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Effects of high temperature on photosynthetic capacity in the leaves of creepers

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ABSTRACT: High temperature induces structural and physiological damage to plants. However, studies on the effects of constant high temperature on climbing plant species are limited. To estimate the response of photosynthetic capacity of two creeper species, *Parthenocissus tricuspidata* (Sieb. et Zucc.) and *Parthenocissus quinquefolia* (L.) Planch, to constant high-temperature treatment at noon, we measured photosynthetic pigments, gas exchange, and chlorophyll fluorescence parameters at 35, 40, and 45 °C (25 °C was the control treatment). High temperature significantly reduced photosynthetic pigment content, whereas carotenoid content showed the opposite trend. Net photosynthetic rate, stomatal conductance, transpiration rate, maximal quantum yield of PSII photochemistry, actual quantum yield of PSII photochemistry, and the coefficient of photochemical quenching all showed a decreasing trend, with increasing stress duration, whereas the non-regulated thermal energy loss and regulated thermal energy loss indexes increased. As temperature increased, intercellular CO_2 concentration initially decreased and then increased. Non-stomatal restriction factors were the main cause of the decrease in photosynthetic rate when temperature exceeded 40 °C. These parameters recovered to pre-stress levels only in plants grown at 35 °C upon stress relief. *P. quinquefolia* showed higher photosynthetic heat resistance and resilience than *P. tricuspidata*. Our results revealed photosynthetic adaptation and recovery mechanisms in two creepers grown under high-temperature stress. Molecular and genetic approaches should be considered to gain deeper insight into the mechanism underlying high temperature adaptation in these two creepers.

KEYWORDS: high-temperature stress, chlorophyll fluorescence, gas exchange, pigment content, creepers

INTRODUCTION

Photosynthetic responses of various plant species under abiotic stress such as water deficit [1] or under biotic stress such as fungus infection [2] have been reported; however, studies on the effect of high temperature on photosynthetic capacity of creepers are limited.

In the coming decades, the global average temperature will gradually increase [3]. Especially in China, the annual mean temperature will have increased by up to 6 °C by the end of this century; concomitantly, the frequency of extreme heat events will increase by up to 40%, with duration potentially increasing by up to 150% [4]. High temperature stress is one of the key factors restricting normal plant growth [5]. Therefore, it is very important to investigate thermal adaptation mechanisms of plants grown in a high-temperature environment for the conservation and breeding of heat-resistant varieties.

Photosynthesis is closely related to plant growth and is considered the first process inhibited before other cell functions [6]. High-temperature stress can induce damage to the photosynthetic apparatus [7], among which, photosystem II (PSII) is considered one of the most temperature-sensitive components [8]. The function of PSII is mainly affected by high-temperature stress in the following three aspects: first, separation of the PSII peripheral antenna complex from its core complex; second, inactivation and dissociation of the oxygen-evolving PSII complexes [9]; and third, redox imbalance between the primary acceptor plastoquinone and the secondary acceptor plastoquinone [10, 11].

In recent years, chlorophyll fluorescence has been widely used to diagnose environmental stress, which mainly comes from PSII and can reflect the structure and function of PSII in terms of different aspects [12, 13]. The maximum quantum yield of PSII photochemistry (F_v/F_m) is one of the most widely used parameters, as it reflects photosynthetic performance and overall photosynthetic plant

health status. A decrease in the F_v/F_m ratio might reveal whether the PSII reaction center is experiencing photoinhibition. Among the many photosynthetic protection mechanisms that have been studied, non-regulated thermal energy loss ($\Phi_{f,D}$) and regulated thermal energy loss (Φ_{NPQ}) are thought to be the most effective in dissipating excess energy absorption [14]. Therefore, chlorophyll fluorescence parameters are often selected as reliable indicators of the activity of the photosynthetic apparatus to evaluate plant stress tolerance [15, 16].

Parthenocissus tricuspidata (Sieb. et Zucc.) Planch and *Parthenocissus quinquefolia* (L.) Planch are considered two of the main vertical greening creepers worldwide, as they can control soil water loss and soil erosion in mountain slopes because of their particularly high growth rate, large coverage area, strong climbing ability, and high adaptability, among other traits [17, 18]. Furthermore, creepers are also valuable in the pharmaceutical industry as sources of polysaccharides and phenols [19]. Unfortunately, owing to the exacerbation of global warming in recent years, frequent overheating of rocky slopes and building surfaces is threatening the healthy growth of creepers, especially during the initial colonization stage.

Previous studies on creeper responses to the environment mainly focused on water stress and nutrient stress, among other adverse conditions [17, 20, 21]. Nevertheless, studies on the effects of high-temperature stress on their photosynthetic capacity are scarce. To reveal the adaptive and recovery mechanisms of *P. quinquefolia* and *P. tricuspidata* grown under high-temperature stress (35, 40, and 45 °C), herein the responses of photosynthetic pigments, gas exchange, and chlorophyll fluorescence were investigated during a seven-day stress period and a two-day recovery period.

MATERIALS AND METHODS

Plant species and treatments

The experiments reported herein were conducted at the North China University of Science and Technology (39°37′ N; 118°37′ E). One-year-old *P. quinquefolia* and *P. tricuspidata* plants of uniform size at the 5–8 fully expanded leaf stage were divided into four groups, each containing five replicate clones and grown in four controlled climate chambers (RXZ-380, Ningbo Jiangnan Co. Ltd., Zhejiang, China) under the same conditions (PPFD, 500 μmol $m^{-2}s^{-1}$; relative humidity, 65% ± 5%), except for temperature. One group was subjected to 25 ± 0.1 °C/18 ± 0.1 °C (day/night temperature) as control treatment. The other groups were kept at constant 35 ± 0.1 °C, 40 ± 0.1 °C, or 45 ± 0.1 °C for 7 days from 10:00–15:00 h. After the high-temperature stress period, all treatment groups were returned to control treatment conditions for 2 days. The selected parameters were measured on days 0, 1, 3, 5, and 7 and then after the 2-day recovery period.

Chlorophyll content

The concentration of chlorophyll was determined according to Arnon [22]. Briefly, fresh plant leaf samples (0.1 g) were extracted in 10 ml extraction solution (absolute ethanol: 95.5% acetone, 1:1, v/v) over 48 h under dark conditions at 25 °C. Subsequently, the content of chlorophyll a (Chl a), chlorophyll b (Chl b), chlorophyll (a+b) (Chl (a+b)) and carotenoids (Car) contents were calculated based on measurements of absorbance of the sample solutions at 470, 645, 652, and 663 nm using a UV-visible spectrophotometer (UC-5500PC; Shanghai Yuanxi Co. Ltd., Shanghai, China).

Gas exchange

The photosynthetic rate (P_n), intercellular carbon dioxide concentration (C_i), stomatal conductance (*gs*), and transpiration rate (Tr) were measured on the third to fifth (from the top of the plants down) fully developed functioning leaves of similar size using a portable LI-6400XT Li-Cor device (Li-Cor, Inc., Lincoln, NE, USA) under 500 μmol $m^{-2}s^{-1}$ PPFD.

Chlorophyll fluorescence measurements

First, minimum fluorescence yield (F_0) and maximum fluorescence yield (F_m) were measured on leaves adapted to darkness for approximately 30 min. Subsequently, the leaves were illuminated continuously. After the leaves were sufficiently photoactivated, steady-state fluorescence, minimum fluorescence, and maximum fluorescence were measured [23]. Illumination at 3000 μmol $m^{-2}s^{-1}$ was used to determine maximum fluorescence levels. The F_v/F_m, Φ_{PSII}, $\Phi_{f,D}$, Φ_{NPQ}, and the coefficient of photochemical quenching (qP) were calculated according to Humplik [24] and Lazar [25].

Statistical analysis

All data were expressed as means ± standard deviations (SD) of five replicates. One-way ANOVA was performed using the SPSS version 19.0 software

(IBM, Chicago, IL, USA) and Duncan's multiple comparison ($p < 0.05$) method was used to determine significant differences among means.

RESULTS

Pigment content

Photosynthetic pigment content of the two creepers under study was negatively affected by high-temperature treatments (Fig. 1). On the seventh day of stress, Chl a content in *P. quinquefolia* decreased by 15.4% at 35 °C, 28.7% at 40 °C, and 47.1% at 45 °C, compared to control leaves (25 °C). In contrast, leaf Chl a content for *P. tricuspidata* decreased by 21.6%, 33.7%, and 51.8% at 35, 40, and 45 °C, respectively. Similarly, Chl b content decreased with increasing temperature. Conversely, Car content and the Car/Chl (a+b) ratio showed the opposite trend. Chl a and Chl b pre-stress contents were almost completely restored in plants of the two creepers grown at 35 °C upon stress relief, but they were only partially restored in plants grown at 40 or 45 °C.

Gas exchange

A significant decline in P_n was observed in plants of both creepers under high temperature (Fig. 2). After 7 days under high-temperature stress, P_n decreased by 19.3%, 30.1%, and 45.2% in leaves of *P. quinquefolia* exposed to 35, 40, and 45 °C, respectively. Meanwhile P_n in leaves of *P. tricuspidata* decreased by 20.2%, 41.6%, and 65.6% at 35, 40 and 45 °C, respectively. In the early stage of high temperature stress, P_n showed a faster and greater decline in *P. tricuspidata* than in *P. quinquefolia*. In turn, gs and Tr in both creepers showed similar trends as P_n, whereas C_i showed an opposite trend at 40 and 45 °C. After a two-day recovery, P_n of both creepers recovered completely only in plants exposed to 35 °C, whereas that of both creepers grown at 40 and 45 °C remained strongly inhibited by high-temperature stress.

Chlorophyll fluorescence

When plants were subjected to high-temperature stress, the F_v/F_m ratio significantly decreased in both creepers (Fig. 3). After 7 days, the values of the F_v/F_m ratio in leaves of *P. quinquefolia* subjected to 35, 40, and 45 °C decreased by 1.35%, 1.98%, and 4.02%, respectively. However, F_v/F_m values exhibited a larger decline in leaves of *P. tricuspidata*, (1.37% at 35 °C, 2.75% at 40 °C, and 4.84% at 45 °C) than in those of *P. quinquefolia*. The extended duration of stress treatment caused $\Phi_{f,D}$ and the Φ_{NPQ} to increase, whereas Φ_{PSII} showed a decreasing trend; further, Φ_{NPQ} showed faster and larger differences in *P. quinquefolia* than in *P. tricuspidata*. Concomitantly, qP of both creepers showed a similar trend as Φ_{PSII}. Upon stress relief, all control values of chlorophyll fluorescence parameters of *P. quinquefolia* grown at 35 and 40 °C were restored completely. On the other hand, chlorophyll fluorescence parameters of *P. tricuspidata* were restored to pre-stress levels only in plants in the 35 °C treatment group.

DISCUSSION

Photosynthetic pigment content and its dynamic accumulation are considered important factors affecting plant biomass, and their level at any given growth stage can reflect the health status of the plants [26]. In this study, high-temperature stress induced a decrease in chlorophyll content, with P_n showing a similar trend. These findings are consistent with the results reported by Xiao et al [27], indicating that the observed decrease in chlorophyll content was one of the reasons for the observed decrease of P_n. Car has been proven to alleviate oxidative damage, and the increase in the Car/Chl(a+b) ratio reflects the initiation of chloroplast self-protection mechanisms [28, 29]. In our experiments, Car content increased, whereas Car/Chl (a+b) decreased when the temperature exceeded 0 °C. This indicated that 45 °C is beyond the heat tolerance range of both experimental creepers.

Photosynthesis is a temperature-sensitive fundamental biological process that allows for organic matter accumulation [4]. In this study, a significant decrease in biomass was observed at 35, 40, and 45 °C, consistent with the report by Greer and Weedon [30]. This indicates that photosynthetic capacity in both creepers was reduced. Further, the decrease in gs suggested that high-temperature stress induced stomatal closure. In addition, a larger decline in Tr than in gs in both creepers indicated that high temperature induced excess leaf water loss. Compared to control plants, C_i in both creepers decreased initially and then increased with the extended duration of heat stress. This indicated that the decrease in P_n was mainly induced by non-stomatal restriction factors when the temperature exceeded 40 °C [31]. Altogether, our data suggested that the photosynthetic capacity of *P. quinquefolia* exhibited a much higher level of resistance to high temperature than *P. tricuspidata*.

The F_v/F_m value is a good proxy of plant health

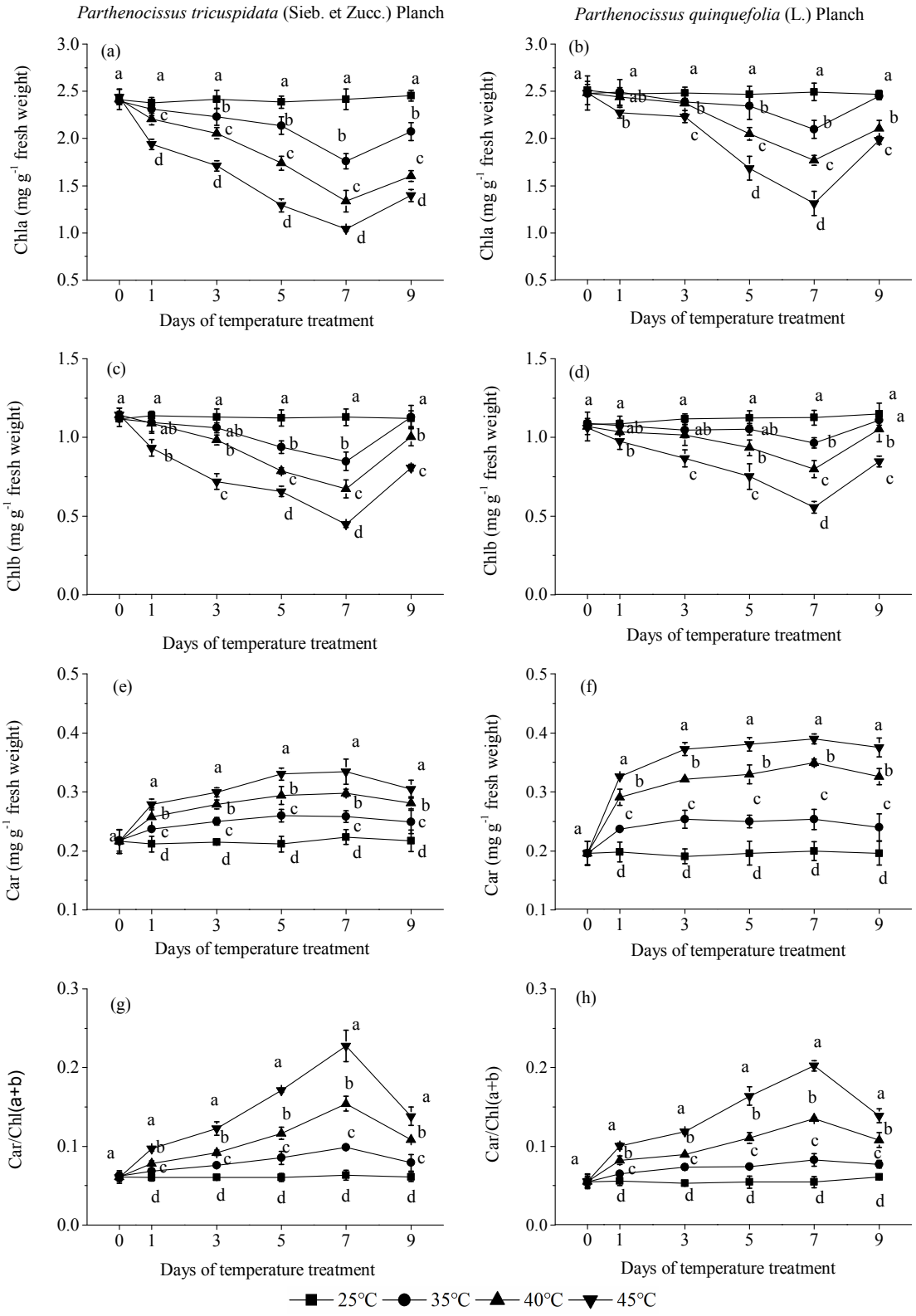

Fig. 1 Effects of constant high-temperature treatments on the content of chlorophyll (Chl) a, Chl b, carotenoid (Car), and Car/Chl (a+b) in the leaves of *P. tricuspidata* (Sieb. et Zucc.) Planch (a, c, e, g) and *P. quinquefolia* (L.) Planch (b, d, f, h).

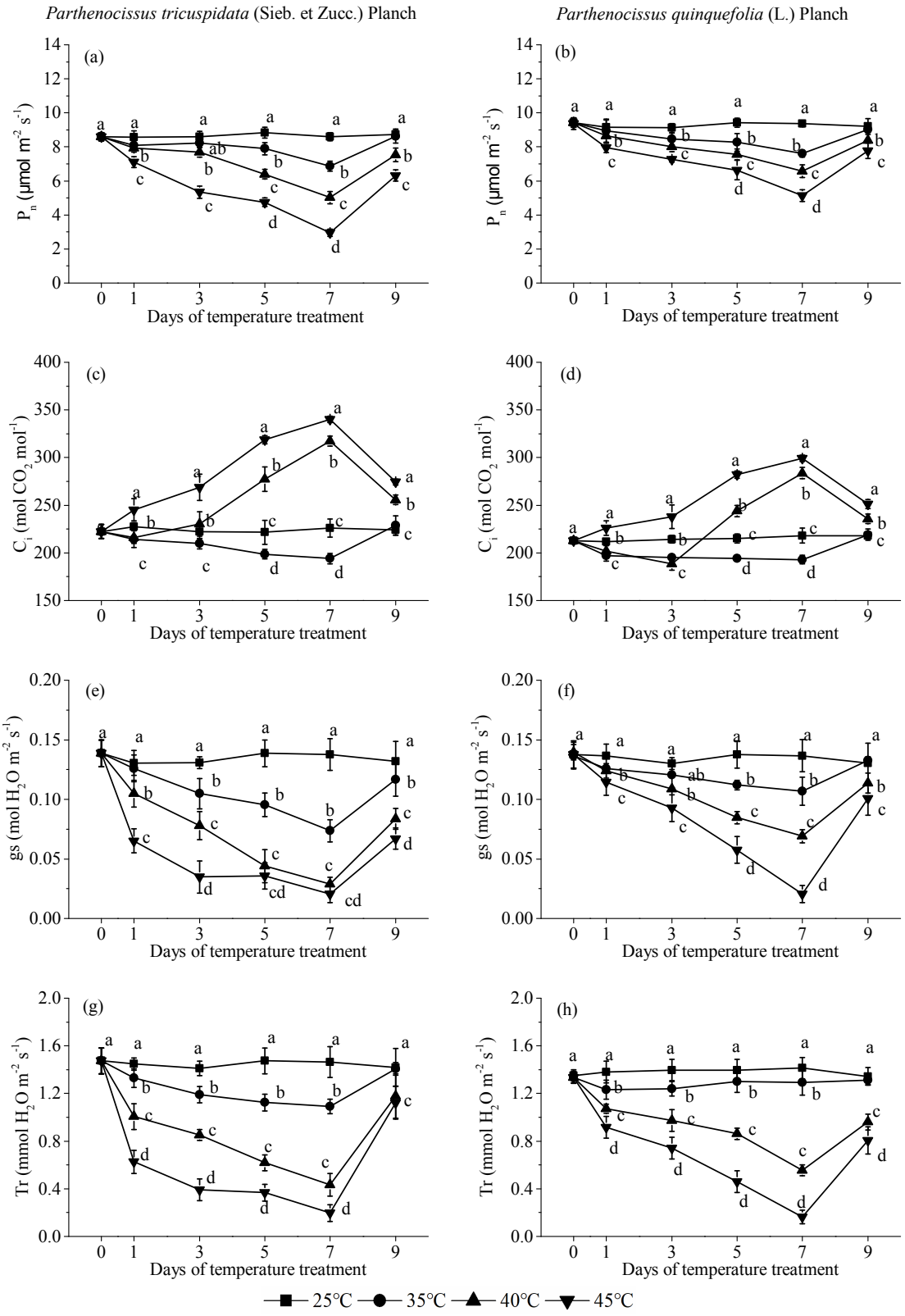

Fig. 2 Effects of constant high temperature treatments on P_n, C_i, gs and Tr in the leaves of *P. tricuspidata* (Sieb. et Zucc.) Planch (a, c, e, g) and *P. quinquefolia* (L.) Planch (b, d, f, h). P_n, photosynthetic rate; C_i, intercellular carbon dioxide concentration; gs, stomatal conductance; Tr, transpiration rate.

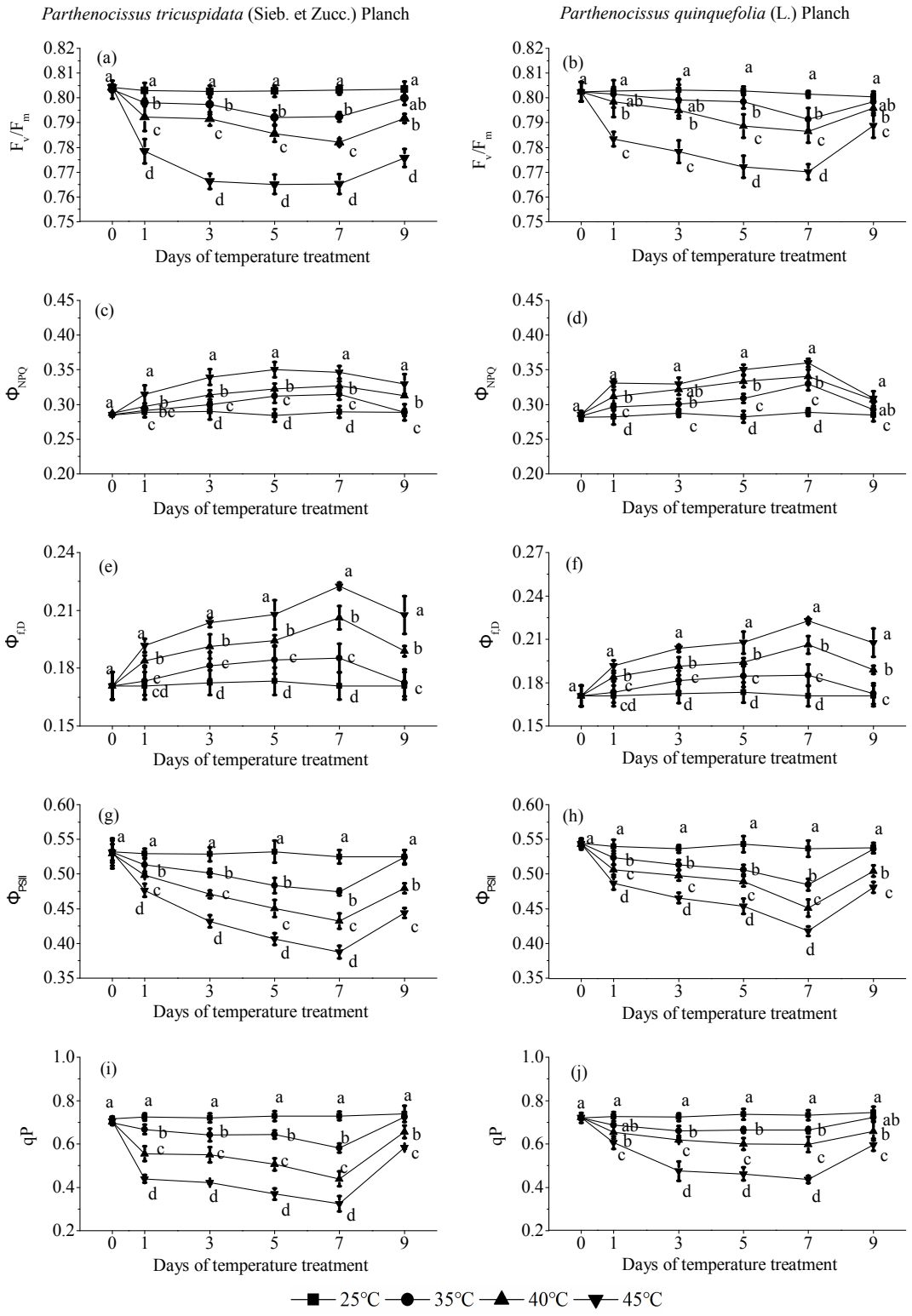

Fig. 3 Effects of constant high temperature treatments on F_v/F_m, Φ_{NPQ}, $\Phi_{f,D}$, Φ_{PSII}, and qP in the leaves of *P. tricuspidata* (Sieb. et Zucc.) Planch (a, c, e, g, i) and *P. quinquefolia* (L.) Planch (b, d, f, h, j). F_v/F_m, quantum yield of PSII photochemistry; $\Phi_{f,D}$, thermal energy loss; Φ_{NPQ}, regulated thermal energy loss; Φ_{PSII}, actual quantum yield of PSII photochemistry; qP, coefficient of photochemical quenching.

status [32]. In the present study, a reduction in F_v/F_m values was observed in both creepers under high-temperature stress; further, the ratio decreased continuously with the prolongation of the stress. This indicated that possible damage occurred to the PSII reaction centers. Compared to control values, Φ_{PSII} and qP showed a decreasing trend, whereas the $\Phi_{f,D}$ showed the opposite trend. This indicated that the activity of PSII was inhibited and that photodamage occurred due to exposure to high-temperature, an effect that increased with increasing stress duration [13, 25].

Absorbed light energy is usually distributed through three main paths, namely, Φ_{NPQ}, $\Phi_{f,D}$, and Φ_{PSII}. These three paths are somewhat interchangeable [13]. To maintain photosynthetic carbon-assimilation ability, chloroplasts must enhance excess-energy dissipation processes through Φ_{NPQ}, whereby the reaction center closes. During the entire duration of stress exposure, Φ_{NPQ} of *P. quinquefolia* showed faster and wider response ranges than Φ_{NPQ} of *P. tricuspidata*. This finding indicated that *P. quinquefolia* has a higher adaptive capacity to high temperature than *P. tricuspidata*.

To further investigate the photosynthetic capacity in both creepers, photosynthetic recovery upon relief of high-temperature stress treatment was analyzed. The results of Greer [30] and Yamori [33] proved that the CO_2 fixation process is also sensitive to high-temperature stress and is likely disrupted. In our study, P_n did not recover in either creeper after they were exposed for 7 days to 40 or 45 °C. This indicated that high temperature might induce irreversible damage to the CO_2 fixation process. Thus, enhancing heat stability of CO_2 fixation might be an effective way for both creepers to deal with the greenhouse effect. The extent of recovery of PSII performance under high-temperature stress can reflect the capacity of photosynthetic components for self-repair.

In the present study, the fluorescence parameters of *P. quinquefolia* showed greater resilience than those of *P. tricuspidata*. This indicated that as far as photosynthesis is concerned, *P. quinquefolia* shows important advantages over *P. tricuspidata* to deal with the challenge posed by global warming.

CONCLUSION

A significant reduction in photosynthetic pigment content was observed in both creepers studied with increasing temperature; concomitantly, Car levels showed the opposite trend. Non-stomatal limitations were the main cause for the decrease in P_n when air temperature exceeded 40 °C. Carotenoids play a key role in the adaptation of both species to high-temperature stress. Simultaneously, the process of excess energy dissipation through Φ_{NPQ} is an important mechanism for protecting the photosynthetic machinery. Overall, *P. quinquefolia* showed greater resistance and resilience to heat stress than *P. tricuspidata*.

Although we discussed the tolerance mechanism of the two creepers to high temperature, a complete understanding of the heat resistance mechanism remains limited. The climatic environment of plants varies among regions. We must further explore the adaptive mechanism of the two creepers under study in different high temperature environments. At the same time, we should also utilize molecular and genetic methods to further reveal the mechanisms underlying the response of the two creepers to high-temperature stress.

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