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High Temperature Suppresses Fruit/Seed Set and Weight, and Cladode Regreening in Red-fleshed 'Da Hong' Pitaya (*Hylocereus polyrhizus*) under Controlled Conditions

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***Abstract.* Following high summer temperatures in Taiwan, erratic fruit production and yellowed cladode have been observed in red-fleshed 'Da Hong' pitaya (*Hylocereus polyrhizus*). However, the specific environmental influences that result in the yield loss and cladode damage are unknown. The aim of this study was to evaluate how high temperature affects fruit production and cladode yellowing of 'Da Hong' pitaya under controlled conditions. One-year-old field-grown potted plants with moderately yellow-colored cladodes were placed in the phytotron at either 40/30 °C ± 1 °C [day/night, high-temperature treatment (HT)] or 30/20 °C ± 1 °C [day/night, control (CK)] during the natural long-day reproductive period. Floral bud development duration, flower opening behavior, fruit set and development, as well as fruit characteristics and seed setting (which was expressed as the estimated number of seeds), and the weight per fruit at harvest were investigated. In addition, the percentage of dry matter and color change (regreening) of cladodes were examined. We found that floral bud development was completed 8 days earlier than the control, but the time of blooming was 2 to 3 hours later within a day; and fruit set, fruit size, seed weight, and peel color were strongly suppressed in HT-treated plants compared with the control. Furthermore, both the estimated seed number and seed weight were positively correlated with fruit weight, suggesting that reduced seed setting and weight arising from incomplete fertilization in the HT plants may have resulted in fruit drop and smaller fruit. Although the color on the sunny (sun-exposed) side of the cladode remained yellow, the percentage of dry matter in the HT cladodes was not significantly different from the control, indicating that the yellow-colored cladodes did not reduce their carbon supply potential. The results indicate that HT during bloom led to poorer fruit set and lower fruit weight, presumably due to lower seed setting/weight per fruit arising from incomplete fertilization. The HT treatment also caused less regreening of cladodes, but this did not seem to impact fruit production. Further study is required to ascertain whether disrupted stamens or pistils resulting from HT treatment lead to incomplete fertilization.**

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Pitaya, or dragon fruit (*Hylocereus* spp.), is a climbing cactus native to South and Central America that grows in the shade of canopy trees (Mizrahi et al., 1997). It is an emerging commercial fruit crop grown worldwide, particularly in Vietnam, Taiwan, Malaysia, Indonesia, and Israel (Mizrahi et al., 1997; Ortiz-Hernández and Carrillo-Salazar, 2012). In Taiwan, the production of pitaya has increased substantially over recent decades (Council of Agriculture, 2019) due to its high price and increasing market demand. Normally, red-fleshed pitaya (*H. polyrizus*) is produced in Taiwan from May to December, and the production peak begins from July to September (Chu and Chang, 2020); however, a night-breaking technique has been used to extend off-season production (Jiang and Yang, 2015).

'Da Hong', also known as 'Big Red', is an elite red-fleshed cultivar preferred by growers in Taiwan and Southeast Asia because of its favorable traits including self-compatibility, abundant yield, large fruit (more than 400 g per fruit), and high total soluble solid content (TSSC, above 20 °Brix) (Jiang and Yang, 2015; Liu et al., 2015). However, unlike the red-fleshed cultivar Fu Gui Hong or VN White, a white-fleshed pitaya (*H. undatus*) cultivar, Da Hong does not produce high fruit yield all of the year in Taiwan (Chien and Chang, 2019). It has been found that although 'Da Hong' produces the most abundant flowers and fruits during the hottest period (August to September), the fruits are small (less than 150 g) and the color of the cladode becomes yellow under field conditions (Y.C. Chu and J.C. Chang, unpublished data; Chiu et al., 2015) and in net-house grown plants (Chien and Chang, 2018). Therefore, these conditions result in an erratic yield and variable fruit quality. It appears that 'Da Hong' may be more vulnerable to high temperature stress compared with 'Fu Gui Hong' and 'VN White'; however, a more detailed clarification of the responses of 'Da Hong' to high temperature stress has yet been done.

Pitaya produces fruit that contains thousands of tiny seeds (Hsu, 2004). Moreover, Weiss et al. (1994) reported a positive relationship between seed weight and fruit/pulp weight in pitaya under favorable conditions; however, there is no information available on how heat stress affects fruit production, such as its effect on yield and quality, in terms of fruit weight and sweetness. It has yet to be reported whether flowering under high summer temperatures results in a decrease in seed setting (which is expressed as the estimated number of seeds), and if seed weight exacerbates fruit drop or reduces fruit size.

Although pitaya has a crassulacean acid metabolism (CAM) characteristic, it is prone to yellowing of the cladode, i.e., slight sunburn with no incidence of necrosis on the sunny (sun-exposed) side of the adaxial cladode that has three flat wavy ribs with one sunny side and two shaded sides in red-fleshed pitaya, during the hot season in Taiwan, followed by regreening during cooler seasons (Chien and Chang, 2019). Of the pitayas, the cladode of the white-flesh pitaya displays the highest total daily net uptake of CO_2 at day/night air temperatures of 30/20 °C, but the total daily net uptake of CO_2 falls remarkably at 40/30 °C (Nobel and De la Barrera, 2002), indicating that dry matter accumulation may be affected by temperature regimes. Cladode necrosis begins to occur after 6 weeks of exposure to 40/30 °C, especially when light intensity exceeds photoinhibition, and severe necrosis occurs with prolonged duration of high temperature (Nobel and De la Barrera, 2002). In Israel, it has been shown that extremely high summer temperatures (38/20 °C) inhibit flower bud formation, which directly leads to yield reduction (Nerd et al., 2002; Nobel and De la Barrera, 2002; Raveh et al., 1998). However, the resulting effects of heat stress on dry matter accumulation and how that change affects flowering, fruit set, and fruit development are still unknown.

The aim of this study was to ascertain whether HT during flowering affects floral bud development duration, flower opening behavior, fruit set, fruit weight, seed setting, which was expressed as the estimated number of seeds, and seed weight per fruit, and cladode discoloration in ‘Da Hong’ red-fleshed pitaya plants under controlled conditions.

Materials and Methods

Plant materials and pretreatments. One-year-old, field-grown, potted red-fleshed ‘Da Hong’ pitaya plants grown at Kaohsiung District Agricultural Research and Extension Station (KDARES) in Pingtung, southern Taiwan (lat. 22.42°N, long. 120.31°E), were used in this study during the Summer of 2015.

Da Hong was selected because it is a popular cultivar that may be sensitive to HT during flowering, which may result in reduced yield and slight sunburn (yellowed) cladodes. Each potted plant was cultivated in a 15-L pot with support from a bamboo pole and had three to five mature cladodes, and at least two to three cladodes were flowering. The potted plants received routine cares following the Taiwan Good Agricultural Process guidelines (Council of Agriculture, 2011). The potted plants were well watered with a drip irrigation system, and balanced N–P–K (15–15–15) liquid fertilizer was added to the drip irrigation system every week to maintain plant growth before treatment. All flower buds were removed before the beginning of the experiment to maintain the plant vigor.

Considering the finite space within the phytotron, which was 3.8 m in length and 2.4 m in width, four uniform and high-vigor potted plants were selected for each treatment (Fig. 1). Although ‘Da Hong’ can set fruit after blooming naturally, and there are 14–16 flowering waves during the natural reproductive period in Taiwan, only 1–2 flowers; and thus, 1–2 fruit per cladode were retained to guarantee fruit quality in each wave of flowering for commercial production (Chen, 2015; Chiu et al., 2015). To avoid excess crop loading affecting the temperature effect and to ensure fruit quality, only one flower and subsequently one fruit were left for each flowering wave of each cladode per potted plant in this study. In total, only one flowering wave and consequently 2–3 fruits were retained per plant.

Three days after flower bud formation (23 July), selected plants were transferred into a phytotron greenhouse to acclimate them for further treatment or applying the conditions of the control. The plant cladodes were slightly yellowed due to suffering moderate HT (average 36/26 °C day/night temperature) and high solar radiation in the field before the beginning of the experiment.

Ambient temperature monitoring and control. A comparative experimental design was implemented to assess the responses of flowering to high temperature and optimal control conditions. The experiment was conducted from July to September in 2015 in the phytotron at KDARES when the natural reproductive photoperiod is 12–13 h, and therefore, no prolonged lighting was required (Jiang et al., 2012). A high temperature of 40/30 °C (day/night; HT treatment) was set and compared with an optimal temperature of 30/20 °C [day/night; control (CK) treatment]. The temperature and relative humidity (RH) were recorded using a data logger (HOBO UX100-003; Onset Computer Corp., Bourne, MA). The actual temperature used ±1 °C of the set temperatures in the phytotron during the experimental period, and the RH were 75% to 85% and 65% to 75% in the CK treatment and HT, respectively. About 20% to 30% (data not shown) of the light intensity was shaded in the phytotron glasshouse compared with that of the open field. However, the reduction of light did not decrease plant growth (data not shown).

Floral bud development duration, flower opening behavior, and flower characteristics. The total targeted flower number in the four potted plants of CK and HT were 9 and 10, respectively. Duration from floral bud formation to flowering and the daytime of opening behavior was recorded. The time of sepal and petal opening and displaying a visible sigma was recorded as initial bloom. Full bloom was recorded when petal opening reached the widest diameter. The time of flower closure on the next day with an invisible stigma was recorded as well.

Flower characteristics, including the length of flower, length of non-ovary organs (comprised of petal, style, stigma, and stamen), length of ovary (Fig. 2), and diameter and perimeter of the ovary were recorded at 1600 HR on days when flowers bloomed.

Fruit and seed set, fruit development and characteristics. All plants were self-compatible and self-pollinated. In this study, fruit drop occurred on the sixth day after bloom in HT plants; therefore, the fruit set was examined 1 week after flowering. The fruit characteristics of nine fruit set on the four CK potted plants and the three fruit set on the three HT potted plants were investigated at harvest.

Fruit length and width of CK and HT were measured every 2 d from the seventh to the 33rd, and the 35th days after blooming, respectively. Fruits of both treatments were harvested 37–38 d after flowering when the peel color of the style end turned red in both treatments. Fruit characteristics, such as individual fruit weight, longitudinal diameter, transversal diameter, flesh weight, peel weight, edible weight, TSSC in the central section at the equatorial zone, seed weight, and seed setting, which was expressed as the estimated number of seeds, and weight were recorded at harvest. The estimated seed number per fruit = seed weight per fruit / (weight of 100 seeds / 100); whereas, the average weights of 100 seeds were 0.113 g and 0.111 g for CK and HT, respectively (data not shown). The HT might have no significant effect on the individual seed weight. Therefore, the estimation of the number of seeds should be valid. In addition, the peel color (mainly expressed as the a* value) at the equatorial zone on both the sunny side and the shaded side of fruit were measured using a spectrophotometer (ColorLite sph860; Katlenburg-Lindau, Germany).

Cladode yellowing and dry weight. Cladode yellowing caused by HT was recorded as a b* value by spectrophotometer (ColorLite sph860). Only the sunny side rather than two shaded sides of the cladode was measured weekly.

Each cladode in each potted plant was cut at harvest, and cladodes with and without fruit were separated for evaluation. The total fresh weight of each cladode was measured. Because the length of each cladode was different, the fresh/dry weight was performed as weight per 10-cm section along with the cladode to account for the different lengths of the cladodes. Cladode dry weights were recorded after oven drying for 1 week at 60 °C to determine the percentage of dry matter and water content.

Fig. 1. The phytotron experiment with potted plants was performed in this study

Fig. 2. Floral morphology and anatomical structure of ‘Da Hong’ pitaya. Non-ovary organs (NO); ovary (O). NO was comprised of sepal (S), petal (P), stamen (STM), stigma (STG), and style (STY).

Table 1. Effects of high temperature on floral bud development duration and flower opening behavior in ‘Da Hong’ pitaya in 2015.

Treatment[z]	Floral bud development duration (day)	Time of initial bloom[y] (daytime)	Time of full bloom[x] (daytime)	Time of flower closure[w] (daytime)
HT	15 b[v]	2000 HR	2300 HR	1000 HR
CK	23 a	1830 HR	2000 HR	0800 HR

[z]Treatment: HT, high temperature: air day/night temperature at 40/30 °C; CK, control: air day/night temperature at 30/20 °C.
[y]Time of sepal and petal opening with visible stigma.
[x]Time of petal opening with the widest diameter.
[w]Time of petal closure with the stigma being covered.
[v]Means within each column followed by the different letters are significantly different at $P < 0.05$ by Unpaired Student’s *t* test, n = 4.

Table 2. Comparison of flower characteristics at bloom and fruit set at the seventh day in ‘Da Hong’ pitaya in 2015.

Treatment[z]	Length of whole flower (cm)	Length of non-ovary organs of flower (cm)	Perimeter of ovary (cm)	Diam of ovary (mm)	Length of ovary (mm)	Fruit set[y] (%)
HT	33.0 b[x]	25.0 b	13.2 a	36.7 a	80.2 a	29.2 b
CK	35.8 a	27.1 a	13.8 a	39.4 a	87.8 a	100.0 a

[z]Treatment: HT, high temperature: air day/night temperature at 40/30 °C; CK, control: air day/night temperature at 30/20 °C.
[y]Fruit set were recorded at seventh day after pollination.
[x]Means within each column followed by the different letters are significantly different at $P < 0.05$ by Unpaired Student’s *t* test, n = 4.

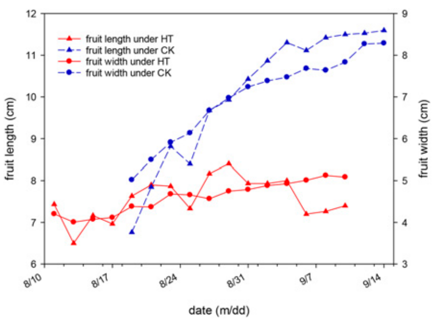

Fig. 3. Fruit growth of ‘Da Hong’ pitaya under control (CK, 30/20 °C) and high temperature (HT, 40/30 °C) treatments in 2015. Fruit length and width of CK (n = 4) and HT (n = 3, initially n = 4) were measured every two days from the seventh day to thirty-third and thirty-fifth days after bloom, respectively.

Statistical analysis. Data were analyzed using an unpaired Student’s *t* test at the 5% significance level ($P < 0.05$) with SigmaPlot 14.0 (Systat Software, Inc, San Jose, CA). The correlations between the seed weight and fruit weight/flesh weight as well as the estimated number of seeds and fruit weight/flesh weight were calculated using SigmaPlot 14.0 (Systat Software, Inc).

Results

Floral bud development duration, flower opening behavior, and flower characteristics. Flowers of HT plants bloomed 15 d after the formation of floral buds, which was eight days earlier than those of CK plants (Table 1).

Flowers of HT plants initially opened (bloomed) and displayed a visible stigma at 2000 HR and withered at 1000 HR the following day (Table 1), which was 2–3 h later than CK plants (Table 1). Furthermore, the lengths of the whole flower and non-ovary organs of HT plants were shorter than CK plants (Table 2), while there was no significant difference in perimeter, diameter, or length of the ovary between the treatments (Table 2).

Fruit and seed set, fruit development and its characteristics. All CK plants set fruit successfully after flowering. Conversely, in HT plants, only 29.2% of the flowers set fruit (Table 2). Due to server fruit drop, only three of the four potted HT potted plants with fruit were investigated in the following study further. In CK plants, the fruit displayed a sigmoid pattern based on the growth rates of fruit length and width and developed rapidly after flowering (Fig. 3), while the fruits of HT plants developed much slower (Fig. 3), and the peel color faded at the beginning of fruit growth. The HT also had no discernable effect on accelerating fruit maturation, and all fruits from both treatments were harvested 37–38 d after flowering.

The average fruit weights of CK and HT plants were 423 g and 110 g, respectively (Table 3). The HT treatment significantly suppressed fruit growth and reduced fruit size, resulting in inferior fruit weight, longitudinal diameter, transversal diameter, flesh weight, and peel weight when compared with the control (Table 3). The edible part of the fruit from the CK- and HT-treated plants constituted 75.7% and 50.7% of the fruit, respectively (Table 3), and HT-treated plants had less fruit flesh. Additionally, HT plants had lower seed weight per fruit than the control. Less than 1 g of seed set from the fruit of HT plants, while 6.4 g of seed set per fruit in CK plants (Table 3). In addition, the estimated number of seeds per fruit (seed setting) of the CK and HT treatments were 5664 and 496, respectively. Positive relationships were observed between seed weight and fruit/pulp weight as well as between the number of seeds and fruit/pulp weight (Fig. 4). However, there was no significant difference in the TSSC between the two treatments (Table 3). The HT treatment not only reduced the fruit size but also caused some fruit to shrivel (Fig. 5).

There was no difference in the peel color (a* value) on the shaded side of the fruit between the two treatments at fruit maturation (Table 4); however, the peel color on the sunny side of the fruit in HT plants had a much lower a* value compared with the control (Table 4).

Cladode yellowing and dry matter accumulation. Under the CK treatment at an optimal temperature, the cladode was moderately yellow before treatment, and it rapidly regreened after being transferred into a controlled environment. There was a significant reduction in the b* value of the adaxial cladode two weeks after treatment (Fig. 6). Although less regreening occurred on the cladode at HT than CK (Fig. 6), there was no incidence of necrosis in cladodes after HT treatment (Fig. 7).

No significant difference in fresh weight of the cladodes was detected between the HT and CK plants (Table 5). Furthermore, no significant difference in the dry matter or water content was recorded between the two treatments either, suggesting that moderate yellowing of cladodes under HT does not reduce the carbon supply potential to fruit. In this study, only 1 fruit was retained per cladode and 1–3 fruits were retained for each potted plant.

Discussion

The study examined the responses of the reproductive process of ‘Da Hong’ pitaya to high temperature stress.

The HT accelerated floral bud development but delayed bloom by about 2 h within a day in red-fleshed pitaya ‘Da Hong’ (Table 1). Previous studies have suggested that both hot as well as cool temperatures lead to later flower closure in pitaya (Zee et al., 2004).

Flower opening and closing are controlled by the petal movement, which is induced by the difference in growth rates of the two sides (van Doorn and van Meeteren, 2003). Cell elongation and turgor pressure are also involved in flower opening (van Doorn and van Meeteren, 2003). Studies with HT over 35/25 °C have reported a reduction in stomata conductance in pitaya (Nobel and De la Barrera, 2002; Yamori et al., 2014). However, there was no significant reduction in the water content in the stems of HT plants

Table 3. Comparison of fruit characteristics in 'Da Hong' pitaya at harvest in 2015.

Treatment[z]	Fruit wt[y] (g)	Longitudinal diam (cm)	Transversal Diam (cm)	Flesh wt (g)	Peel wt (g)	Edible Part (%)	Seed wt per fruit (g)	Estimated number of seeds per fruit[x]	Total soluble solid content (°Brix)
HT	110 b[w]	7.7 b	4.8 b	59 b	51 b	50.7 b	0.6 b	496 b	20.3 a
CK	423 a	10.8 a	8.3 a	322 a	101 a	75.7 a	6.4 a	5664 a	19.2 a

[z]Treatment: HT, high temperature: air day/night temperature at 40/30 °C; CK, control: air day/night temperature at 30/20 °C.
[y]Fruits were harvested at around 37–38 d after pollination.
[x]Estimated seed number per fruit = seed weight per fruit / (weight of 100 seeds / 100); the average weight of 100 seeds was 0.113 g and 0.111 g at CK and HT, respectively.
[w]Means within each column followed by the different letters are significantly different at $P < 0.05$ by Unpaired Student's *t* test, n = 3(HT), n = 4(CK), respectively.

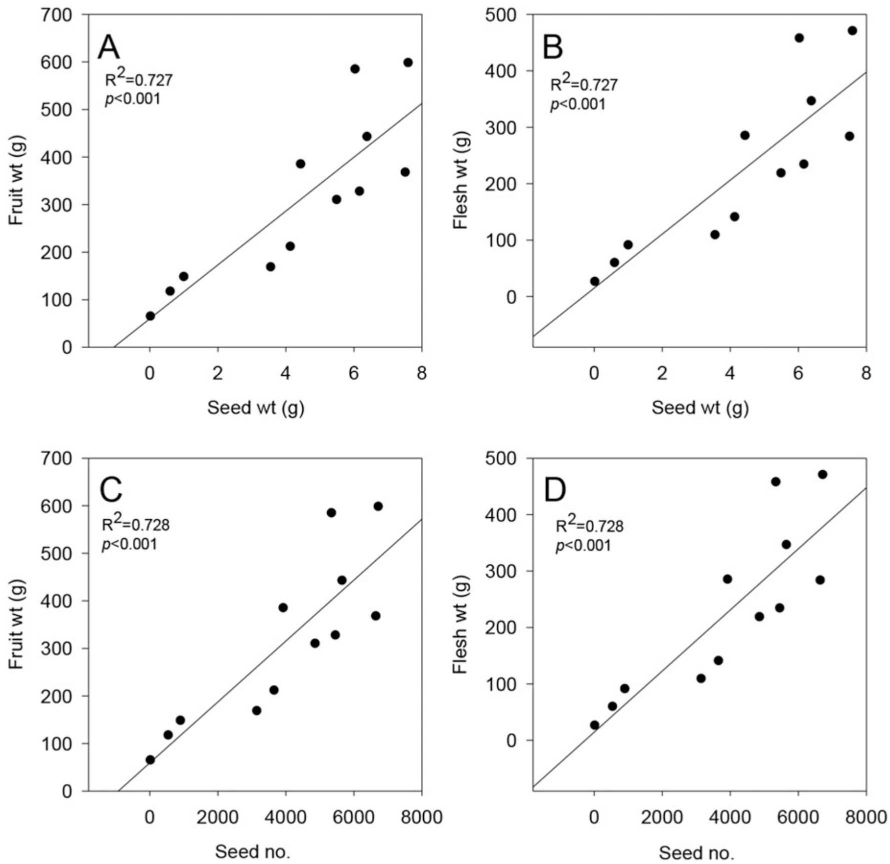

Fig. 4. The relationships between seed weight and fruit weight (**A**) / flesh weight (**B**) per fruit as well as the relationship of the number of seeds and fruit weight (**C**) / flesh weight (**D**) per fruit of 'Da Hong' pitaya harvested in 2015; n = 12 fruit harvested from the two treatments.

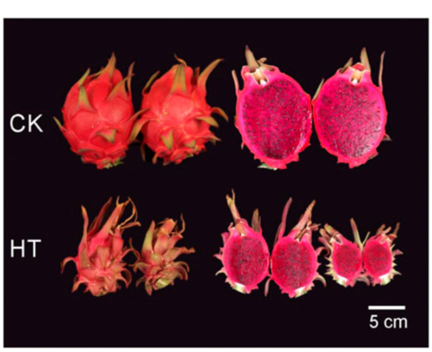

Fig. 5. Fruits characteristics of 'Da Hong' pitaya at harvest under control (CK, 30/20 °C) and high temperature (HT, 40/30 °C) treatments in 2015.

(Table 5), and the cell turgor pressure and water potential were not measured in this experiment, suggesting that further examination is required to determine whether water deficiency, as a consequence of heat stress, may have delayed blooming. Moreover, HT plants had a similar flower opening sequence during the daytime to CK plants despite the heat delaying blooming (Table 1), indicating that floral structure and self-compatibility in 'Da Hong' might not be changed by HT.

The HT resulted in significantly shortened flower lengths, especially in the non-ovary organs (Table 2), which may be in part because of shorter floral bud development duration (Table 1). Nevertheless, there was no significant decrease in the ovary characteristics (Table 2) unlike the peach, HT (25 to 30 °C) reduced both flower size and ovary diameter (Kozai et al., 2004). However, in this study HT caused a remarkable fruit drop in 'Da Hong' (Table 2). Moreover, the remaining fruit in HT plants only had one-fourth of the fruit weight and one-tenth of the seed set as fruit from CK plants (Table 3). Consistent with the results reported by Hsu (2004) and Weiss et al. (1994), an increase in fruit/pulp weight along with increasing seed weight and an additional number of seeds was found in this study, also (Fig. 4). Overall, HT during floral bud development until fruit ripening suppressed fruit set and fruit weight in 'Da Hong' pitaya (Tables 2 and 3), which may have been caused by lower seed set per fruit arising from incomplete fertilization.

'Da Hong' is a well-known, self-compatible variety with abundant yield; thus, the fertilization is unaffected by self-pollination. Cheng and Weng (2000) reported that 25 to 30 °C is the optimal incubation temperature for pollen germination of 'DR3' *H. polyrhizus* in vitro, and less than 20% of the pollen germinates at 35 to 40 °C. Moreover, Weiss et al. (1994) indicated that lower pollen germination caused the poor fruit set and smaller fruit production in pitaya. Therefore, unlike HT causing reduction of fruit setting by the abnormal embryo sac instead of pollen viability in peach (Kozai et al., 2004), the lower fruit set and seed setting/weight seemed to be a result of incomplete fertilization under HT as a consequence of the poor pollen viability in this study. However, degradation of the embryo sac under HT could not be excluded because a high temperature effect on embryo sac fertility is yet to be examined. There is a need for further study to clarify whether poor seed weight results from incomplete fertilization due to abnormal stamens and pistils under HT in 'Da Hong' pitaya.

It is worth noting that Nerd et al. (2002) reported that extreme heat reduced the number of flower buds in pitaya. Nevertheless, in that study, the fruit set of 'clone C' (*H. polyrhizus*) was still relatively high, and the fruit size was unaffected in Qetura, an extremely hot region in Israel. Conversely, our findings suggest that HT is the main factor driving low yield and poor quality after flowering in 'Da Hong' in Taiwan, indicating that the type and extent of damage in fruit production due to HT is highly variable among cultivars and locations; in Qetura, the plant is grown in an open field, with conditions fluctuating every day compared with the stable conditions of the phytotron.

Consistent with results reported by Huang and Lin (2008) and Nerd et al. (1999), fruit growth in the current study also exhibited a sigmoid pattern under optimal temperatures (CK plants), while heat stress resulted in plants that did not show a typical sigmoid

Table 4. Comparison of peel color in 'Da Hong' pitaya fruit at harvest in 2015.

Treatment[z]	Shaded side L	Shaded side a*	Shaded side b*	Sunny side L	Sunny side a*	Sunny side b*
HT	36.50 a[y]	29.31 a	–0.19 a	30.37 b	6.55 b	7.18 a
CK	38.90 a	36.12 a	5.25 a	39.60 a	31.05 a	6.03 a

[z]Treatment: HT, high temperature: air day/night temperature at 40/30 °C; CK, control: air day/night temperature at 30/20 °C.
[y]Means within each column followed by the different letters are significantly different at $P < 0.05$ by Unpaired Student's *t* test, n = 3(HT), 4(CK), respectively.

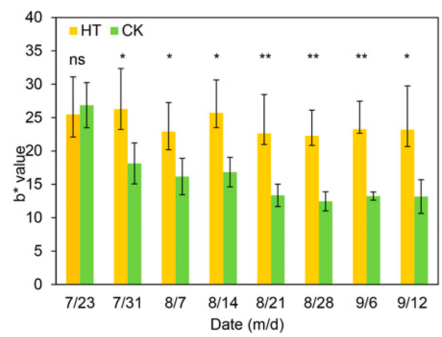

Fig. 6. Color change of cladode was described as b* value in 'Da Hong' pitaya during the control (CK, 30/20 °C) and high temperature (HT, 40/30 °C) treatments. ns = not significant at 5% level; *, ** indicates significant at 5% and 1% levels, respectively. Each value represents the mean ±SD of four potted plants; three stems were measured in each potted plant.

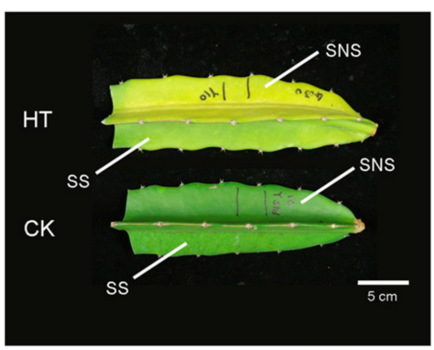

Fig. 7. Cladode regreening on adaxial end in 'Da Hong' pitaya at the end of the experiment under HT and CK treatment in 2015. Sunny side (SNS); shaded side (SS).

fruit growth pattern and dramatically suppressed fruit growth (Fig. 3). However, under both treatments, fruit still ripened 37–38 d after bloom. Even though HT significantly reduced the weight and edible part of the fruit, there was no significant difference between the treatments in terms of the TSSC (Table 3).

Nomura et al. (2005) indicated that the accumulated temperature (AT) from pollination in pitaya along with the a* value of the peel color reaching a plateau is a reliable index for estimating harvest. Although the average temperature under HT treatment was 10 °C higher than the control during this study, there was no significant difference in the duration from flowering to harvest. Thus, AT does not seem to be a consistent method for determining harvest time under extremely HT.

Betacyanins accumulate in the peel of mature fruit and form a desirable red color in pitaya (Stintzing et al., 2002). Compared with field-grown plants, shading with 50% to 75% netting resulting in 6 to 7 °C lower temperatures in 'Shih Huo Chuan' red-fleshed pitaya increased the accumulation of betacyanins in the peel (Chang et al., 2016), indicating that high light intensity accompanied with elevated temperature may delay the accumulation of betacyanins or degradation of chlorophyll. The accumulation of betacyanins on the sunny sides of fruits was also likely suppressed under the HT treatment of 40/30 °C (Table 4), leading to a consequent reduction in coloration and commercial value (Fig. 5).

Based on vacuolar uptake of neutral red pigment by chlorenchyma cells following different temperature treatments, it has been shown that pitaya has a lower tolerance for HT than 18 other species of cactus native to desert areas (Nobel and De la Barrera, 2002; Smith et al., 1984). Furthermore, while heat/chilling tolerance has been demonstrated to be inducible through moderating high/low temperatures in prickly pear (*Optunia ficus-indica*) (Nobel and De la Barrera, 2003), heat tolerance of *H. undatus* does not improve after exposure to high temperature compared with other cactus species (Nobel and De la Barrera, 2002). Both temperatures over 35 °C and high light intensity resulted in slight sunburn, i.e., yellowed cladodes of pitaya, and similar responses have also been observed in 'VN White' white-flesh and 'Shih Huo Chuan' red-fleshed pitaya in Taiwan (Chang et al., 2016; Chu et al., 2015; Nobel and De La Barrera, 2004).

In a study reported by Nobel and De la Barrera (2002), visible necrosis occurred on cladodes 6 weeks after treatment at 40/30 °C. It has also been reported that a reduction in total daily net CO_2 uptake resulted in cladode damage in *H. undatus* (Nobel and De la Barrera, 2002, 2004). However, in the current study, HT treatments cladodes without necrosis showed less regreening on the sunny side than that of CK treatment cladodes by the end of the experiment (8 weeks) (Figs. 6 and 7), implying that there was no severe reduction of CO_2 uptake occurring under HT treatment during the short experimental period. The reduced cladode damage may be attributable to cultivar characteristics and acclimation to a moderated HT of 36/26 °C before the experiment. Irrespective of high light intensity, heat caused yellowing of cladodes under control conditions, suggesting that heat stress is the primary cause of yellowing in cladodes.

In Israel, high summer temperatures of 38/20 °C in the Qetura and Gilgal regions caused yield reduction due to inhibition of flower bud formation (Nerd et al., 2002); however, whether HT reduced dry matter accumulation leading to poorer fruit set and fruit development was not evaluated. In the current study, although the cladodes of HT plants exhibited less regreening (Fig. 6) and may have had somewhat reduced CO_2 uptake, flower bud formation and development were not inhibited (Tables 1 and 2). In addition, much less yellow color was maintained on the two shaded sides than on the sunny side of cladodes in HT plants (Fig. 7), indicating that HT did not substantially result in lower CO_2 uptake during the experiment in the whole plant. Moreover, Chang et al. (2016) reported that no differences were recorded in fruit weight between the cladodes that exhibited less regreening because of sunburn, and that the cladodes show more regreening as a result of netting the pitaya for a short shading experiment.

The accumulation of dry matter was related to CO_2 uptake under varied temperature conditions in pitaya has been reported by Nobel and De la Barrera (2002). They found a dramatic reduction in dry mass gain after 19 weeks at the temperature of 40/30 °C. However, there was no significant difference in dry matter content in the cladodes with/without fruit in this study (Table 5), suggesting there was no difference in carbon supply potential between HT and CK plants, and cladode yellowness likely did not reduce fruit production.

Conclusions

Our findings confirmed that HT during the period from floral bud development until fruit ripening resulted in an inferior fruit set and reduced fruit weight. Based on our findings, this is largely due to less seed setting/weight per fruit likely arising from incomplete fertilization. The HT also caused less regreening of the cladode, but it did not appear to play a part in poor fruit production during the short duration of the experiment. However, how HT causes incomplete fertilization remains unclear. Overall, there is a need for further study to clarify whether poor seed weight resulted from incomplete fertilization due to

Table 5. The fresh weight, dry weight per 10-cm stem in length and dry matter percentage of 'Da Hong' pitaya in the phytotron with high temperature (HT) and control (CK) treatments in 2015.

Treatment[z]	Fresh wt (g/10 cm)	Dry wt (g/10 cm)	Dry matter (%)	Water content (%)
Stem with fruit				
HT	22.8 a[y]	3.4 a	15.1 a	84.9 a
CK	27.4 a	3.5 a	12.8 a	87.2 a
Stem without fruit				
HT	24.2 a[x]	3.6 a	14.8 a	85.2 a
CK	26.7 a	3.3 a	12.3 a	87.7 a

[z]Treatment: HT, high temperature: air day/night temperature at 40/30 °C; CK, control: air day/night temperature at 30/20 °C.
[y]Means within each column followed by the different letters are significantly different at $P < 0.05$ by Unpaired Student's *t* test, n = 3 (HT), 4 (CK), respectively.
[x]Means within each column followed by the different letters are significantly different at $P < 0.05$ by Unpaired Student's *t* test, n = 4.

abnormal stamens and pistils under HT in 'Da Hong' pitaya.

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