Crown-cooling Treatment Induces Earlier Flower Bud Differentiation of Strawberry under High Air Temperatures

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Global warming is predicted to increase air temperatures. With the aim of ensuring future stable production of strawberry under high autumn air temperatures, we examined the effect of a crown-cooling treatment on flower bud differentiation, flowering characteristics and fruit yield in a June-bearing strawberry (Fragaria × ananassa Duch. cv. Fukuoka S6). We forced strawberries under high air temperature conditions (controlled day/night temperatures of 30/27°C) to simulate future global warming. For approximately 40 d after transplanting in August, strawberry crowns were cooled using a crown-cooling tube filled with water controlled to temperatures of 10, 15, 20 and 25°C. The crown-cooling treatments of 10, 15 and 20°C significantly (P < 0.05) promoted flower bud differentiation in the first inflorescence compared with controls. This earlier differentiation resulted in quicker anthesis, and led to an increase in marketable fruit yield in December. However, continuous cooling treatments of 10 and 15°C after flower bud differentiation negatively affected anthesis and fruit yield. These data suggest that crown-cooling treatment for an appropriate period may be able to stabilize strawberry production under high air temperatures.

Keywords: crown temperature, flowering, forcing culture, global warming, stable production

INTRODUCTION

Over 90% of Japanese strawberry farmers employ forcing to enable harvest from winter to the following spring (Yamasaki, 2013). However, because available production area continues to decline, new techniques to obtain consistently high yields are required. Many factors contribute to fruit yield in strawberry production (Hidaka et al., 2014a). Fruit yield per plant is influenced by factors including per unit fruit weight, fruit number, flower budding, photosynthetic partitioning, leaf photosynthesis, and water and nutrient uptake by roots. These factors are affected by the growing environment (e.g., light intensity, photoperiod, temperature, CO2 concentration, humidity, and wind velocity) and the genetic potential of each cultivar. In our previous studies, we explored the development of environmental control techniques, such as supplemental lighting and CO2 enrichment, to achieve high increases in fruits yield through acceleration of leaf photosynthesis (Hidaka et al., 2013; 2014b; 2015; 2016). However, seeking to increase yields through environmental controls relies on the assumption that flower bud differentiation will be induced normally.

Global warming has recently been reported to have serious potential impacts on water resources, ecosystems, food production and other aspects of life. The Japanese Ministry of Agriculture, Forestry and Fisheries has reported on agricultural issues already known to result from global warming, including high-temperature-related injuries to rice (cracked rice), abnormal fruit coloration, changes in fruit growing zones, and increased incidences of pests and disease (2008). Further, effects of recent warming on agricultural production have been observed throughout the whole of Japan (Sugiura et al., 2012).

Japanese strawberry producers usually use June-bearing cultivars, and flower bud differentiation in these cultivars is induced by short days and low temperatures (Ito and Saito, 1962). However, recently there have been concerns that rising air temperatures in August and September will cause delayed flower bud differentiation in first inflorescences. Many types of localized temperature control systems have been developed to stabilize flower bud differentiation under high-temperature conditions (Mukai and Ogura, 1988; Ikeda et al., 2007; Yamazaki et al., 2007; Miyoshi et al., 2013). Our research group also developed a technique to control the temperature of the strawberry crown, which is the organ containing the shoot apical meristem (Dan et al., 2015). However, few studies have examined the effect of such cooling systems under the high temperatures expected with future global warming.

We calculated likely future air temperatures in the study area based on past recorded temperatures and predictions of future global warming and reproduced these temperature conditions in a greenhouse. We examined the effect of crown-cooling treatments on flower bud differentiation, flowering characteristics and yield under high air temperature with the aim of achieving stable future production of strawberry.

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MATERIALS AND METHODS

Plant materials and growth conditions

Plants were grown on benches installed in a 37 m × 9 m section of a large greenhouse (37 m long × 27 m wide × 4.5 m high) at the National Agriculture and Food Research Organization Kyushu Okinawa Agricultural Research Center, Japan (33°18.4′N, 130°32.8′E). In early June 2015, 250 nursery plants of the June-bearing strawberry (Fragaria × ananassa Duch. cv. Fukuoka S6) selected from mother stock plants were transplanted into plastic pots (6-cm diameter; 0.2 L volume). Connections from the mother plants to the nursery plants were retained through runners. The 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 rooting, the nursery plants were severed from the mother plants in late June, and were supplied with nutrient solution thereafter. The 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. From August 15th, 2015, nutrient supplementation was halted to induce anthesis, and only water was supplied. On August 17th, 2015, the nursery plants, which were still undifferentiated at the first inflorescence in the shoot apical meristem, were transplanted into substrate-filled 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 supplied with only water until September 30th, 2015, and, thereafter, were supplied with nutrient solution at the aforementioned rate until March 31st, 2016. Substrates and nutrient solutions were the same as those used to cultivate the nursery plants, with approximately 3 L substrate per plant. Flower pollination was performed by bees. Fruit thinning was not conducted.

Experimental air temperature conditions

To produce the high air temperatures expected to occur under global warming, we established threshold air temperatures in the greenhouse by using past data for outside air temperatures at the experimental site (Kurume City, Fukuoka, Japan) and predictions from the Japan Meteorological Agency (2013) to simulate potential future air temperatures. Hourly temperature data for the period from August to September 1980 to 2014 for Kurume City were obtained from the Automated Meteorological Data Acquisition System of the Japan Meteorological Agency. Using these data, we calculated the daytime-, nighttime- and daily average air temperatures for the months of August and September from 1980 to 2014. Data from 06:00 to 17:00, 18:00 to 05:00 the following day, and 06:00 to 05:00 the following day were used to calculate the average daytime-, nighttime- and daily air temperature values, respectively.

Figure 1 shows yearly changes in averaged values of daytime-, nighttime- and daily outside air temperatures (Tₑ) in Kurume City in August (a) and September (b) from 1980 to 2014. The average daytime and nighttime temperatures for August gradually increased over time, and the average daily air temperature in the 2010s was about 2°C higher than that of the 1980s. A similar pattern of gradual increases in daytime-, nighttime- and daily average air temperatures was also observed for September. However, the nighttime average air temperature for September showed a remarkably sharper increase over time than that for August. According to a report of projected global warming in Japan (Japan Meteorological Agency, 2013), current daytime-, nighttime- and daily average air temperatures in Fukuoka, which were defined as the average values from 1980 to 1999, will rise by about 3°C each in the future (approximately 2076–2095).

According to our analysis (Fig. 1a, b), the current (1980–1999) average values for daytime- and nighttime air temperatures during August to September were approximately 27°C and 24°C, respectively. Therefore, we estimated that daytime- and nighttime average air temperatures during August to September in Kurume City would be approximately 30 and 27°C, respectively, in the future (approximately 2076–2095).

Based on the air temperature data analysis (Fig. 1) and global warming projections, we decided to maintain the daytime (06:00–18:00) and nighttime (18:00–06:00) air temperatures in the greenhouse to 30 and 27°C using a fuel-burning heater (HK2027TEV, Nepon Inc., Tokyo, Japan) and a pad and fun evaporative cooling system (Kuchen Kogyo. Co., Ltd., Fukuoka, Japan). This high air temperature treatment was conducted in 2015 from August 19th, 2 d after transplanting the nursery plants, to...
September 30th. Thereafter, the daytime air temperature was maintained below 27°C by the pad and fun evaporative cooling system, and the nighttime air temperature was maintained above 8°C with heating provided by a fuel-burning heater until the last day of cultivation (March 31st, 2016). The daytime CO2 concentration inside the greenhouse was maintained at 1,000 μmol mol⁻¹ with a fuel-burning CO2 generator (CG-254S1, Nepon Inc., Japan) from October 2015 to March 2016.

**Crown-cooling treatment**

Figure 2 shows the crown-cooling system. The system consisted of a chiller (CA-1112, Tokyo Rikakikai Co., Ltd., Tokyo, Japan) and a crown-cooling tube (Fig. 2a) and a crown-cooling tube (Fig. 2b). The crown-cooling treatment was carried out by controlling the temperature of water flowing in the crown-cooling tube (made of polyvinyl chloride, 3 cm × 11 m each) placed on the strawberry crown (Fig. 2c). We applied the crown-cooling treatment at four different temperatures, 10°C, 15°C, 20°C, 25°C as well as no treatment (control). The water temperature in the tube was maintained at the threshold temperatures by regulating cooling with the chiller thermostat. Individual crown-cooling systems were used in the respective treatments. The crown-cooling treatments were conducted continuously from August 19th to September 30th, 2015.

**Measuring environmental conditions**

During the experiment, we monitored the air temperature inside the greenhouse. A temperature recorder (TR-76Ui, T&D Corporation, Nagano, Japan) was placed in the center of the greenhouse. The water temperature in the crown-cooling tube and soil temperature in the beds were also measured. Temperature sensors (TR-52i, T&D Corporation, Japan) were set on the circulation water tank in the chiller and 10 cm below the base of plants to measure water and soil temperatures, respectively. Air, water and soil temperatures were automatically recorded every 10 min. Crown temperature was also measured by setting thermocouples between the crown-cooling tube and plant crowns (Fig. 2c). Crown temperatures were automatically recorded every 10 min by a data logger (GL200A, Graphtec Co., Ltd., Yokohama, Japan).

**Analyses of flower bud differentiation, flowering characteristics and fruit yield**

To analyze the effects of the crown-cooling treatment on flower bud differentiation under high air temperatures, we investigated changes in the flower bud development stage of the first inflorescence in the apical meristem. Five plants from each treatment were harvested each week on the 24th and 31st of August, and the 4th, 7th, 14th, 21st, and 28th of September, 2015. All expanded leaves were removed from the harvested plants. Then, unexpanded leaves enclosing the terminal apex were removed by a sharp needle while looking through a stereomicroscope (SMZ-2T, Nikon Corp., Tokyo, Japan). This was done to make the terminal apex visible. The terminal apex was then stained with methyl blue, and microphotographs were taken to determine the flower bud development stage. From the microphotograph examination and using a reference report (Jahn and Dana, 1970), flower bud development was classified into 9 stages (Fig. 3). These stages were: 0, the vegetative apex stage; 1, the early apex enlargement stage; 2, the middle apex enlargement stage; 3, the later apex enlargement stage; 4, the apex division stage; 5, the sepal development stage; 6, the stamen development stage; 7, the pistil development stage; and 8, the epidermal hair development stage. In this study, the timing of flower bud differentiation was determined at the apex division stage (stage 4).

To analyze the effects of crown-cooling treatment on flowering under high air temperatures, we recorded the flower bud emergence and flowering dates. These were defined as the dates of emergence and anthesis of the first flower, flowering of the first and second inflorescences, and the number of flowers in the first inflorescence. We...
analyzed 10 plants per treatment.

To determine the effects of crown-cooling treatment on yield under high air temperatures, marketable fruit (fresh weight ≥ 6 g per fruit) were harvested from 10 plants in each treatment. Harvested fruits were weighed, and the number of fruits was recorded.

**Statistical analysis**

Data for flowering characteristics and fruit yield were analyzed by one-way analysis of variance. Significant differences between means for different treatments were determined using the Tukey-Kramer test. For flower bud development stages, significance differences between means for different treatments were tested with the Wilcoxon rank sum test. All statistical analyses were performed using SAS software version 9.2 and JMP version 11.2 (SAS Institute Inc., Cary, NC, USA).

**RESULTS AND DISCUSSION**

Figure 4 shows diurnal changes in air temperature inside the greenhouse (a), water temperatures in the crown-cooling tubes (b), soil temperatures in the beds (c) and crown temperatures (d) under the different crown-cooling treatments. Under the heating treatment, the air temperature inside the greenhouse was maintained at approximately 30°C in the daytime (06:00–18:00). In the nighttime (18:00–next 06:00), the air temperature was maintained at approximately 27°C. Thus, the daytime- and nighttime air temperatures were adequately controlled at threshold temperatures. Thus, the air temperature conditions in the greenhouse sufficiently simulated the air temperatures predicted for future global warming conditions.

Water temperatures in the 10, 15, 20 and 25°C crown-cooling treatments were adequately controlled at the desired threshold temperatures throughout the experiment. Soil temperature in the control increased starting at 06:00 and reached a maximum temperature of 29°C at 16:00; after 18:00, the temperature decreased. More gradual increases and decreases were observed in soil temperatures than air temperatures under all treatments (Fig. 4a, c). Under the crown-cooling treatments, soil temperatures decreased. Approximately 4 and 1°C decreases in soil temperature were observed under the 10 and 20°C treatments, respectively, at 12:00 compared with that of the control. After 06:00, crown temperature in the control increased with air temperature, and reached 30°C at 12:00. Crown temperatures in the 10, 15, 20 and 25°C treatments fluctuated around 11–13°C, 15–17°C, 20–22°C and 25–27°C, respectively. Under the crown-cooling treatments, crown temperatures decreased by approximately 18, 13, 8 and 4°C under the 10, 15, 20 and 25°C treatments at 12:00 compared with that of the control. Thus, the crown-cooling treatment has a much greater effect on crown temperatures than soil temperatures under high air temperature conditions (Fig. 4c, d).

Figure 5 shows temporal changes in flower bud development under the different crown-cooling treatments. In the control, flower bud development showed almost no change from stage 0 until September 14th. From this point, flower bud development in the control progressed to stage 1 by September 21st, and reached to almost stage 4 by September 28th. Under the 10°C crown-cooling treatment, flower bud development reached stage 4 by September 14th, indicating that cooling treatment promoted faster bud development. Flower bud development under the 15, 20 and 25°C treatments reached stage 4 on September 15th, 18th and 26th, respectively. On September 28th, flower bud development had reached stage 8 in the 10°C treatment, stage 7 in the 15 and 20°C treatments and stage 5 in the 25°C treatment group.

We investigated significant differences in flower development stages between treatments on September 14th and 28th (Fig. 4a, b). On September 14th, flower bud development in the 10, 15 and 20°C treatment groups had progressed significantly faster than in the 25°C treatment and control groups. In the 10°C treatment group, in particular, flower bud development had already reached the apex division stage. On September 28th, flower bud
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Development in the 10, 15 and 20°C treatment groups had progressed significantly faster than in the 25°C treatment and control groups. Further, bud development under the 10°C treatment had progressed significantly faster than that of the 20°C group. Significant differences between stages in the 25°C treatment and control groups were not observed for September 14th or 28th.

Nitrogen levels affect flower bud differentiation in June-bearing strawberry (Furuya et al., 1988). Fertilizing plants during flower bud development causes plants to revert from reproductive growth to vegetative growth (Morishita and Yamakawa, 1991), which may cause subsequent delays in anthesis and harvest times. Therefore, determining the timing of flower bud differentiation, which is necessary for subsequent fertilization, is very important to the stable yield of fruits. Morishita and Yamakawa (1991) suggested that flower bud differentiation should be determined based on the stages later after the middle apex enlargement stage (stage 2 in Fig. 3); however, this middle stage can easily be mistaken for the early stage (1) and later stage (3) of apex enlargement because they are very similar in appearance. Therefore, the timing of flower bud differentiation in this study was determined by the apex division stage (stage 4), which is more easily distinguished by the shape of the terminal apex than the stages of apex enlargement (stages 1–3).

The 10°C treatment induced earlier flower bud differentiation than in the control, which still showed an undifferentiated apex on September 14th. Flower buds in the 15 and 20°C treatments were also differentiated by the 15th and 18th of September, which was significantly earlier than in the control (September 28th). According to these results, the crown-cooling treatments clearly promoted earlier flower bud differentiation in strawberry grown under high air temperature conditions, and this effect became more pronounced as the treatment temperatures were lowered.

Table 1 shows the effect of crown-cooling treatments on flowering characteristics. Crown-cooling treatments clearly promoted flower bud emergence in the first inflorescence. The dates of flower bud emergence in the 10, 15, and 20°C treatment groups were approximately 8, 8, and 5 d earlier than that of control. Furthermore, crown-cooling treatment also hastened anthesis. The dates of anthesis in the 10, 15, and 20°C treatment groups were approximately 7, 6, and 4 d earlier than that of control. Crown-cooling treatment also affected flower number; the greatest and least numbers of flowers were observed in the 20°C treatment and control groups, respectively. Flower numbers in the 15 and 10°C treatment groups were lower than that of the 20°C treatment group, and numbers in the 10°C treatment group were slightly lower than those in the 15°C treatment group. For the second inflorescence, only the 20°C treatment showed a tendency towards earlier flower bud emergence among all the groups. Furthermore, the date of anthesis was also earliest in the 20°C treatment.

Different responses to the crown-cooling treatments were observed in flowering characteristics between the first and second inflorescences. In the first inflorescence, the crown-cooling treatment clearly promoted earlier flower bud emergence and subsequent anthesis of plants grown under high air temperature conditions. This effect became more pronounced as the treatment temperature was
Yoshida et al. (1991) reported that flower bud development and anthesis were only 8 and 7 d earlier than those of control. However, although the date of flower bud differentiation under the 10°C treatment was 14 d earlier than that of the control, the dates of bud emergence and differentiation under the 10°C treatment was 14 d earlier (Figs. 5 and 6). However, although the date of flower bud differentiation by the crown-cooling treatment (see Table 1) was hastened under high temperature conditions after the pistil differentiation stage. Therefore, it is likely that crown-cooling treatment promotes flower bud differentiation, but after flower bud differentiation, treatment delays bud emergence and subsequent anthesis. Thus, the less pronounced effect of the crown-cooling treatments in the anthesis stage (Table 1) compared with the flower bud development stage (Fig. 5) may relate to a delay in plant growth caused by continuous crown-cooling treatment after flower bud differentiation.

In the second inflorescence, although the crown temperatures under the 10 and 15°C treatments were lower than under the 20°C treatment (Fig. 4d), flower bud emergence and anthesis were later under the cooler treatments. This was probably caused by a delay in plant growth under continuous crown-cooling treatment after flower bud differentiation. According to Fujime and Yamasaki (1988), dormancy, which causes dwarfing and suspension of growth, was induced in ‘Hoko-wase’ strawberries grown under the comparatively low temperature of 15°C. At 10 and 15°C, continuous crown-cooling treatment may have induced dormancy, which perhaps resulted in the later bud emergence and anthesis compared with the 20°C treatment.

Figure 7 shows the average fruit weight, number of fruits, and marketable yield under the different crown-cooling treatments. A tendency toward lower average fruit weights were observed in the 10, 15 and 20°C treatment groups compared with those in the 25°C and control groups, but significant differences were not observed. Fruit numbers in December in the 10 and 15°C treatment groups were higher than that of the control group. Throughout the entire growing season (December to March), fruit numbers in the 20 and 25°C treatment groups were about 1.3 and 1.2 times greater than that of the control. However, fruit numbers in the 10 and 15°C treatment groups were almost the same as that in the control. Marketable yield per plant had a similar trend to fruit number; and the marketable yields in December in the 10 and 15°C treatment groups were 2.8 times higher than that of control. Throughout the entire season, fruit yields in the 20 and 25°C treatment groups were about 1.1 times higher than that of the control. However, fruit yields in the 10 and 15°C treatment groups were almost the same as that in the control.

The marketable yield reflected fruit number to a greater extent than the average fruit weight and followed an almost identical trend to fruit number. In December, the marketable yield was almost identical trend to fruit number. In December, the

Table 1  Effect of crown-cooling treatment on flowering characteristics.

| Crown-cooling Treatment | First inflorescence | Second inflorescence | Leaf number between 1st and 2nd inflorescence |
|-------------------------|---------------------|---------------------|----------------------------------------------|
|                         | Bud emergence      | Anthesis            | Flower number                                | Bud emergence | Anthesis |                                |
| Control                 | Nov. 7 ± 1 a       | Nov. 18 ± 1 a       | 10.1 ± 0.9 b                                 | Jan. 19 ± 4 a | Feb. 17 ± 3 a | 5.2 ± 0.1 ab |
| 10°C                    | Oct. 30 ± 1 c      | Nov. 11 ± 1 b       | 11.9 ± 1.6 ab                                 | Jan. 18 ± 4 a | Feb. 12 ± 3 a | 4.7 ± 0.2 ab |
| 15°C                    | Oct. 30 ± 2 c      | Nov. 12 ± 1 b       | 12.1 ± 0.9 ab                                 | Jan. 19 ± 4 a | Feb. 15 ± 3 a | 5.3 ± 0.2 ab |
| 20°C                    | Nov. 2 ± 1 bc      | Nov. 14 ± 1 ab      | 15.8 ± 1.4 a                                 | Jan. 6 ± 10 a | Jan. 28 ± 11 a | 4.2 ± 0.5 b  |
| 25°C                    | Nov. 5 ± 1 ab      | Nov. 17 ± 1 a       | 13.4 ± 1.2 ab                                 | Jan. 24 ± 4 a | Feb. 19 ± 2 a | 5.7 ± 0.2 a  |

*, ** indicate significant differences at P<0.05, P<0.001, NS, not significant (P≥0.05).

Control, no treatment; 10°C, crown-cooling at 10°C; 15°C, crown-cooling at 15°C; 20°C, crown-cooling at 20°C; 25°C, crown-cooling at 25°C. Data are mean ± S.E. (n=10). Results of one-way analysis of variance with crown-cooling treatment are shown in each column. Different letters indicate significant differences by Tukey-Kramer test for 5 treatments (P<0.05). *, ** indicate significant differences at P<0.05, P<0.001. NS, not significant (P≥0.05).

lowered. This promotion of earlier flower bud emergence and anthesis may be the result of the promotion of flower bud differentiation by the crown-cooling treatment (see Figs. 5 and 6). However, although the date of flower bud differentiation under the 10°C treatment was 14 d earlier than that of the control, the dates of bud emergence and anthesis were only 8 and 7 d earlier than those of control. Yoshida et al. (1991) reported that flower bud development
market price for strawberry is high in Japan, making it an optimal time for harvest. In this study, the 10 and 15°C treatments resulted in an increase in December fruit yield. This December yield increase may have resulted from the fact that strawberries were ready to harvest earlier because of the earlier flower bud differentiation and subsequent anthesis (Figs. 5, 6 and Table 1). The positive effects from the 10 and 15°C treatment groups decreased in March. This may reflect a delay in plant growth under continuous crown-cooling treatment after flower bud differentiation. The higher yield from the 20 and 25°C treatment groups may have resulted from normal growth due to moderate crown temperatures compared with the high crown temperatures in the control (Fig. 4d).

From these results, we see that the crown-cooling treatments promoted earlier flower bud differentiation, and increased the volume of the December fruit yield. However, after flower bud differentiation, continuous low temperature treatments (at 10 and 15°C) negatively affected anthesis and fruit yield.

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