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Effect of growth temperature levels on photosynthetic ability and fruit quality of 'KU-PP2', a new low-chill peach cultivar

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Key words: forcing culture, high temperature, protected culture, *Prunus persica*, stress response.

Abstract: Temperature is a crucial factor in growing plants in a forcing system. Our goal was to introduce low-chill peach cultivars into a forcing culture for early-season peach production with high fruit quality. However, the effects of growth temperature on plant growth and fruit quality during fruit development of the 'KU-PP2' peach cultivar have not yet been evaluated. 'KU-PP2' trees were grown in containers and transferred to phytotrons after fruit set in April 2019. The air temperature was set at 20, 25, and 30°C until harvest. Photosynthetic ability, leaf characteristics, and fruit quality under each treatment were determined. Long exposure to lower growth temperatures did not cause a change in leaf characteristics or a reduction in photosynthetic ability and fruit quality in the 'KU-PP2' peach cultivar. In contrast, the 30°C was found to be associated with a decrease in leaf size and thickness, stomatal density, photosynthesis, chlorophyll content, and fruit size. Conversely, the high-temperature condition enhanced coloration of the fruit peel and hastened the harvesting period, compared with the lower-temperature treatments. These results indicated that long-term exposure to the moderately high temperature of 30°C negatively affected plant growth and fruit productivity through changed leaf characteristics and a disrupted photosynthesis.

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1. Introduction

Air temperature is a crucial factor that affects fruit production. Excessive high temperatures disrupt normal plant functions such as carbon assimilation, respiration, fertilization, cell differentiation, and fruit maturation (Cui *et al*., 2006; Efeoglu and Terzioglu, 2009; Lin-Wang, 2011; Hao *et al*., 2019). Previous report indicated that chlorophyll (Chl) *a* content, total Chl content, and the Chl *a/b* ratio in soybeans, which were grown under high temperatures (38/28°C), decreased 7, 3, and 18%, respectively (Hasanuzzaman *et al*., 2013). Additionally, Sugiura *et al*.

(2003) showed that higher temperatures significantly change the fruit quality of apple. A reduction in acid concentration and softening of fruit flesh were observed resulting from exposure to high temperatures during fruit development. The effect of elevated temperatures on plants differs depending on the stages of development and timescale. Continuing heat stress can lead to slowing of growth and development and inducing an imbalance in carbohydrate metabolism between photosynthesis and respiration. As a result, carbohydrate reserves decline, leading of yield loss, and possibly plant death (Hall, 1992; Wahid *et al*., 2007).

Photosynthesis comprises a few principal components that are highly sensitive to temperature: photosynthetic pigments, electron transport chain, Photosystem I (PS I), and Photosystem II (PS II). The decline in photosynthesis under high-temperature conditions results from inhibition of the redox reaction and metabolic pathways occurring in PS I, PS II, the cytochrome complex, and photosynthetic enzyme activities (Taiz and Zeiger, 2006). Moreover, elevated temperatures can also affect photosynthesis via physical processes. Previous studies have shown that heat stress is involved with leaf water status, leaf gas exchange, and stomatal conductance (*gsw*) caused by changes in hydraulic conductance (Fredeen and Sage, 1999; Greer and Weedon, 2012). Under high-temperature conditions, intercellular CO_2 concentration in leaves frequently declines because of stomatal closure and reduced CO_2 uptake and transport, leading to impaired photosynthetic CO_2 assimilation (Centritto *et al*., 2001).

'KU-PP2' is a new yellow flesh peach with a low-chilling requirement that produce excellent yield and high fruit quality. It was bred and released in 2016 for use in subtropical regions and particularly for use in forcing culture system to expand the harvesting season of fresh peach (Manabe *et al*., 2015). Understanding the effect of growth temperatures on 'KU-PP2' peach trees is crucial for optimizing plant growth, physiological functioning, and increasing productivity. The effect of chilling accumulation and heating temperatures on bud burst and flowering of 'KU-PP2' have been clarified. However, the influence of temperature during fruit development on low-chill peach cultivars has not been elucidated. Previous studies on Japanese high-chill peach cultivars indicated that high temperatures dramatically hasten fruit growth and the onset of fruit maturation (Sugiura *et al*., 2003; Hayama *et al*., 2007). In addition, optimal heating could save energy costs for plant production in heated plastic houses. Therefore, the aim of this study was to investigate the effect of growth temperature during fruit development on plant physiology and to determine the optimal growth temperature for plant growth, which can enhance fruit quality of the low-chill peaches under controlled conditions. Additionally, the knowledge gained could be used to design a heating program and cultivation management practices for growing the low-chill peach trees in plastic houses.

2. Materials and Methods

Plant materials

This experiment was conducted at the research field of the Faculty of Agriculture, Kagawa University, which is located in southwest Japan. Six healthy and uniform of seven-year-old 'KU-PP2' peach trees were selected for this study. All plants were grafted onto 'Tsukuba 1 Gou' peach rootstock and planted in containers. 'KU-PP2' flowers were hand-pollinated with fresh pollen from another 'KU-PP2' tree. Three weeks after pollination, two plants were transferred to each temperature regimes and the fruits were thinned by hand to 6-7 fruits per tree. The air temperature in the phytotrons was set at 20, 25, and 30°C during the experimental period from 13 April to 8 July 2019. Cultural practices and fertilization were performed according to standard peach growing practices in Japan (Sugiura *et al*., 2003).

Leaf morphology and anatomy observation

Leaf length and width were measured for five mature leaves per tree for each treatment using a digital caliper at the end of the experiment. Leaf width was measured across the widest part of the leaf. Five fully expanded leaves were collected and weighed immediately to determine fresh weight. These leaves were dried in a hot air oven at 80°C and weighed after 72 h of drying to determine their dry weight (Fanourakis *et al*., 2017). Leaf dry matter (DM) was calculated as the ratio between dry mass and fresh mass. DM was expressed as the percentage of fresh weight For anatomical analysis, five leaf samples from each plant were collected and preserved in formalin-acetic acid-alcohol (FAA; formaldehyde 1:acetic acid 1: 99.5% ethanol 9:deionized water 9) solution. Cross-sections were made using a rotary microtome at a thickness of 5 µm. The cross-sections

of samples were observed and photographed using a light microscope equipped with a microscope camera (Olympus DP-25, Olympus Co. Ltd., Japan). The following anatomical characteristics were measured: the thickness of the adaxial and abaxial epidermis, spongy mesophyll, and palisade cells, as well as the number of stomata per square millimeter.

Evaluations of chlorophyll content and SPAD value

The Chl content and SPAD value of five mature leaves from each tree were analyzed during the harvesting period. SPAD values were measured using a portable chlorophyll meter (SPAD-502, Minolta, Japan). Chlorophyll in the same leaves was analyzed as described by Lichtenthaler and Wellburn (1983). Leaf disks (2.5 cm^2 per disk) were homogenized with 10 mL of cold 95% acetone and incubated at 4°C in darkness for 3 h. These mixtures were centrifuged at 3,500 rpm for 10 min. After centrifugation, absorbance of the supernatants was determined using the spectrophotometer. The optical density for the blank and the mixtures were measured at 645 and 663 nm, respectively. These absorbance values were used to calculate Chl *a*, Chl *b*, and total chlorophyll (Chl *a+b*) and expressed as mg L^{-1}.

Leaf gas exchange measurement

Photosynthetic gas exchange was measured using a Portable Photosynthesis System (LI-6800; LI-COR Biosciences, Lincoln, NE, USA) from 9:00 to 12:00. The rate of net CO_2 assimilation, stomatal conductance, transpiration, and intercellular CO_2 concentration were measured weekly until the end of the experiment. Ten newest fully expanded leaves, which were outside of the canopy and fully exposed to sunlight, were randomly selected and used for the measurements. The reference CO_2 concentration and flow rate inside the chamber were maintained at 400 µmol mol^{-1} and 800 µmol m^{-2} s^{-1}, respectively. Photosynthetically active radiation (PAR) was set to 1,200 µmol s^{-1}. The chamber temperature was comparable to the growth temperatures, and relative humidity (RH) was kept at 60% (Marchi *et al*., 2008). The data were recorded at a steady state, in which gas exchange parameters were stable.

Fruit quality assessment

Five fruits per treatment were collected on the commercial harvest date for phytochemical analysis. After the harvest, all fruits were immediately transferred to the laboratory and weighed. Flesh firmness and total soluble solids (TSS) were measured from two opposite fruit cheeks. Flesh firmness was determined using a manual penetrometer with a 4.5-mm tip. TSS was measured using a digital refractometer (PR-101α; Atago Co. Ltd., Japan) and were expressed as degree Brix (°Brix). Titratable acidity (g L^{-1} of malic acid) was determined by titrating fruit juices with 0.05 mol L^{-1} of sodium hydroxide (NaOH) using Acidity Titrator (TA-72; DKK-TOA Co. Ltd., Japan). The fruit development period was calculated as the days from full bloom to first commercial harvest. Fruit coloring was estimated visually according to a scale from 1 (none) to 9 (hiding ground color) using ECPGR priority descriptors for peach (UPOV, 2010). The fruit coloring was expressed as the percentage of over color extent.

Statistical analysis

All data from each treatment were subjected to analysis of variance (ANOVA) using the Statistical Analysis System (SAS) university edition (SAS Institute Inc., Cary, NC). The differences between means were separated by Tukey's honestly significant difference (HSD) test at $p<0.05$. The results were expressed by means followed by the standard errors.

3. Results

Leaf morphology and anatomy response to growth temperature

At the end of the experiment, the significant differences in leaf dimensions ($p < 0.0001$) and dry matter ($p<0.0001$) between growth temperature levels were observed (Table 1). 'KU-PP2' peach trees that were forced at 25°C had the longest leaf length, followed by the 20°C and the 30°C treatments, while the leaf width of each treatment was comparable (p= 0.0864). The stomatal density increased by 7% with the increase in growth temperature from 20 to 25°C and reached its maximum value at 25°C. However, raising the growth temperature from 25 to 30°C significantly diminished stomatal density by 32%. In contrast, the leaf dry matter content slightly increased when the growth temperature increased. Compared with 20 and 25°C, the 30°C treatment increased leaf dry matter by a mean value of 5% FW.

The growth temperatures not only changed the leaf morphological characteristics but also affected leaf anatomical traits (Table 1). The higher temperature significantly decreased the thickness of leaves, palisade mesophyll, and spongy mesophyll ($p <$ 0.0001). The leaves that were forced at the highest growth temperature (30°C) were thinner than those

Table 1 - Leaf morphological and anatomical characteristics, percentage of leaf dry matter (DM), and stomatal density of the 'KU-PP2' peach cultivar at the end of the experiment. The peach trees were grown under three growing temperatures (20, 25, and 30°C)

Parameter	Growth temperature			*p-value*
	20°C	25°C	30°C	
Leaf length (cm)	17.1 ± 0.6 a [z]	18.6 ± 0.2 a	13.7 ± 0.5 b	< 0.0001
Leaf width (cm)	4.6 ± 0.1	4.5 ± 0.1	3.9 ± 0.3	0.0864
Percentage of leaf dry matter (% FW)	44.9 ± 1.35 b	44.5 ± 0.46 b	50.8 ± 0.56 a	< 0.0001
Leaf thickness (µm)	58 ± 1.6 a	41 ± 1.0 b	37 ± 1.1 b	< 0.0001
Adaxial epidermis thickness (µm)	6 ± 0.3	5 ± 0.3	5 ± 0.5	0.7828
Abaxial epidermis thickness (µm)	4 ± 0.3	4 ± 0.4	3 ± 0.2	0.4418
Palisade thickness (µm)	28 ± 0.7 a	18 ± 0.4 b	15 ± 0.2 c	< 0.0001
Spongy thickness (µm)	20 ± 0.5 a	13 ± 0.6 b	14 ± 0.6 b	< 0.0001
Stomatal density (no. mm^{-2})	242 ± 2 b	260 ± 3 a	176 ± 4 c	< 0.0001

[z] Data are mean values ± standard errors (n = 10). The different lowercase letters within the same row indicate significant differences at p ≤ 0.05 (Tukey's test).

from the trees grown at 25 and 20°C, as well as palisade and spongy mesophyll layers. On the other hand, the different growing temperatures did not significantly change the adaxial and abaxial epidermis thickness (p= 0.7828 and p= 0.4418, respectively) throughout the temperature treatments. Figure 1 shows the light microscopy pictures of leaf cross-sections for all temperature treatments, measured at the end of treatment.

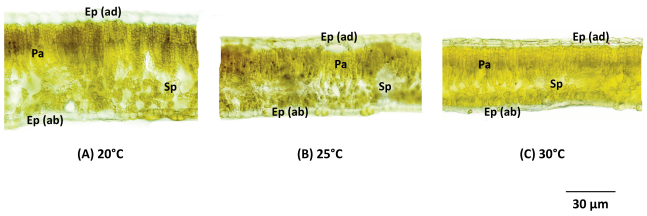

Fig. 1 - Anatomical comparison of leaf cross-section of 'KU-PP2' peach trees under (A) 20°C, (B) 25°C and (C) 30°C at the end of the experiment. The cross-sections of samples were observed and photographed under a light microscope. Ep (ad) = adaxial epidermis; Pa = palisade mesophyll layer; Sp = spongy mesophyll layer; and Ep (ab) = abaxial epidermis. These pictures were taken on 15 November 2019.

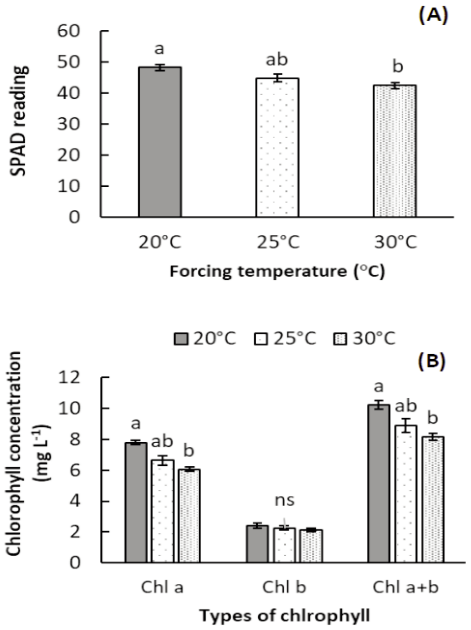

Fig. 2 - SPAD value (A) and chlorophyll content (B) in response to growth temperature treatments. Data represent means ± standard error (n= 5). Different letters indicate significant differences according to Tukey's test (p < 0.05) and NS denotes non-significant.

SPAD values, chlorophyll contents, photosynthetic rate, and gas exchange parameters

Figure 2 shows the high-temperature conditions caused a reduction in SPAD values (p= 0.0206) and loss of Chl content, especially Chl *a* (p= 0.0029) and Chl *a+b* (p= 0.0133). The SPAD reading for the 30°C treatment showed decreases by 12.5%, compared with the 20°C treatment. However, the SPAD values for the 20 and 30°C treatments were not significantly different from that of the 25°C treatment. Similarly, the Chl content decreased when exposed to an increasing temperature compared with the 20°C treatment. The maximum reduction in Chl *a* content (22.3%) occurred with 30°C, the Chl *a+b* concentration for 30°C decreased by 20.1%, while the Chl *b* content was not significantly affected (p= 0.3494).

The responses of the net photosynthetic rate (P_n) and the gas exchange parameters to growth temperature differed significantly depending on the levels and duration of the temperature treatments (Fig. 3). One week after temperature treatment started, the P_n for all treatments increased considerably

(p<0.0001). The P_n of the 30°C treatment was higher than the other treatments in this period (p=0.005). Subsequently, the P_n of the 20 and 25°C treatments steadily increased and remained stable at a higher level than at the beginning of treatment until the harvesting period. Conversely, the P_n of the 30°C treatment dramatically declined in the second week (p=0.0007) and after that gradually decreased and reached its lowest level in the eighth week (p<0.0001) after temperature treatment started (Fig. 3A). The average P_n values of the mature leaves under the 20°C treatment was higher than those in the 25 and 30°C treatments by 12.8 and 47.7%, respectively (p<0.0001). The changes in stomatal conductance (*gsw*) of each treatment were similar to those of the P_n values. The maximum *gsw* for 30°C was observed in the first week after the beginning of treatment while the peak *gsw* for 20 and 25°C occurred in the third week (Fig. 3B). The averages of *gsw* in both lower-temperature treatments were not different (p= 0.2578). The *gsw* of the higher-temperature treatment rapidly decreased in the second (p<0.0001) and eighth weeks (p= 0.02) after treatment started. Similarly, the peak of leaf internal CO_2 concentration (C_i) was observed one week after the beginning of treatment (Fig. 3C). A higher growth temperature had greater effects on C_i, with a considerable reduction in C_i occurring twice; in the second and eighth weeks after treatment started (p<0.0001). The lower growth temperatures (20 and 25°C) had comparative effects on the values of transpiration rate (E). The mature leaf E under the 20 and 25°C treatments declined more slowly than under the 30°C treatment, with the average E for the lower temperatures (20 and 25 °C) being higher than that for the high-temperature treatment by 30−35% (p = 0.004; Fig. 3D).

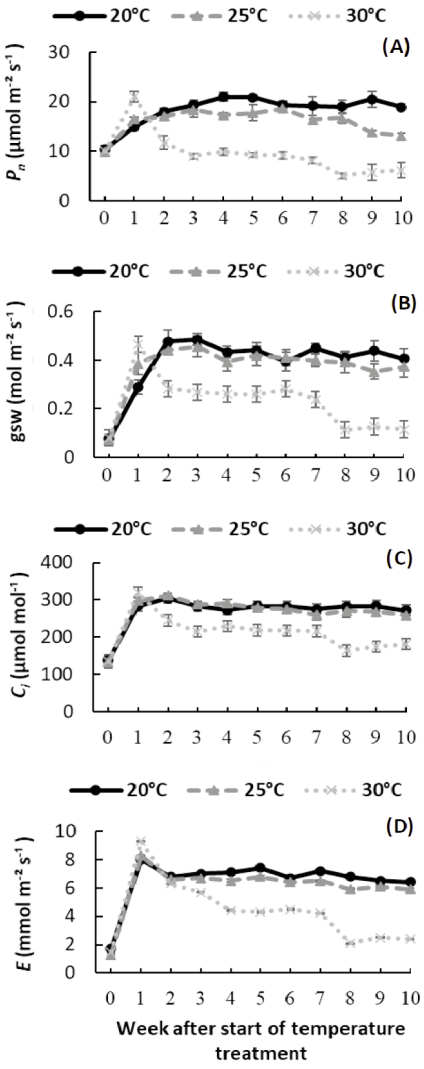

Fig. 3 - Effect of growth temperatures on (A) leaf net photosynthesis, (B) stomatal conductance, (C) leaf internal CO2 concentration, and (D) transpiration rate of the 'KU-PP2' peach trees. Data represent means ± standard error (n= 5).

Effect of growth temperature on fruit quality indexes

The morphological characteristics and chemical compositions of the ripe fruit are shown in Table 2. The results indicated that a high growth temperature strongly affected only the fruit morphological characteristics (p=<0.0001) of the 'KU-PP2' fruit and fruit weight (Table 2). However, significant differences in fruit shape (p = 0.0631) and chemical compositions of the fruit (p = 0.0881) were not found. An increase in growth temperature decreased fruit weight, fruit diameter, and fruit length. As shown in figure 4, there were significant contrasts in skin coloration for the 'KU-PP2' peaches with the different treatments. During the harvesting period, the fruit from the 30°C treatment showed a higher level of red coloration than the fruit from the 20 and 25°C treatments, indicating that increasing the temperature could accelerate the reddening of the fruit skin. Further, at 30°C, the fruit development period became shorter than under the 20 and 25°C conditions, with maturation occurring 14 days earlier.

4. Discussion and Conclusions

Long-term exposure to a moderate high-temperature regime (30°C) can result in cellular and physio-

Table 2 - Fruit quality characteristics of the 'KU-PP2' peach trees for each growth temperature treatment

Parameter	Growth temperature			p-value
	20°C	25°C	30°C	
Fruit weight (g)	164.34 ± 7.48 a [z]	131.89 ± 6.16 b	97.83 ± 7.05 c	< 0.0001
Fruit cheek diameter (mm)	68.1 ± 1.2 a	62.1 ± 1.4 b	56.2 ± 1.4 c	0.0002
Fruit suture diameter (mm)	69.9 ± 1.3 a	64.0 ± 1.0 b	58.5 ± 1.5 c	0.0002
Fruit length (mm)	59.9 ± 0.7 a	57.7 ± 1.0 a	50.0 ± 0.8 b	< 0.0001
Total soluble solids (°Brix)	15.0 ± 0.7	13.8 ± 0.2	13.3 ± 0.6	0.0881
Titratable acidity (g L^{-1})	0.21 ± 0.07	0.29 ± 0.01	0.24 ± 0.03	0.2331
Over color extent (%)	10–15 b	10–15 b	60–75 a	0.0013
Fruit development period (days)	96 a	91 a	81 b	0.0023

[z] Data are mean values ± standard errors (n = 10). The different lowercase letters within the same row indicate significant differences at p≤ 0.05 (Tukey's test).

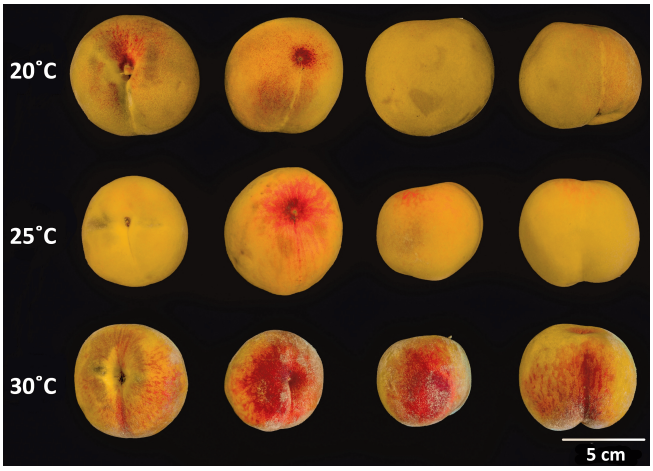

Fig. 4 - Effect of growth temperature on the coloration of the 'KU-PP2' fruits during the commercial ripening period.

logical adaptation of 'KU-PP2'. The responses of the peach trees to a high growing temperature could breakdown Chl, change leaf structure, reduce P_n, hasten fruit maturity, and could further explain the decrease in fruit quality under high temperatures in the present study. Similar to previous studies, high-temperature conditions induced closure of the stomata and generation of reactive oxygen species (ROS), damaged chloroplast structure and PS II and decreased photosynthetic pigments and enzyme activities (Takahashi and Murata, 2006; Ashraf and Harris, 2013; Chen *et al*., 2017; Jumrani *et al*., 2017).

Under high-temperature regimes, plants avoid heat damage and reduce excessive energy absorption on their leaves by decreasing leaf size, covering leaf surfaces with a thick waxy cuticle as well as trichome, changing leaf shape, or increasing the number of stomata. Small leaves can also reduce water loss and have less surface area exposed to solar radiation (Hasanuzzaman *et al*., 2013). Plants with thinner leaves and high stomatal densities can evacuate heat to the environment quicker than large leaves. A similar response to high temperatures was found in this study, in which leaf size and thickness of the leaf blades, including the epidermal and mesophyll layers, decreased. Elevating the temperature from 20 to 25°C increased the stomatal density, but the number of stomata sharply decreased when the growth temperature increased from 25 to 30°C. Previous study found similar results: the stomatal density of blueberry decreased when the temperature exceeded the optimum growth temperature (Hao *et al*., 2019). They suggested that increasing stomatal density may be an efficient strategy for evacuating more heat by evaporative cooling, but this strategy is inefficient under higher temperatures (Xu, 2015). It has been reported that a high temperature limits CO_2 and H_2O diffusion, resulting in increased resistance to gas exchange (Mukohata *et al*., 1971; Monson *et al*., 1982). In this study, we found that the transpiration rate (*E*) of the leaves under the 30°C treatment sharply decreased at four weeks after temperature treatment started, while the *E* of the leaves under both the 20 and 25°C treatments remained constant or slightly increased. The reduction in *E* under high-temperature conditions reflected the low efficiency of leaf cooling. In other words, the convective processes of heat through transpiration were reduced, resulting in excessive leaf temperature above an optimum point. The trees grown at 25°C tended to maintain transpiration cooling by increasing stomatal density, which reduces the negative

effects of excessive heat on their foliage, leading to the maintaining of high *E* and P_n.

The higher temperature decreased the concentration of Chl *a* and Chl *a+b*. As was also observed in this study, Chl contents have been reported to be sensitive to high-temperature conditions. The decline in Chl pigments may correlate to impaired Chl biosynthesis, exacerbated Chl breakdown, or both. The inhibition of Chl biosynthesis and the increase in Chl degradation under high temperature results from the destruction and construction of several enzymes (Efeoglu and Terzioglu, 2009). Additionally, the reduction in Chl content observed under high temperature is associated with physical damage to thylakoid membranes by excessive ROS accumulation (Halliwell and Gutteridge, 2007). Chl is embedded in the thylakoid membranes; therefore, damage to these membranes could result in Chl loss (Mathur *et al*., 2014; Chen *et al*., 2017; Jumrani *et al*., 2017). The imbalance between Chl biosynthesis and degradation disrupts the photosynthesis apparatus resulting in decreased photosynthetic efficiency, eventually influencing plant growth and fruit quality (Shanshan *et al*., 2020).

Changes in P_n have been directly linked to the level and duration of high-temperature exposure (Hao *et al*., 2019). In this study, one week after temperature treatment started, the P_n of 'KU-PP2' increased rapidly with the initial rise in growth temperature; as the forcing condition continued, P_n under a moderately high-temperature treatment (30°C) dramatically decreased, whereas the P_n under both the 20 and 25°C conditions steadily increased and remained constant until the harvesting period. The response of P_n to growth temperature can depend on two factors - non-stomatal and stomatal (Cui *et al*., 2006; Chen *et al*., 2014), which can be indicated by the difference in *gsw* and C_i patterns (Farquhar and Sharkey, 1982). If *gsw* decreased or stabilized but C_i increased, the decline in P_n can be attributed to non-stomatal factors. If both *gsw* and C_i decreased simultaneously, P_n could be ascribed to stomatal factors. In this study, the increase in P_n and C_i at the onset of treatment may result from the increase in enzyme activities in the photosynthetic system catalyzed by high temperatures. Therefore, an increase in P_n in this period could be identified as a non-stomatal factor.

Furthermore, the decrease in P_n under the prolonged higher-temperature treatment (30°C) can be divided into two periods: 2-7 weeks and 8-13 weeks after the onset of forcing. For 2-7 weeks, the decrease in P_n can be ascribed to a non-stomatal limitation, with *gsw* significantly decreasing and C_i increasing. The non-stomatal factors play a role in the reduction of P_n in the 2-7 weeks period after temperature treatment started through damage to the structures of the chloroplast, impairment of Chl biosynthesis, and increased Chl degradation. This hypothesis is supported by the reduction in Chl *a* and Chl *a+b* observed in this study. With exposure to forcing conditions over an extended period, P_n, C_i, and *gsw* of the 30°C treatment gradually decreased and reached their lowest levels in the eighth week after temperature treatment started, indicating that P_n in this period might be limited by stomatal factors through changes in stomatal density and modified leaf morphological and anatomical characteristics. Our study showed that the size and thickness of the leaves, including the epidermal and mesophyll layers, decreased with the elevated growth temperature, and thus led to the decline in P_n as stomatal limitations.

The differences in fruit morphological characteristics, such as fruit weight and fruit size of the trees under high-temperature conditions, might be associated with the decline in the fruit development period and P_n. Previous studies reported that the relationships between fruit development period (FDP) and fruit weight and diameter were observed in apple and peach (Sugiura *et al*., 2013; Giovannelli *et al*., 2014). In the 30°C treatment, fruit size was lower than those in the 20 and 25°C treatments, which was expected according to the length of their FDP. Additionally, previous studies indicated that a low P_n causes a steep reduction in fruit size because most of the energy used in fruit development is generated via photosynthesis during the year (Pavel and DeJong, 1993; Grossman and DeJong, 1995) Similarly, Lopez and DeJong (2007) reported that high temperature during fruit development increases the potential of fruit growth without enough resources to subsidize fruit growth, resulting in smaller fruit size. High temperatures not only depress photosynthesis but also increase leaf respiration. Plants grown under high-temperature conditions may consume much more energy because of increased leaf respiration caused by increased temperatures (Corelli-Grappadelli and Lakso, 2004; Hao *et al*., 2019). This result is supported by the increase in both the number and size of mitochondria in *Arabidopsis* thaliana, indicating that more starch and soluble sugar are consumed by leaf

respiration and rapid growth because of increased temperature (Jin *et al*., 2011). Hence, the reduction in fruit size of 'KU-PP2' grown under high temperatures may be supported by the above conclusion.

In this study, we found that the red coloration in 'KU-PP2' peel at 30°C was higher than those at 20 and 25 °C. Previous study showed the red coloration in plum (*P. salicina* Lindl.) peel increases under high-temperature conditions (35°C) (Junping *et al*., 2017). Conversely, the biosynthesis of anthocyanin in grape and apple is suppressed by high temperatures (Lin-Wang, 2011; Mori *et al*., 2017). Junping *et al*. (2017) showed that high temperatures can stimulate red skin coloration in plum by increasing respiration and ethylene production. Long-term forcing under high-temperature conditions may increase the respiration rate in 'KU-PP2' peach fruits, and hence enhance red coloration in the fruit peel. Moreover, the development of red coloration in peach fruit skin is positively related to light conditions (Corelli-Grappadelli and Coston, 1991; Kataoka and Beppu, 2004). Previous study showed that 'Redhaven' peach fruits that develop in the shade have less red coloration than those that develop in full sunlight (Erez and Flore, 1986). In our study, the fruit grown under the 30°C treatment had smaller leaves, leading to a decrease in canopy shade. Thus, the peach fruits grown under the 30°C treatment were exposed to more sunlight, which might result in higher red skin coloration.

In conclusion, this study illustrated the effect of growth temperature on plant development and fruit quality of 'KU-PP2' peach trees. Air temperatures directly affect leaf morphology, leaf anatomy, and the photosynthetic ability of plants. The decline in carbon assimilation due to exposure to excessive temperatures could diminish the plant's ability to efficiently support fruit development, resulting in low yield and poor fruit quality. All these data show high-temperature stress in the 'KU-PP2' peach cultivar caused by long-term exposure to moderately high temperatures. Therefore, a better understanding of plant adaptability to high temperatures is crucial for growing low-chill peach cultivars in plastic houses with a heating system.

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