |
| Benihoppe | Non-lighting | 9.09±0.22 cd | 0.56±0.02 b | 1.61±0.06 b |
| | Lighting | 10.59±0.16 ab | 0.69±0.02 a | 1.69±0.12 b |

Data are mean ±S.E. ($n=8$). Different letters indicate significant differences by Tukey-Kramer test among treatments in different cultivars ($P<0.05$).

fruit in 'Benihoppe' (1.4 times higher than in non-lighting). In 'Sagahonoka', supplemental lighting was observed to result in an increasing trend of average fruit weight, but the difference was not significant, while no significant effect was also found in 'Ookimi' and 'Akihime'. Within cultivars, 'Ookimi' and 'Akihime' had the highest and lowest average fruit weight, respectively, with the weight of the former being more than twice as high in the latter. Supplemental lighting resulted in an increase in the total number of fruits harvested from December to the next May in 'Sagahonoka', 'Akihime' and 'Benihoppe'. In 'Ookimi', significant differences in fruit numbers were not observed between lighting and non-lighting treatments. The observed yield of marketable fruit followed almost the same pattern as the observed number of fruits produced in all cultivars, and in lighting treatment, the total yield of 'Sagahonoka', 'Akihime' and 'Benihoppe' was 1.8, 1.6 and 1.9 times that in non-lighting treatment, respectively. However, positive effect of supplemental lighting was not observed on fruit yield in 'Ookimi'.

In this study, the effects of supplemental lighting on average fruit weight and fruit number, factors that contribute to fruit yield, were different in each cultivar. Supplemental lighting resulted in increased average fruit weight and number in 'Benihoppe'; both of these contributed and increase in yield. Roussos et al. (2009) found fruit size can be enhanced by increasing the supply of assimilate to fruit. Furthermore, Sung and Chen (1991) reported that accelerated leaf photosynthesis increases fruit set per plant. Hidaka et al. (2013; 2014) also found that the supplemental lighting enhances average fruit weight and number using another cultivar of 'Fukuoka S6'. Therefore, we can attribute the observed increases in average fruit weight and number under the supplemental lighting to the higher allocation of photosynthate to fruit. In 'Sagahonoka' and 'Akihime', supplemental lighting preferentially affected the fruit number more than the average fruit weight, although especially in 'Akihime', supplemental lighting only affected the fruit

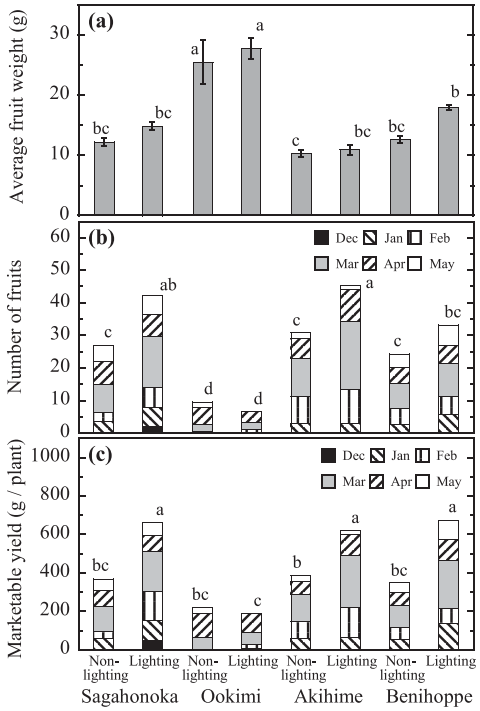


**Fig. 3** Effect of supplemental lighting treatments on average fruit weight (a), number of fruits (b) and marketable yield (c) from December to the next May among different four cultivars. Data are mean ± S.E. ($n=5$). Different letters indicate significant differences by Tukey-Kramer test among treatments in different cultivars ($P<0.05$).

number. Therefore, increasing the fruit number is believed to have mainly contributed to the increase in yield in 'Sagahonoka' and 'Akihime'. In 'Akihime', the acceleration of leaf photosynthesis with supplemental lighting directly resulted in an increase in flower number per inflorescence (Table 1). Supplemental lighting also increased flower number in 'Sagahonoka' (Table 1), but the degree of increase was lower than that in 'Akihime'. Although these different increases in flower numbers were observed between 'Sagahonoka' and 'Akihime', supplemental lighting resulted in almost the same total number of harvested fruits in both these cultivars (Fig. 3b). In 'Sagahonoka', supplemental lighting accelerated leaf photosynthesis (Fig. 1b), which shortened the period from flower bud differentiation to anthesis thorough the promotion of the growing speed of plants. This may have caused early flowering of the 1st, 2nd and subsequent inflorescences, successively.

The data of fruit numbers and marketable yield in the early season (December to the following January) would reflect varietal differences of flowering earliness and flower number under supplemental lighting. Increases of fruit number and marketable yield under supplemental lighting were observed in 'Sagahonoka' and 'Benihoppe' but were not observed in 'Akihime' (Fig. 3b and c). As a result, the total number of harvested fruits (December to the following May) under supplemental lighting may have been almost the same in both 'Sagahonoka' and 'Akihime'.

In addition, a positive effect of supplemental lighting was not observed on either average fruit weight, number of fruits or fruit yield of 'Ookimi' through the inhibition of flower bud differentiation in this treatment. The upper limit of flower number in 'Ookimi' is definitely hereditary (Table 1), and Sone et al. (2008) reported that flower numbers of first inflorescence in 'Ookimi' was only half of those in other ordinarily cultivars. This genetic limitation of flower number may have increased the partitioning of photosynthate to fruit when 'Ookimi' was compared with that of other cultivars. Therefore, the much higher observed average fruit weight in 'Ookimi' may be caused by the increased accumulation of the photosynthate in each fruit. Furthermore, without supplemental lighting, an increase in the accumulation of photosynthate in the fruit of 'Ookimi' may enable an increase in potential fruit size; this would explain the lack of a difference in average fruit size between the lighting and non-lighting treatments in 'Ookimi'. Therefore, the effect of supplemental lighting on fruit yield was remarkably affected by the varietal characteristics such as the light sensitivity for flower bud differentiation, the increased number of flowers produced during higher accumulation of photosynthates provided to bud primordia and the upper limit of flower number per inflorescence.

Figure 4 shows the *NAR*, *LAI*, *SLW*, *CGR*, $GR_S$ and $GR_R$ before fruit set with and without supplemental lighting for the four cultivars studied here. In the stage before fruit set, supplemental lighting resulted in significantly higher *NAR* among all cultivars. This pattern of increase was almost the same as the results of leaf photosynthesis (Fig. 1). Within cultivars, *NAR* was significantly higher in 'Akihime' than in the other three cultivars. Supplemental lighting was not observed to have a positive effect on *LAI* in all cultivars, although it resulted in significantly higher *SLW* among all cultivars. Similar to the *NAR* results, supplemental lighting significantly increased *CGR* among all cultivars, and the *CGR* was higher in 'Akihime' than in the other cultivars. Supplemental lighting resulted in an increase in $GR_S$ in 'Sagahonoka', 'Ookimi', 'Akihime' and 'Benihoppe' by 1.8, 1.8, 1.3 and 1.5 times, respectively. By supplemental lighting, remarkable increases in values of $GR_S$ were observed in 'Sagahonoka' and 'Ookimi' but were not observed in 'Akihime' and 'Benihoppe'. Supplemental lighting resulted in significantly increased $GR_R$ in 'Ookimi', 'Akihime' and 'Benihoppe'; the values in 'Sagahonoka', 'Ookimi', 'Akihime' and 'Benihoppe' were 1.8, 2.0, 3.5 and 2.2 times higher than those under the non-lighting treatment, respectively.

The significant increase in each cultivar's *NAR* under supplemental lighting would be caused by the acceleration of the leaf photosynthetic rate (Fig. 1). This higher *NAR* of illuminated leaves would have affected *SLW* rather than *LAI*. Chabot and Chabot (1977) detected increases in leaf thickness and *SLW* under high light conditions, and suggested that the observed leaf thickening was related to increases in mesophyll cell size and amounts of mesophyll tissue produced. In our previous study, the higher *SLW* value and leaf thickening under supplemental lighting were

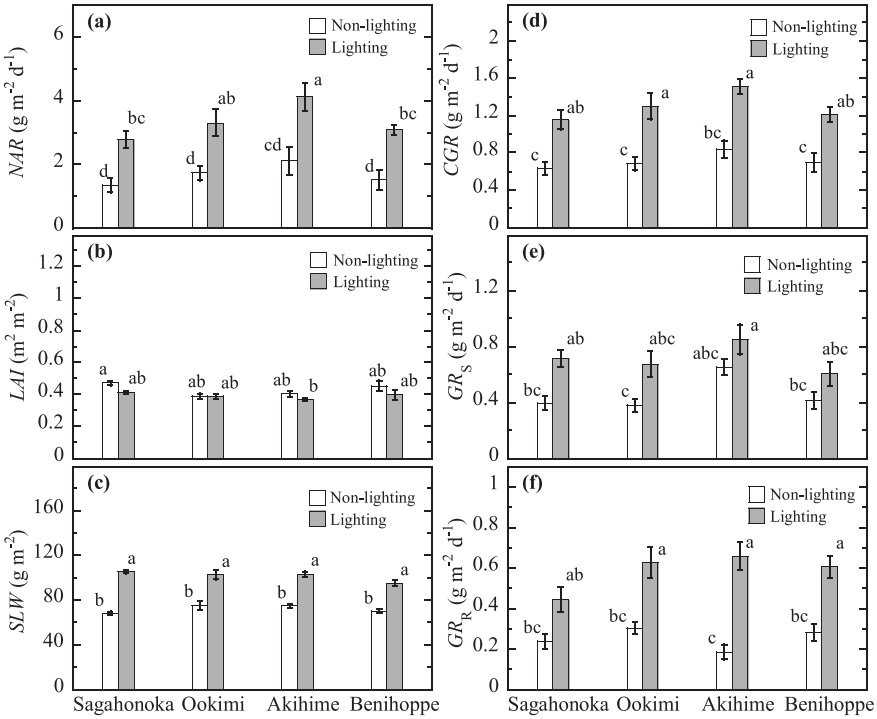


**Fig. 4** Effect of supplemental lighting treatments on net assimilation rate (*NAR*, a), leaf area index (*LAI*, b), specific leaf weight (*SLW*, c), crop growth rate (*CGR*, d), shoot growth rate ($GR_S$, e) and root growth rate ($GR_R$, f) before fruit set among different four cultivars. Data are mean ±S.E. ($n=5$). Different letters indicate significant differences by Tukey-Kramer test among treatments in different cultivars ($P<0.05$).

also observed (Hidaka et al., 2014). Thus, it can be considered that the acceleration of leaf photosynthesis under supplemental lighting treatment contributes to leaf thickening rather than an enlargement of leaf area among all cultivars in the stage before fruit set. Dry matter partitioning to shoot and root under supplemental lighting in the stage before fruit set was different in each cultivar. In 'Sagahonoka' and 'Ookimi', the rate of increase between $GR_S$ and $GR_R$ under supplemental lighting was almost the same, but in 'Akihime' and 'Benihoppe', the rate of increase of $GR_R$ was higher than that of $GR_S$. Therefore, in the stage before fruit set, supplemental lighting may accelerate plant growth through the acceleration of leaf photosynthesis, and thereafter result in well-balanced partitioning of photosynthates between shoot and root in 'Sagahonoka' and 'Ookimi', and a higher partitioning to root than shoot in 'Akihime' and 'Benihoppe'.

Figure 5 shows the *NAR*, *LAI*, *SLW*, *CGR*, $GR_S$, $GR_R$ and $GR_F$ after fruit set with and without supplemental lighting for the four cultivars studied here. In the stage after fruit set, supplemental lighting resulted in increased *NAR* by all cultivars, although the increase was significant only in 'Sagahonoka' and 'Akihime'. Within cultivars, *NAR* was significantly lower in 'Ookimi' than those in the other three cultivars. Under supplemental lighting, *LAI* tended to increase in 'Sagahonoka' and 'Ookimi', but the difference was not significant between lighting and non-lighting treatments. Supplemental lighting resulted in a significant increase in *SLW* among all cultivars. Although supplemental lighting increased *CGR* among all cultivars, the increase was significant only in 'Sagahonoka'. Supplemental lighting resulted in increased $GR_S$ in 'Sagahonoka', 'Ookimi' and 'Akihime' that increased by 2.3, 3.0 and 1.7 times, respectively, but a significant difference was only observed in 'Ookimi'. Supplemental lighting resulted in a increase of $GR_R$ in 'Sagahonoka', but increase was not significant. With supplemental lighting, $GR_F$ increased significantly in 'Sagahonoka', 'Akihime' and 'Benihoppe' by 3.3, 1.5 and 1.9 times higher than those under non-lighting, respectively. Supplemental lighting was not observed to have a positive effect on $GR_F$ in 'Ookimi'.

In the stage after fruit set, supplemental lighting resulted in an increase in *NAR* in all cultivars; this would also be caused by the accelerated leaf photosynthetic rate with the same results as observed in the stage before fruit set. Supplemental lighting also caused a higher *SLW* that was caused by leaf thickening; leaf thickening was brought by the accelerated leaf photosynthesis as it did in the stage before fruit set. Supplemental lighting remarkably increased *CGR* (more than three times over that of non-lighting) in 'Sagahonoka'. 'Ookimi' had the lowest *CGR* of the four cultivars. The higher *CGR* in illuminated 'Sagahonoka' and lower *CGR* in 'Ookimi' may be affected by the partitioning of photosynthates to fruits.

The *CGR* value reflects the growth of all plant organs. By dividing *CGR* into $GR_S$, $GR_R$ and $GR_F$, the effect of supplemental lighting on $GR_F$, which is an index of the rate of partitioning photosynthates to fruits, was found to be highest in 'Sagahonoka'. This can be attributed to an increase in yield during the early season through early flowering that is in turn caused by an acceleration of leaf photosynthesis as discussed above. The lowest value of $GR_F$ of the

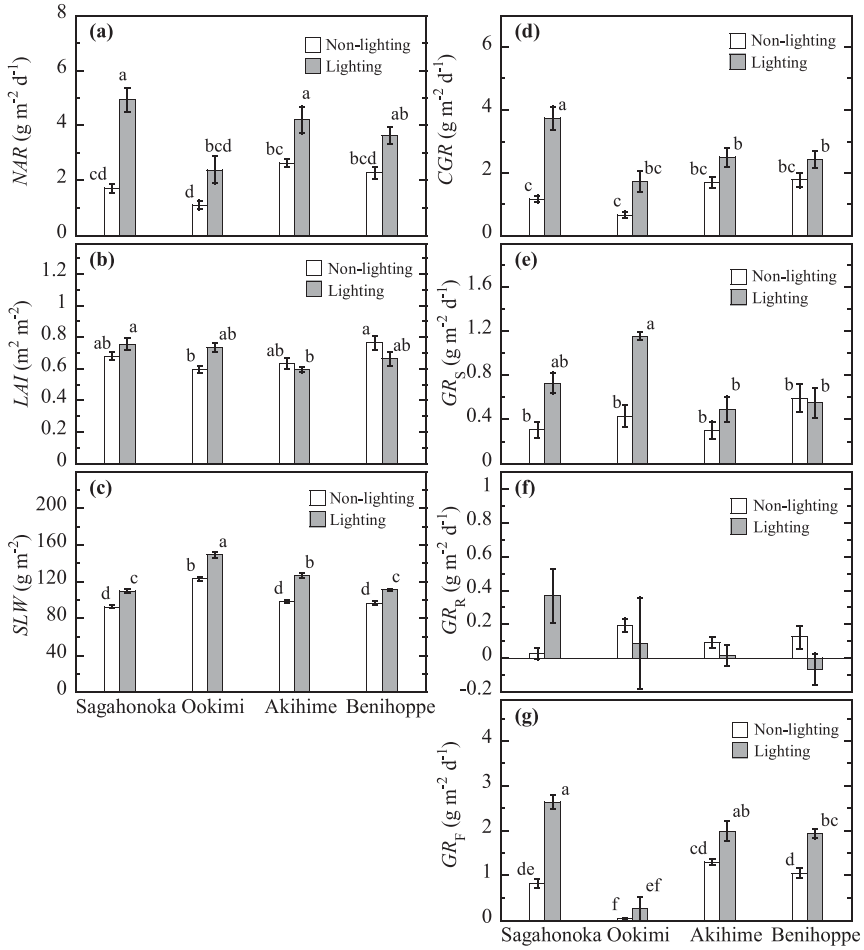


**Fig. 5** Effect of supplemental lighting treatments on net assimilation rate (*NAR*, a), leaf area index (*LAI*, b), specific leaf weight (*SLW*, c), crop growth rate (*CGR*, d), shoot growth rate ($GR_S$, e), root growth rate ($GR_R$, f) and fruit growth rate ($GR_F$, g) after fruit set among different four cultivars. Data are mean ±S.E. ($n=5$). Different letters indicate significant differences by Tukey-Kramer test among treatments in different cultivars ($P<0.05$).

four cultivars was observed in 'Ookimi'. Under the non-lighting treatment, $GR_F$ in 'Akihime', the cultivar with the largest number of flowers per inflorescence (Table 1), was higher than those of the other three cultivars. The percentages of $GR_F$ as part of the *CGR* in 'Sagahonoka', 'Akihime' and 'Benihoppe' were over 50%, and exceeded 70% under supplemental lighting. The percentages of $GR_S$ to *CGR* in 'Sagahonoka', 'Akihime' and 'Benihoppe' were about 20–30%. Although the percentages of $GR_R$ to *CGR* in the before fruit set were about 40% in all cultivars, after fruit set they fell below 10%. Therefore, in the stage after fruit set, most photosynthates were translocated to the fruits despite the increasing amount of photosynthates that resulted from supplemental lighting; this drastically limited photosynthate partitioning to roots. This was probably caused by a remarkably higher sink strength of fruits than other organs (shoots, roots) as was seen in our previous study (Hidaka et al., 2014). This unbalanced partitioning of photosynthates may provide opportunities for increasing crop yield in the future. In 'Ookimi', the partitioning of photosynthate to shoots after fruit set was remarkably high compared with the low partitioning to fruits, but dry matter production of whole organs was lower in 'Ookimi' than that of the other three cultivars. Therefore, total dry matter production of plants may be influenced by whether fruits were setting.

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