Effect of Temperature on Photosynthesis Characteristics in the Passion Fruits ‘Summer Queen’ and ‘Ruby Star’

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The effects of temperature and light on photosynthetic, chlorophyll fluorescence characteristics under high temperature in the passion fruits ‘Summer Queen’ (P. edulis × P. edulis f. flavicarpa) and ‘Ruby Star’ (P. edulis × P. edulis f. flavicarpa) were examined. Photosynthetic rates of both cultivars markedly and linearly increased up to 300 μmol·m⁻²·s⁻¹, and less markedly increased from 300 to 1500 μmol·m⁻²·s⁻¹ under several light conditions. Their light saturation points were recorded at around 1200 μmol·m⁻²·s⁻¹ photosynthetic photon flux densities (PPFD). Regarding the relationship between temperature and photosynthesis, the maximum value of the apparent photosynthetic rate of ‘Summer Queen’ was observed at 30°C, and it was lower at both lower and higher temperatures. In ‘Ruby Star’, on the other hand, the maximum value was observed at 20 to 30°C, and this decreased at 35 and 40°C. The gross photosynthetic rate of ‘Summer Queen’ decreased over 30°C whereas in ‘Ruby Star’, it decreased to a lesser extent. The transpiration rate of ‘Ruby Star’ was higher than that of ‘Summer Queen’ at 40°C. Dark respiration increased from 20 to 40°C in both cultivars. Concerning chlorophyll fluorescence characteristics, ‘Summer Queen’ showed high-temperature injury at 40°C and all parameters were significantly decreased at 45°C. On the other hand, Fv/Fm showed only a slight decrease at 45°C in ‘Ruby Star’. These results indicate that ‘Summer Queen’ is susceptible to heat stress and that the range of its optimal temperature for photosynthesis is lower than ‘Ruby Star’.

Key Words: chlorophyll fluorescence, high temperature, non-photochemical quenching (NPQ), photosynthetic rate, transpiration rate.

Introduction

Passion fruit (Passiflora edulis Sims.) is a climbing perennial herbaceous fruit tree belonging to the Passifloraceae Passiflora. Although the Passifloraceae has 12 families, including approximately 600 species, only about 10 species have been cultivated for food production (Yonemoto, 2009). The origin of passion fruit is considered to be the Amazon river basin from Brazil to Paraguay, and northern Argentina, and it is grown in the highlands of tropical areas or temperate zones with mild winters. The main producer countries are located in the tropics to subtropics, such as Brazil, Southeast Asia, and Australia. In Japan, it is cultivated in subtropical areas such as Kagoshima Prefecture, Okinawa Prefecture, and the Bonin Islands, where it is suitable for growing without frost damage. In particular, Kagoshima Prefecture produced 260 tons of passion fruit in 2013. This accounted for about 60% of the national production. Recently, the cultivation area has expanded northward to include Tateyama City, Chiba Prefecture.

There are several problems with passion fruit cultivation under high-temperature conditions since it originated from the highlands of tropical areas. Flower buds differentiate stably at 25/20°C day/night temperatures, but do not develop at high temperatures over 30°C (Chang and Cheng-Yung, 1992). The Japanese summer is too hot for flower and set fruit. Furthermore, the fruit quality is adversely affected by high-temperature conditions. In purple passion fruit (P. edulis Sims var. edulis), small and low sugar content fruits were produced under high-temperature regimes such as 33/28°C (Utsunomiya, 1992). Coloration of the peel was also inhibited by a high night temperature (30°C) in ‘Summer Queen’ (P. edulis × P. edulis f. flavicarpa) (Kozai et al.,...
In the leading cultivars of Kagoshima Prefecture, ‘Summer Queen’ and ‘Ruby Star’ (*P. edulis* × *P. edulis f. flavicarpa*), high temperatures have adverse effects such as causing immature fruit drop. In Japan, many passion fruits are cultivated in greenhouses and summer temperatures inside rise up to around 40°C. In addition, since the air temperature has risen due to the effect of global warming in recent years, it is considered that heat injury will also increase.

Photosynthesis is an indispensable reaction used to produce carbohydrates in higher plants. A high photosynthetic ability is necessary for healthy plant growth and the production of fruit with a high quality. It is known that photosynthetic ability is decreased by higher temperatures. Under such conditions, tree growth and fruit quality deteriorate (Higuchi et al., 1998, 1999). Tomato yield was positively correlated with the photosynthetic rate, transpiration rate, and stomatal conductance (Nkansah and Ito, 1994). Thus, it is important to elucidate the relationship between temperature and photosynthetic characteristics for the stable production of high-quality fruit in a given fruit species. Chlorophyll fluorescence measurements are used for the clarification of photosynthetic characteristics. Light energy is used to drive the photochemical reaction in photosystem II (PSII). However, unused energy is released as heat dissipation and chlorophyll fluorescence. Chlorophyll fluorescence is measured by this reaction. Chlorophyll fluorescence measurements combined with gas exchange measurements can be used to comprehensively estimate the photosynthesis reaction and ability. Furthermore, they can be used for the evaluation of heat tolerance in several plants (Greer, 2015; Yamada et al., 1996b).

In passion fruit cultivation in Kagoshima Prefecture, problems of heat injury related to poor flowering and fruit-set and insufficient peel color have been more severe in ‘Summer Queen’ than in ‘Ruby Star’. Therefore, there is a possibility that varietal differences in photosynthetic ability exist. It is well-known that varietal differences in temperature reactions concerning the photosynthetic rate or chlorophyll fluorescence exist in various vegetables and fruit trees (Guo et al., 2006; Sato et al., 2002; Xu et al., 2014). Varietal differences in photosynthetic ability under shade treatment in passion fruits were studied (Pires et al., 2011). Varietal differences in photosynthetic characteristics within the same species were also reported (Gama et al., 2013). However, varietal differences in the effect of temperature on photosynthetic characteristics have yet to be clarified.

Therefore, the objectives of the present study were 1) to measure the photosynthetic rate, transpiration rate, stomatal conductance, and dark respiration under several light and temperature conditions in two major passion fruit cultivars in Kagoshima Prefecture, ‘Summer Queen’ and ‘Ruby Star’ and 2) to study chlorophyll fluorescence characteristics at high temperatures to elucidate the effects of high temperatures on the photosynthetic characteristics of the two cultivars.

**Materials and Methods**

**Photosynthetic characteristics of the passion fruits ‘Summer Queen’ and ‘Ruby Star’**

One-year-old passion fruits ‘Summer Queen’ and ‘Ruby Star’, planted in plastic pots (ca. 10852 cm³), grown in a greenhouse at Toso Orchard, Faculty of Agriculture, Kagoshima University (Kagoshima City, Kagoshima Prefecture, Japan), were used. Fully expanded leaves (15–20th from the terminus) had their photosynthetic characteristics measured under several light and temperature conditions in September 2015. The plants were trimmed to a single shoot and each shoot was trained in a circular pattern. The effects of the illumination intensity and temperature on the photosynthetic characteristics were measured using a portable gas exchange system (LCpro+; ADC, UK). This instrument can arbitrarily set photosynthetic photon flux densities (PPFD), CO₂ concentration, temperature, and humidity in a chamber (measured leaf area: 6.25 cm², chamber size (H × W × D): 300 × 80 × 75 mm). Measurements were taken between 09:00 and 13:00 on a clear day (average temperature: 30.6°C). This measurement was for plants watered the day before.

Photosynthetic rates under several PPFD: 0, 100, 200, 300, 500, 700, 900, 1200, and 1500 μmol·m⁻²·s⁻¹, were measured. Photosynthetic conditions were as follows: 380 ppm CO₂, 28°C air temperature, and 200 μmol·s⁻¹ flow rate. The photosynthetic rate, transpiration rate, stomatal conductance, and dark respiration at several air temperatures: 20, 25, 30, 35, and 40°C, were also measured. Photosynthetic conditions were as follows: 380 ppm CO₂, 0 or 1200 μmol·m⁻²·s⁻¹ PPFD, and 200 μmol·s⁻¹ flow rate. Dark respiration was measured at a photosynthetic rate of 0 μmol·m⁻²·s⁻¹ PPFD. Measurement time was about one or two minutes with the leaf sandwiched in the chamber.

**Chlorophyll fluorescence characteristics of the passion fruits ‘Summer Queen’ and ‘Ruby Star’ at high temperature**

One-year-old passion fruits ‘Summer Queen’ and ‘Ruby Star’, planted in plastic pots, grown in a greenhouse at Toso Orchard, Faculty of Agriculture, Kagoshima University, were used. Fully expanded leaves (15–20th from the terminus) had their chlorophyll fluorescence characteristics measured under several temperature conditions. ‘Summer Queen’ and ‘Ruby Star’ experiments were conducted in August or September 2012 and 2013, respectively. The effects of the high temperature on the chlorophyll fluorescence characteristics were measured using a kinetic imaging fluorometer (Handy FluorCam 701MF; PSI, Czech). Leaf discs cut from the detached sample leaves were
wrapped in wet filter paper and then aluminum foil before treatments. Leaves were kept at 35, 40, and 45°C for 15, 30, 45, 60, 90, and 120 min in a temperature-controlled incubator (MTI-203; EYELA, Japan). The chlorophyll fluorescence parameters, quantum yield of electron transport \[ \Phi_{II} = (Fm' - Fs)/Fm' \], maximum quantum efficiency of PSII \[ Fv/Fm = (Fm - Fo)/Fm \], photochemical quenching factor \[ qP = (Fm' - Fs)/(Fm' - Fo') \], and non-photochemical quenching \[ NPQ = (Fm - Fm')/Fm' \] were measured before and after treatments. These parameters were automatically calculated by a kinetic imaging fluorimeter. These experiments were conducted at 27°C under dark conditions.

**Statistical analysis**

Results were subjected to analysis of variance (ANOVA) and mean values were compared by the Tukey’s test at \( P \leq 0.05 \).

**Results**

**Photosynthetic characteristics of the passion fruits ‘Summer Queen’ and ‘Ruby Star’**

Photosynthetic rates of the passion fruits ‘Summer Queen’ and ‘Ruby Star’ markedly and linearly increased up to 300 \( \mu \text{mol·m}^{-2}·\text{s}^{-1} \), and then less markedly increased from 300 to 1500 \( \mu \text{mol·m}^{-2}·\text{s}^{-1} \) under several light conditions (Fig. 1). The maximum photosynthetic rate of ‘Summer Queen’ was recorded at 1200–1500 \( \mu \text{mol·m}^{-2}·\text{s}^{-1} \) PPFD, and that of ‘Ruby Star’ was recorded at around 1200 \( \mu \text{mol·m}^{-2}·\text{s}^{-1} \) PPFD (Fig. 1).

The apparent photosynthetic rate, gross photosynthetic rate, transpiration rate, stomatal conductance, and dark respiration of the passion fruits ‘Summer Queen’ and ‘Ruby Star’ under several temperature conditions are shown in Figure 2. The apparent photosynthetic rate of ‘Summer Queen’ was increased until 30°C, and then decreased markedly at higher temperatures. On the other hand, that of ‘Ruby Star’ was stable at 20 to 30°C, and it moderately decreased at a higher temperature (Fig. 2A, B). The effect of temperature on the gross photosynthetic rate of ‘Summer Queen’ was similar to that on the apparent photosynthetic rate. On the other hand, the gross photosynthetic rate of ‘Ruby Star’ was less markedly decreased at a higher temperature.

**Chlorophyll fluorescence characteristics of the passion fruits ‘Summer Queen’ and ‘Ruby Star’ at high temperature**

All chlorophyll fluorescence parameters except for NPQ of ‘Summer Queen’ decreased up to 60 min as the temperature or duration of treatment increased (Fig. 3). The \( \Phi_{II} \) value decreased markedly at 45°C within 60 min after the start of treatment and was stable from (Fig. 2A, B). The transpiration rate of ‘Summer Queen’ and ‘Ruby Star’ showed a similar response to temperature; the higher the temperature, the higher transpiration rate under dark conditions. However, under light conditions, the transpiration rate of ‘Summer Queen’ was similar to those at 35 and 40°C. On the other hand, the transpiration rate of ‘Ruby Star’ was higher at 40°C than at 35°C. (Fig. 2C, D). Stomatal conductance of ‘Summer Queen’ and ‘Ruby Star’ did not show a constant trend, varying enormously depending on the temperature and light conditions (Fig. 2E, F). Dark respiration of ‘Summer Queen’ increased from 20 to 40°C. However, dark respiration of ‘Ruby Star’ was constant from 20 to 30°C and increased from 30 to 40°C (Fig. 2G, H).
60 to 120 min. At 40°C, the ΦII gradually decreased. At 35°C, it was stable until 120 min. The Fv/Fm value decreased markedly at 45°C, whereas at 35°C it was maintained up to 120 min. At 40°C, the Fv/Fm gradually decreased. The qP value decreased at 45°C up to 60 min after the start of the treatment and was stable from 60 to 120 min. At 35°C, the qP slightly decreased up to 30 min and was stable from 30 to 120 min. The NPQ value gradually increased at 35°C after the start of the treatment. At 40°C, the NPQ increased within 15 min after the start of the treatment and moderately decreased from 15 to 120 min. On the other hand, at 45°C, it decreased markedly from 15 to 120 min.

The ΦII value of ‘Ruby Star’ slightly decreased 15 min after the start of the treatment and was stable after 15 min in all treatments (Fig. 4). The Fv/Fm value was stable up to 120 min at 35 and 40°C. At 45°C, the Fv/Fm decreased from 45 to 60 min and was stable from 60 to 120 min. The qP value was stable up to 120 min at 35°C. At 40°C, the qP decreased until 45 min and recovered from 45 to 120 min. At 45°C, the qP decreased up to 15 min and was stable from 15 to 120 min. The NPQ value increased markedly within 15 min after the start of the treatment, and this was maintained from 15 to 120 min at 35 and 40°C. At 45°C, the NPQ gradually increased within 45 min after the start of the treatment and was stable from 45 to 120 min. The NPQ value at 45°C was maintained at a lower level than those at 35 and 40°C from 15 to 120 min.

**Discussion**

Passion fruit is generally cultivated using one-year-old cutting-propagated plants and new plants are planted every year in Japan. Hence, it was considered that the environmental conditions of the present study were similar to that of commercial of passion fruit cultivation. Photosynthetic rates of the passion fruits ‘Summer Queen’ and ‘Ruby Star’ markedly and linearly increased up to 300 μmol·m⁻²·s⁻¹, and less markedly increased from 300 to 1500 μmol·m⁻²·s⁻¹ under several light conditions. The maximum photosynthetic rate of both cultivars was recorded at approximately 1200 μmol·m⁻²·s⁻¹ PPFD (Fig. 1). A rectilinear increase up to 500 μmol·m⁻²·s⁻¹ is a characteristic of C₃ plants. On the other hand, the photosynthetic rate of C₄ plants continues to increase linearly until 1000 μmol·m⁻²·s⁻¹ (Ye et al., 2013). Thus, passion fruit showed typical C₃ plant photosynthesis characteristics.

Effects of temperature on the characteristics of photosynthesis were different in ‘Summer Queen’ and ‘Ruby Star’. The maximum apparent and gross photosynthetic rates of ‘Summer Queen’ were observed at 30°C, being lower at both lower and higher temperatures. The apparent photosynthetic rate of ‘Ruby Star’ was moderately decreased over 35°C, although the gross photosynthetic rate was less markedly decreased (Fig. 2A, B). Dark respiration increased from 30 to 40°C in both cultivars (Fig. 2G, H). The apparent and gross photosynthetic rates of ‘Summer Queen’ were more affected by high temperatures than ‘Ruby Star’. However, the gross photosynthetic rate of ‘Ruby Star’ was less affected by high temperatures than ‘Ruby Star’. As in studies of citrus (Iwasaki and Oogaki, 1985) and grapes (Shiraishi et al., 1996), varietal differences in photosynthetic rates within the same species were also observed in passion fruits.

Regarding the transpiration rate and stomatal conductance, ‘Ruby Star’ showed higher values than ‘Summer Queen’, especially for the transpiration rate above 35°C (Fig. 2C, D, E, F). High transpiration rates and stomatal conductance explain the maintenance of the photosynthetic rate at high temperatures in ‘Ruby Star’.

Since the photosynthetic characteristics of ‘Summer Queen’ and ‘Ruby Star’ differed over 35°C, the characteristics of chlorophyll fluorescence above 35°C were
studied. Characteristics of chlorophyll fluorescence were different in ‘Summer Queen’ and ‘Ruby Star’. The causes of the decrease in ΦII varied with the temperature. Decreases in ΦII result in abnormal photosynthetic electron transport. The reduction correlates with a reduction in Fv/Fm and qP and an increase in NPQ. When Fv/Fm decreases, the maximum quantum efficiency and function of PSII decrease. When qP decreased, the functions of the components downstream of PSII such as cytochrome b/f complex, PSI, and carbon dioxide fixation loses, decreased. When NPQ increases, the heat dissipation efficiency increases (Sonoike, 2009). In ‘Summer Queen’, the qP value slightly decreased and NPQ value increased at 35°C. Thus, it was considered that the heat dissipation efficiency and downstream PSII were mildly adversely affected. At 40°C, the Fv/Fm value decreased and it was considered that PSII was also damaged. The ΦII, Fv/Fm, qP, and NPQ values decreased markedly at 45°C. Therefore, it was inferred that ‘Summer Queen’ was severely damaged in terms of PS function. Moreover, the NPQ gradually increased within 15 min after the start of the treatment and decreased from 45°C. It was reported that the NPQ increased markedly at a high temperature (40°C) and decreased markedly over 40°C in Arabidopsis (Shao et al., 2007). Furthermore, the NPQ was correlated with the xanthophyll cycle. Accumulated zeaxanthin acts as a safety valve for eliminating excess energy to receive energy from chlorophyll (Sonoike, 2007). From these results in ‘Summer Queen’, injury to PSII was reduced by the release of excess energy as heat up to 40°C, while at 45°C, it was considered that this buffer effect was ineffective to release excess energy as heat. On the other hand, the NPQ increased with all treatments in ‘Ruby Star’. Thus, it was considered that the heat dissipation system was functional at high temperatures. However, it always retained a high heat dissipation ability. Thus, it was considered that heat dissipation for eliminating excess energy was effective in ‘Ruby Star’. It was inferred that PSII was also slightly damaged because of the decrease in Fv/Fm at 45°C. However, it was considered that PS was not influenced because it maintained the ΦII value at 45°C. The characteristics of chlorophyll fluorescence under high-temperature stress differed among the same species in the raspberry (Molina-Bravo et al., 2011) and tropical fruits such as the mango and longan (Yamada et al., 1996a). ‘Ruby Star’ maintained a high NPQ value up to 45°C. Thus, it was considered that heat dissipation for eliminating excess energy in ‘Ruby Star’ worked more effectively than that in ‘Summer Queen’.

In conclusion, we could elucidate varietal differences in photosynthetic characteristics between ‘Summer Queen’ and ‘Ruby Star’ at high temperatures. Significant injury at high temperatures occurred in ‘Summer Queen’. It was considered that this impaired PS was due to a decrease in all chlorophyll fluorescence parameters. This may reduce the function of PS and the photosynthetic rate. On the other hand, ‘Ruby Star’ maintained its transpiration and NPQ values at high temperatures, and they acted as a safety valve for eliminating heat in leaves. Thus, the high-temperature injury was not so severe. Therefore, ‘Summer Queen’ is susceptible to heat stress, and the optimal temperature for photosynthesis is lower than ‘Ruby Star’. However, since the optimal temperature for photosynthesis was 30°C or less in both cultivars, cultivation at 30°C or less is preferable to achieve good tree growth and stable production of high-quality fruit. Some temperature-lowering technologies such as shading (Wada et al., 2006), root-zone cooling (Kinoshita et al., 2012), fogging (Harel et al., 2013), or a water curtain (Iwasaki et al., 2011) of greenhouse, plants, as well as soil under high-temperature conditions have been established. These technologies should be used for the cultivation of passion fruit in the Japanese summer to prevent high-temperature injury which leads to poor flowering and an inadequate peel color.

Literature Cited
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