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Response of Dahlia Photosynthesis and Transpiration to High-Temperature Stress

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Abstract: The high temperature may cause difficult growth or bloom in the summer, which is the key problem limiting the cultivation and application of dahlia. The photosynthetic physiological mechanisms of dahlia under high temperature stress were studied to provide a theoretical basis for expanding the application range of cultivation and annual production. Two dahlia varieties, 'Tampico' and 'Hypnotica Tropical Breeze', were used as test materials and were treated for 1 d or 2 d at temperatures of 35/30 °C or 40/35 °C (day/night: 14 h/10 h) and then recovered at 25/20 °C for 7 d. A 25/20 °C treatment was used as the control. The results are as follows: (1) High-temperature stress resulted in the chlorophyll (Chl) content, *Fv*/*Fm*, transpiration rate (*Tr*), net photosynthetic rate (*Pn*), and water potential decreasing significantly, and the Chl content, *Tr*, and stomatal density of 'Tampico' were higher than those of 'Hypnotica Tropical Breeze' during the same period. (2) After the two dahlia varieties were treated with high-temperature stress and recovered at 25/20 °C for 7 d, the plant morphology and various physiological indices under the 35/30 °C treatment gradually returned to normal, with 'Tampico' in better condition than 'Hypnotica Tropical Breeze'. (3) Both dahlia varieties could not withstand the stress of 40/35 °C for 2 days.

Keywords: dahlia; high-temperature stress; photosynthesis; transpiration

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1. Introduction

In recent years, frequent summer high temperatures and record-breaking high temperatures [1] have brought great challenges to plant growth and development. High temperatures can cause wilted and dried leaves, the dropping of flowers and fruits, plant lodging, slow growth, and even plant death, which seriously affect production. *Dahlia pinnata* is a perennial bulbous flower of the Asteraceae family and has earned the reputation of "world-famous flower" by virtue of its colorful flowers, diverse flower types, and long flowering period [2,3]. However, high temperatures, especially extreme heat in the summer, result in dahlia plants being subjected to high-temperature stress in a short period of time, leading to plant dormancy or even death, which seriously affects its production and applications.

In response to unfavorable high-temperature environmental conditions, plants have evolved complex physiological and biochemical response mechanisms [4], among which photosynthesis is one of the most sensitive physiological processes in response to high-temperature stress [5]. High temperatures can reduce photosynthetic pigment synthase activity and reduce chlorophyll (Chl) synthesis, resulting in a reduction in Chl content, which can directly weaken photosynthesis [5,6]. At the same time, the enhanced photorespiration and dark respiration rates at high temperatures lead to a decreased net photosynthetic rate (*Pn*). High-temperature stress can destroy the integrity of the chloroplast and thylakoid membranes, resulting in a loss of cell membrane permeability, which affects the photosynthetic process, reduces photosynthetic efficiency [7], and inhibits plant growth. Chl fluorescence is the light signal emitted by the Chl molecule from the first singlet state back to the ground state after absorbing light energy [8], and the change in fluorescence can reflect the status of the photosynthetic apparatus and is often used as a reliable indicator of the structural activity of the photosynthetic system to evaluate the stress on plants [9]. High-temperature stress can damage the structure of the photosynthetic system; photosystem II (PSII) is considered the most temperature-sensitive component, and the ratio of variable to maximum fluorescence (Fv/Fm) can reflect the light energy conversion efficiency of the PSII reaction center [10]. Heat stress can lead to a decrease in the Fv/Fm and damage to the PSII active center, resulting in photoinhibition [11].

The main location of plant transpiration is the leaf, and the main form of leaf transpiration is stomatal transpiration [12]. The feedback of transpiration on stomatal conductance (*Gs*) can be described by the leaf water potential. Under high-temperature stress, plants reduce the leaf temperature by regulating the transpiration rate (*Tr*) and stomatal characteristics [13], while stomatal opening is positively correlated with *Gs* and *Tr* [14]. Plants exhibit avoidance or acclimation mechanisms under short-term high-temperature conditions [15], and the *Tr*, stomatal opening, and *Gs* increase with increasing temperature [16]. Under long-term high-temperature conditions, plants prevent excessive water loss by reducing stomatal opening or even closing the stomata, resulting in reduced leaf water potential, *Tr*, and *Pn* [17,18] and thus protecting plants from high-temperature stress. When the temperature exceeds the limit of plant growth and the root system is in an environment with sufficient water, due to the limited regulation of stomata, photosynthesis can be weakened or even stopped, but the stomata would not be completely closed to maintain the conduction function to enable continuous transpiration [19], and transpiration and photosynthesis are decoupled. The change in stomata is also closely related to the heat tolerance of plants. Studies in *Rhododendron* [20] and *Calendula officinalis* [21] have shown that the higher the stomatal density is, the stronger the heat resistance is; cotton with strong heat resistance [22] has a high *Gs*, and 20 broad-leaved evergreen trees/shrubs have been shown to reduce leaf temperature by increasing *Gs* under high-temperature stress [18]. Therefore, plant stomatal characteristics, leaf temperature, or canopy temperature can be used to characterize plant heat tolerance [23,24].

Dahlia is widely used as potted flowers, cut flowers, and garden plants, and because of its high inulin content, dahlia is also a high-quality raw material for the production of inulin and fructans [25]. Meanwhile, the petals of dahlia are excellent sources of flavonoids and floral pigment glycosides, and they can be eaten raw or made into salad. Leaf extracts have a very high antimicrobial activity [26] and a strong analgesic ability [27]. Therefore, dahlia is an excellent plant species with both ornamental, medicinal, and edible values. High temperatures in the summer are one of the most important stress factors affecting the widespread application of dahlias. To date, research on dahlia has mainly focused on the selection of varieties [28], the postharvest physiology of cut flowers [29], and the extraction and function of tuberous root inulin [30]. However, there are few studies on the heat resistance of dahlias, and the relationship between high temperature and photosynthesis and transpiration in dahlias is rarely reported. The main purpose of this study was to use the two summer flowering dahlia varieties, 'Tampico' and 'Hypnotica Tropical Breeze', as test materials to evaluate the effects of different high-temperature treatments on the morphology and photosynthetic physiology of dahlias and to compare the heat resistance between varieties in order to lay a theoretical basis for the promotion of the application of dahlias in gardens and the production of dahlias for different purposes.

2. Materials and Methods

2.1. Test Materials

'Tampico' and 'Hypnotica Tropical Breeze', summer flowering, being popular in market, showed heat resistance differences in the culturing process and previous tests, were used as the test materials. 'Tampico' and 'Hypnotica Tropical Breeze' cuttings were supplied by Yunnan Yihua Horticulture Co., Ltd. (Kunming, China) and planted in plastic pots. The pots were filled up with a 3:1 mixture of peat and perlite and kept in a greenhouse (115°29′24″ E, 38°51′21″ N) from March to June 2022. Water-soluble compound fertilizer was applied with watering every 2 weeks. The relative humidity of the substrate was maintained at 50–60% (LTS-W Soil Temperature and Humidity Automatic Recorder (De Aupos Scientific, Jiangsu, China)), and the air humidity was 65–75%. High-temperature treatments were carried out when the cuttings were at the blooming florescence stage (ligulate flowers fully expanded, nearly perpendicular to the pedicel, tubular flowers beginning to appear). There were three replicated plots. Basic information is shown in Table 1.

Table 1. Basic information of the tested dahlias.

Variety Name	Basic Information
Tampico	Plant height: 29.99 ± 0.75 cm; number of branches per plant: 8–10; stem thickness: 8.67 ± 0.21 mm; large leaves and small number of leaves per plant; large flower diameter; number of flowers open at one time 4–5.
Hypnotica Tropical Breeze	Plant height: 27.35 ± 0.45 cm: number of branches per plant: 10–14; stem thickness: 7.82 ± 0.25 mm; small leaves and large number of leaves per plant; small flower diameter; number of flowers open at one time: 6–8.

Note: The above basic information was randomly selected for observation and determination of each morphological index before the experimental treatment. Plant height: The distance from the growth point to the surface of the pot soil was determined by a rice ruler. Stem thickness: The diameter of the stem at approximately 1 cm above the pot soil was determined with a Vernier caliper.

2.2. High-Temperature Stress Treatment

The healthy, uniform cuttings were transferred into a GXZ-158B intelligent light incubator (Ningbo Southeast Instrument Co., Ltd., Ningbo, China) at 25/20 °C (day/night) with a light intensity of 10,000 Lux and a light–dark cycle of 14/10 h for 3 d of acclimatization before experiments were performed. The relative humidity of the substrate was 50–60% during the experimental period, and the air humidity was 70%.

During the high-temperature stress treatment, the day and night temperatures were set at 35/30 °C and 40/35 °C, respectively, and the other parameters were the same as those during the adaptation period. Taking 25/20 °C as the control, a 1−d treatment, a 2−d treatment, and a 7−d recovery at the control temperature after the 2−d treatment were conducted, with five pots per treatment and three repeated measurements.

2.3. Index Determination and Method

2.3.1. Heat Injury Index

Immediately after the treatment was completed, the plants were evaluated for heat injury. The heat injury symptoms were graded according to Zhao [31], i.e., grade 0: no damage symptoms, plant condition is good overall; grade 1: the mature leaves at the base are slightly dehydrated or the tips of the leaves are slightly withered, leaf area exhibiting withering or shriveling is <1/3, the leaves are stretched, the plants are slightly wilted, and the flowers are in good shape; grade 2: 1/3 < leaf area exhibiting withering or shriveling <1/2, the plants are wilted, the leaves are drooping, and the outer ligulate flowers are wilted; grade 3: 1/2 < leaf area exhibiting withering or shriveling <1, the plant is shriveled, the leaves are drooping, and the overall dehydration of the flowers is severe; grade 4: the leaves and flowers are all withered. The heat injury index is calculated using Equation (1):

$$\text{eat injury index }\% = \frac{\Sigma(\text{number of plants in the grade } \times \text{ grade level})}{\text{highest grade level } \times \text{ total number of treated plants}} \times 100 \quad (1)$$

2.3.2. Recovery Index

The recovery condition of the dahlia plants after 7 d of recovery was graded according to Jia et al. [32], i.e., grade 0: the whole plant is dry and dead; grade 1: although the stem remains green, the leaves are all withered and do not recover; grade 2: the stem remains green and 30% of the leaves are green; grade 3: the stem is green, 80% of the leaves are recovered, and the leaves are turning green; grade 4: flower buds bloom and the whole plant is restored. The recovery index is calculated using Equation (2):

$$\text{recovery index }\% = \frac{\Sigma(\text{number of plants in the grade } \times \text{ grade level})}{\text{highest grade level } \times \text{ total number of treated plants}} \times 100 \quad (2)$$

2.3.3. Determination of Stomatal Characteristics

After the treatment was completed, the mature leaves at the third node from the top of the stem were selected, and nail polish was applied to the middle part of the leaf using the rubbing method. After drying, the epidermis was removed, and the stomata were observed under a microscope (100×) to count the total number and calculate the stomatal density. The stomatal length and width were measured to calculate the stomatal opening according to Ohsumi et al. [33]:

$$\text{stomatal opening} = \pi ab \quad (3)$$

where a is 1/2 of the stomatal length and b is 1/2 of the stomatal width.

2.3.4. Determination of Water Potential

Three mature leaves were selected from the top of the stem, counting down to the third node, and the leaf water potential measurements were taken at about 9:00–10:00 a.m. using a Model 615 portable pressure chamber instrument (PMS Instrument Company, Alban, WI, USA).

2.3.5. Determination of Photosynthetic Pigments

Mature leaves at the third node from the growing point were selected, and the 95% ethanol extraction method was used. Approximately 0.1 g of dahlia leaves were cut into pieces and placed in 10 mL of 95% ethanol. After extracting in the dark for 72 h, the contents of chlorophyll a (Chl a), chlorophyll b (Chl b), and carotenoids (Car) were determined by the optical density (OD) at 665 nm, 649 nm, and 470 nm, respectively, using a spectrophotometer. The equations for calculating the Chl content are as follows [34]:

$$\text{Ca} = 13.95\text{A}_{665} - 6.88\text{A}_{649} \quad (4)$$

$$\text{Cb} = 24.96\text{A}_{649} - 7.32\text{A}_{665} \quad (5)$$

$$\text{Chl a content (mg/g)} = \frac{\text{Ca} \times \text{V}}{\text{M} \times 1000} \quad (6)$$

$$\text{Chl b content (mg/g)} = \frac{\text{Cb} \times \text{V}}{\text{M} \times 1000} \quad (7)$$

$$\text{Car content (mg/g)} = \frac{(1000\text{A}_{470} - 2.05\text{Ca} - 111.48\text{Cb}) \times \text{V}}{\text{M} \times 1000 \times 245} \quad (8)$$

where Ca represents the concentration of Chl a (mg/L); Cb represents the concentration of Chl b (mg/L); V represents the total volume of the extract (mL); and M is the mass of the fresh sample (g).

2.3.6. Determination of Chl Fluorescence Parameters

Selected mature leaves at the third node from the growing point were clamped with dark-adaptive leaf clips for 20 min, and a Yaxin-1105 portable fluorometer (Beijing Yaxin Liyi Technology Co., Ltd., Beijing, China) was used to measure the fast chlorophyll fluorescence induction curve (OJIP) (the light intensity was set to 3000 μmol/m^{2}s, and the measurement duration was 10 s). The measurement indicators were the maximum photochemical quantum yield of PSII (Fv/Fm), the initial Chl fluorescence (F_0), and the maximum fluorescence yield (Fm).

2.3.7. Determination of Photosynthetic Parameters

The Yaxin-1105 portable fluorometer (BeiJing YaXin LiYi Technology Co., Ltd., Beijing, China) in the open-circuit automatic mode with the external light source (air flow was set to 0.5 L/min, and the intensity of the external light source was set to 1000 μmolE/m^{2}s) was used to determine the photosynthetic physiological characteristics of the two dahlia varieties. Each measurement was conducted at 8:00–10:00 am. Mature leaves from the third node below the growth point were selected to measure the *Pn* and *Tr*.

2.4. Data Analysis

This study used Excel 2019 and IBM SPSS Statistics 20 software to analyze the data and Origin 2021 software to plot the figures. The significance between groups was analyzed using an independent sample *t* test, and multiple comparison analysis was performed using the Waller–Duncan K-ratio *t*-test.

3. Results

3.1. External Morphology

After high-temperature stress, the middle and lower leaves of the two dahlia varieties showed heat injury symptoms, which manifested as scorched leaf edges or even withered leaves. The high temperature also accelerated flower senescence, and rigid and black flower buds appeared (Figures 1 and 2). After being stressed at 40/35 °C for 2 d, the heat injury index of the two dahlia varieties reached a maximum of 35.00% and 60.00%, respectively. After being stressed at 35/30 °C for 2 d, the plants all returned to a normal growth state (Figures 1f and 2f). After high-temperature stress, the overall heat injury index of ‘Tampico’ was lower than that of ‘Hypnotica Tropical Breeze’ (Table 2). After being stressed at 40/35 °C for 2 d, the heat injury to the plants was too serious, and the plant condition after the 7−d recovery was even worse than that immediately after the 2−d stress, i.e., a small number of new leaves were growing on ‘Tampico’, while all ‘Hypnotica Tropical Breeze’ plants were dead (Figures 1i and 2i). Therefore, only the physiological indicators obtained after the 7−d recovery following the 2−d treatment at 35/30 °C were analyzed, while those obtained after the 7−d recovery following the 2−d treatment at 40/35 °C were excluded.

Table 2. Heat injury index and recovery index of dahlia.

Treatment	Heat Injury Index (%)		Recovery Index (%)	
	Tampico	Hypnotica Tropical Breeze	Tampico	Hypnotica Tropical Breeze
25/20 °C 1 d	0.00	0.00	—	—
25/20 °C 2 d	0.00	0.00	100.00	100.00
35/30 °C 1 d	5.00	5.00	—	—
35/30 °C 2 d	12.50	15.00	100.00	100.00
40/35 °C 1 d	17.50	25.00	—	—
40/35 °C 2 d	35.00	60.00	15.00	0.00

Figure 1. Morphological change in 'Tampico' after high-temperature stress (**a**) 25/20 °C 1 d; (**b**) 25/20 °C 2 d; (**c**) 25/20 °C 7−d recovery; (**d**) 35/30 °C 1 d; (**e**) 35/30 °C 2 d; (**f**) 35/30 °C 7−d recovery; (**g**) 40/35 °C 1 d; (**h**) 40/35 °C 2 d; (**i**) 40/35 °C 7−d recovery.

Figure 2. Morphological changes in 'Hypnotica Tropical Breeze' after high-temperature stress (**a**) 25/20 °C 1 d; (**b**) 25/20 °C 2 d; (**c**) 25/20 °C 7−d recovery; (**d**) 35/30 °C 1 d; (**e**) 35/30 °C 2 d; (**f**) 35/30 °C 7−d recovery; (**g**) 40/35 °C 1 d; (**h**) 40/35 °C 2 d; (**i**) 40/35 °C 7−d recovery.

3.2. Stomatal Characteristics

Leaf heat damage symptom levels for stomatal characterization of 'Tampico' and 'Hypnotica Tropical Breeze' are shown in Tables 3 and 4.

Table 3. Heat Damage Levels of 'Tampico' leaves.

Variety Name	Tampico								
Treatment	25/20 °C			35/30 °C			40/35 °C		
Duration (d)	1	2	Recover 7	1	2	Recover 7	1	2	Recover 7
Leaf heat damage symptom level	0	0	0	0	1	1	1	1	3

Table 4. Heat Damage Levels of 'Hypnotica Tropical Breeze' leaves.

Variety Name	Hypnotica Tropical Breeze								
Treatment	25/20 °C			35/30 °C			40/35 °C		
Duration (d)	1	2	Recover 7	1	2	Recover 7	1	2	Recover 7
Leaf heat damage symptom level	0	0	0	1	1	1	1	2	4

High-temperature stress can affect the stomatal density and stomatal opening of dahlias. At 25/20 °C, the stomatal densities of 'Tampico' and 'Hypnotica Tropical Breeze' were 61.00/mm^2 and 44.44/mm^2, respectively, with a significant difference between the two varieties ($p < 0.01$). After high-temperature treatment, 'Tampico' stomatal density decreased and then increased, with significant differences in stomatal density after the high-temperature treatment compared to the control ($p < 0.05$). The stomatal density of 'Tampico' under the 1−d 35/30 °C treatment was the smallest at 49.00/mm^2 and was the highest under the 2−d 40/35 °C treatment, reaching 66.33/mm^2 (Figure 3a). 'Hypnotica Tropical Breeze' stomatal density showed no significant difference after temperature or treatment, and under the 1−d 40/35 °C treatment, it was the smallest at 36.67/mm^2 (Figure 3b). After the 7−d recovery, the stomatal densities of the two varieties were not significantly different from those before recovery and those of the control ($p < 0.05$).

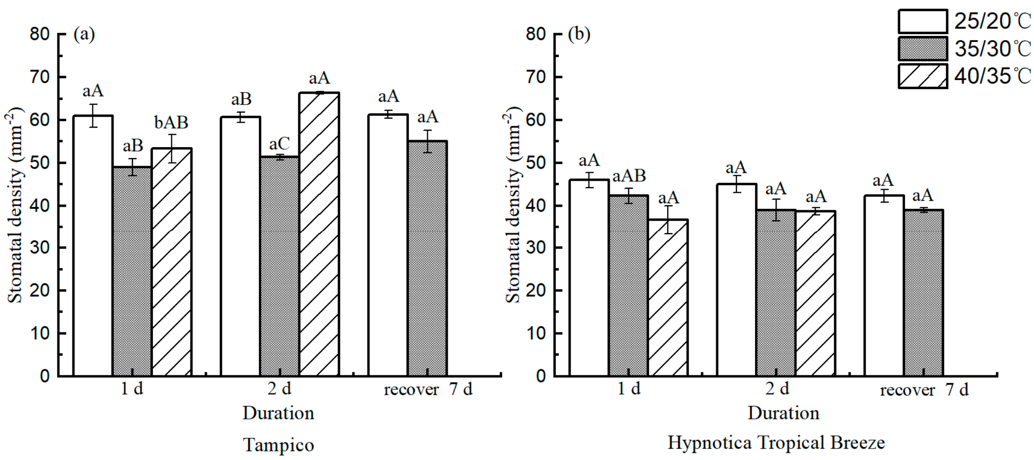

Figure 3. Changes in stomatal density per 1 mm^{-2} leaf area in 'Tampico' (**a**) and 'Hypnotica Tropical Breeze' (**b**) after high temperature stress. Lowercase letters indicate the significance of different treatment times at the same temperature (Waller−Duncan test, $p < 0.05$), and capital letters indicate significant differences in different treatment temperatures for the same treatment days (Waller−Duncan test, $p < 0.05$).

In terms of stomatal opening, at 25/20 °C, the stomatal opening of 'Tampico' was significantly larger than that of 'Hypnotica Tropical Breeze' ($p < 0.01$). After high-temperature stress, the stomatal opening of 'Tampico' reached a maximum under the 1−d 40/35 °C treatment, with an increase of 18.26% compared with the control, and reached a minimum under the 2−d 35/30 °C treatment, with a decrease of 6.80% compared with the control (Figure 4a). After high-temperature stress, the stomatal opening of 'Hypnotica Tropical Breeze' first decreased and then increased. Stomatal opening reached a maximum under the 1−d 40/35 °C treatment, with an increase of 20.93% compared with the control, and reached a minimum under the 1−d 35/30 °C treatment, with a decrease of 15.16% compared with the control (Figure 4b). After the 7−d recovery, the stomatal openings of both varieties were significantly increased compared with those before recovery, and there was no significant difference compared with the control ($p < 0.05$).

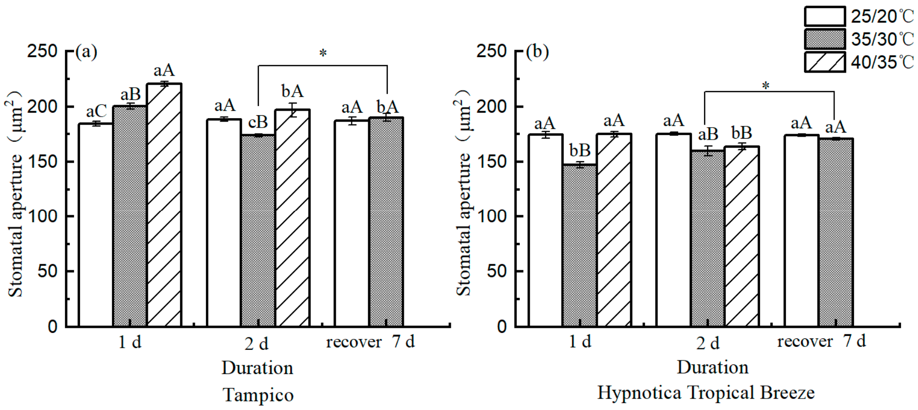

Figure 4. Change of stomatal aperture in 'Tampico' (**a**) and 'Hypnotica Tropical Breeze' (**b**) after high-temperature stress. Lowercase letters indicate the significance of different treatment times at the same temperature (Waller-Duncan test, $p < 0.05$), and capital letters indicate significant differences in different treatment temperatures for the same treatment days (Waller–Duncan test, $p < 0.05$). * is significantly different at the 0.05 probability levels (t-test).

3.3. Leaf Water Potential

Under the control conditions, there was no significant difference in leaf water potential between the two dahlia varieties, with a mean of − 0.41 MPa. After high−temperature stress, the leaf water potential of both varieties decreased. The leaf water potential under the 1−d 35/30 °C treatment was not significantly different from that of the control, while the leaf water potentials under the other treatments were significantly lower than that of the control ($p < 0.05$). Under the 2−d 40/35 °C treatment, the leaf water potentials of 'Tampico' and 'Hypnotica Tropical Breeze' were 6.68-fold and 7.76−fold lower than those of the control, respectively. After the 7−d recovery, the leaf water potential of both varieties rose to a level that was not significantly different from that of the control ($p < 0.05$) but was extremely significantly higher than that before the recovery ($p < 0.01$) (Figure 5).

3.4. Photosynthetic Pigment Content

At 25/20 °C, the Chl a and Car contents in the leaves of 'Tampico' were significantly higher than those of 'Hypnotica Tropical Breeze' (Figure 6a,b,e,f), and the Chl b content in the leaves was not significantly different between the two dahlia varieties ($p < 0.05$) (Figure 6c,d). After high-temperature stress, the Chl a and Chl b contents in the leaves of both varieties decreased, and there was no significant difference between the 1−d 35/30 °C treatment and the control, but the Chl a and Chl b contents under the other treatments decreased significantly compared to the control ($p < 0.05$). The Chl a content of 'Tampico' was higher than that of 'Hypnotica Tropical Breeze' during the same period. Under the 2−d 40/35 °C treatment, the Chl a content of 'Tampico' and 'Hypnotica Tropical Breeze' decreased by 24.49% and 20.76%, respectively, compared with the control; the Chl b content of 'Tampico' and 'Hypnotica Tropical Breeze' decreased by 22.81% and 25.81%, respectively, compared with the control. The Car content in the leaves of the two dahlia varieties first decreased and then increased, reaching a minimum under the 1−d 35/30 °C treatment. After the 7−d recovery, the Chl a, Chl b, and Car contents in the leaves of both dahlia varieties all increased and reached levels that were not significantly different from those of the control ($p < 0.05$).

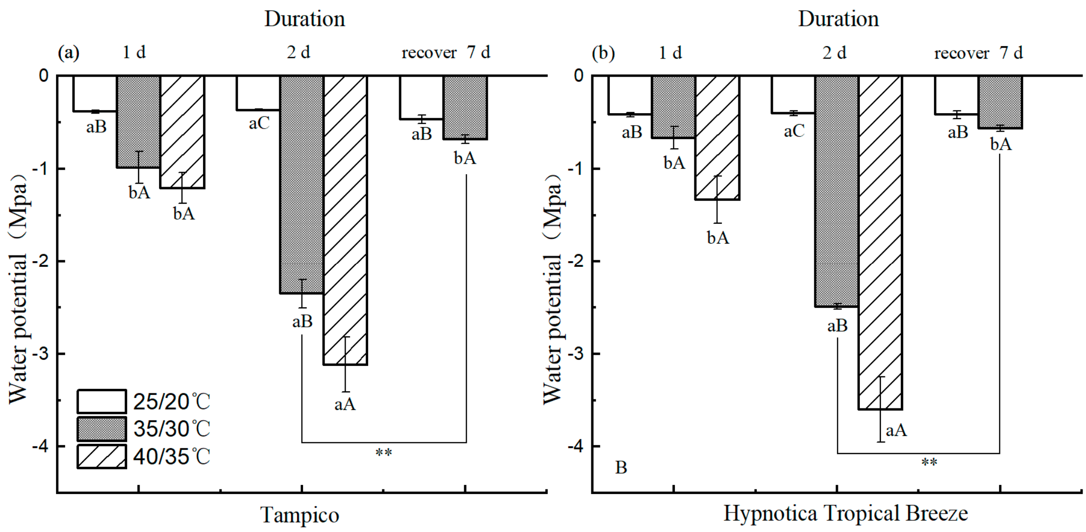

Figure 5. Change of the leaf water potential in 'Tampico' (**a**) and 'Hypnotica Tropical Breeze' (**b**) after high-temperature stress. Lowercase letters indicate the significance of different treatment times at the same temperature (Waller−Duncan test, $p < 0.05$), and capital letters indicate significant differences in different treatment temperatures for the same treatment days (Waller−Duncan test, $p < 0.05$). ** is significantly different at the 0.01 probability levels (*t*-test).

3.5. Chl Fluorescence Parameters

With increasing temperature and time, the F_0 of the two dahlia varieties increased significantly ($p < 0.05$). Under the 2−d 40/35 °C treatment, the F_0 increased by 27.15% and 33.51%. After the 7−d recovery, the F_0 decreased compared with that before the recovery but was still significantly higher than that of the control ($p < 0.05$). The F_0 of 'Tampico' (Figure 7a) was larger than that of 'Hypnotica Tropical Breeze' (Figure 7b) during the same period.

At 25/20 °C, the Fm of 'Tampico' (Figure 8a) and 'Hypnotica Tropical Breeze' (Figure 8b) was 1473.56 and 1377.67, respectively. The Fm of the two dahlia varieties decreased after the high-temperature stress. Under the 2−d 40/35 °C treatment, the Fm of the two dahlia varieties decreased by 43.39% and 45.02% compared with the control; after the 7−d recovery, the Fm of the 'Tampico' and 'Hypnotica Tropical Breeze' increased significantly by 26.80% and 34.37%, respectively, compared with that before the recovery ($p < 0.01$) and were significantly higher than that of the control ($p < 0.05$). The Fm values of 'Tampico' were all larger than those of 'Hypnotica Tropical Breeze' during the same period.

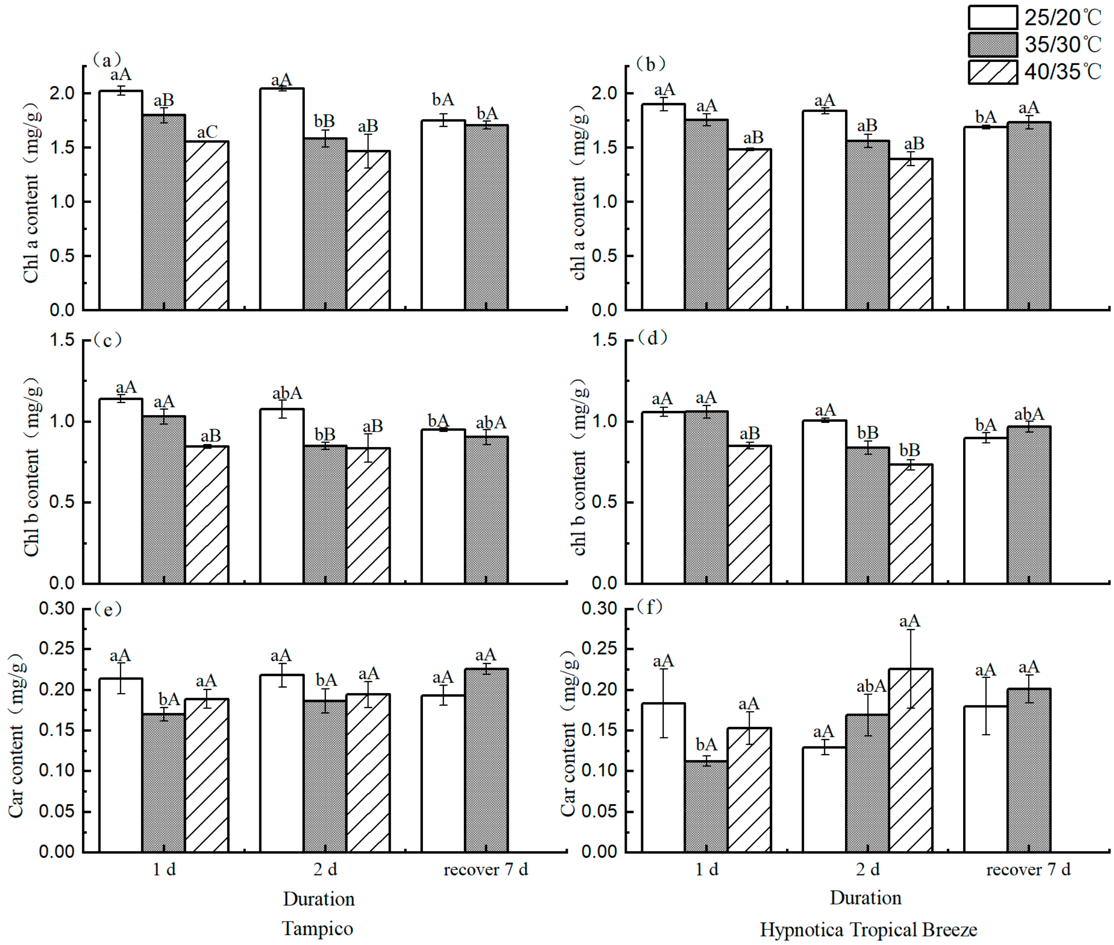

Figure 6. Change of Chl a, Chl b and Car content in 'Tampico' (**a**,**c**,**e**) and 'Hypnotica Tropical Breeze' (**b**,**d**,**f**) after high-temperature stress. Lowercase letters indicate the significance of different treatment times at the same temperature (Waller−Duncan test, $p < 0.05$), and capital letters indicate significant differences in different treatment temperatures for the same treatment days (Waller−Duncan test, $p < 0.05$).

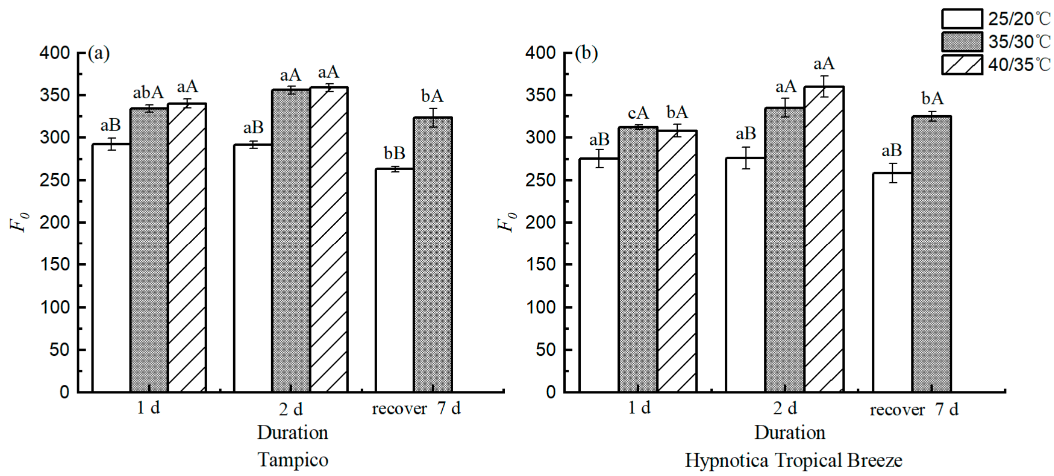

Figure 7. Change of F_0 in 'Tampico' (**a**) and 'Hypnotica Tropical Breeze' (**b**) after high-temperature stress. Lowercase letters indicate the significance of different treatment times at the same temperature (Waller−Duncan test, $p < 0.05$), and capital letters indicate significant differences in different treatment temperatures for the same treatment days (Waller−Duncan test, $p < 0.05$).

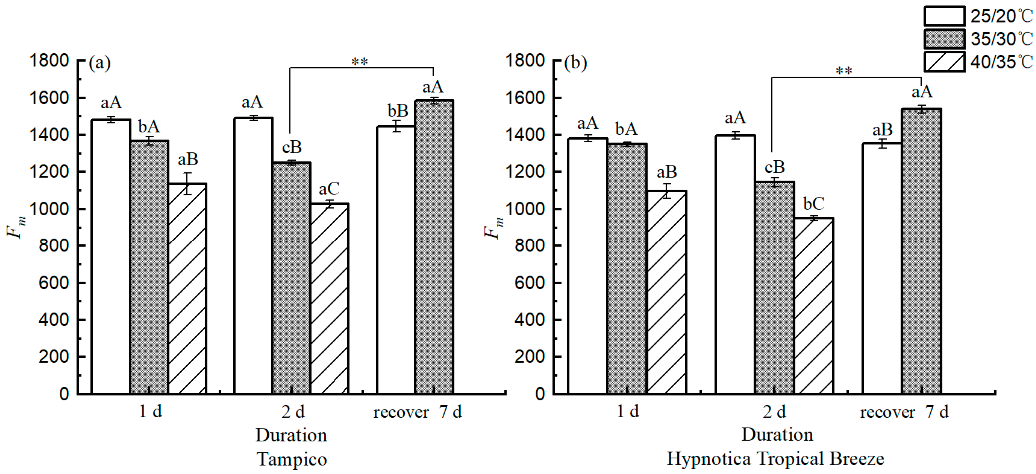

Figure 8. Change of *Fm* in 'Tampico' (**a**) and 'Hypnotica Tropical Breeze' (**b**) after high-temperature stress. Lowercase letters indicate the significance of different treatment times at the same temperature (Waller−Duncan test, $p < 0.05$), and capital letters indicate significant differences in different treatment temperatures for the same treatment days (Waller−Duncan test, $p < 0.05$). ** is significantly different at the 0.01 probability levels (*t*-test).

At 25/20 °C, the Chl fluorescence parameter *Fv*/*Fm* of the leaves of the two dahlia varieties was 0.81, with no significant difference. After high-temperature treatment, the *Fv*/*Fm* of the two varieties decreased, and 'Tampico' (Figure 9a) reached the minimum of 0.65 and 'Hypnotica Tropical Breeze' (Figure 9b) reached 0.62 under the 2−d 40/35 °C treatment, with a decrease of 24.45% and 30.47%, respectively, compared with the control. After the 7−d recovery, *Fv*/*Fm* of the leaves of both dahlia varieties significantly increased compared with that under the 2−d 35/30 °C treatment but was significantly lower than that of the control ($p < 0.05$).

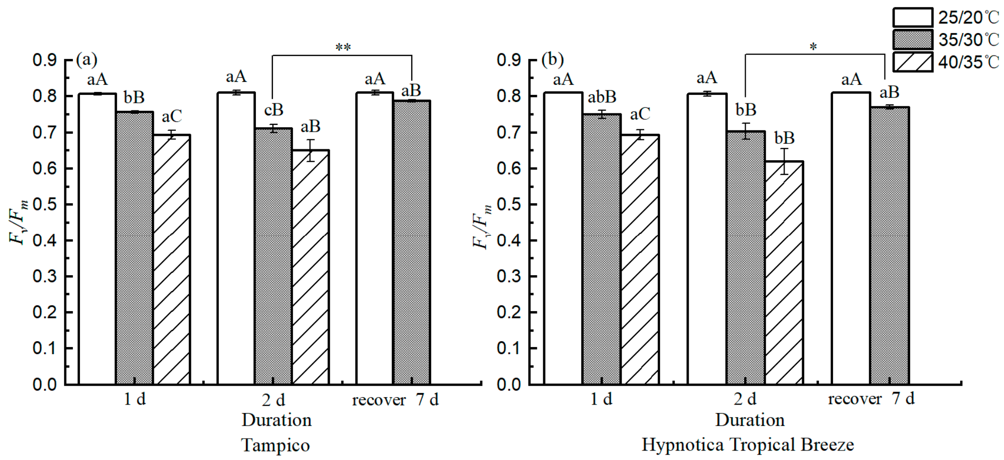

Figure 9. Change of *Fv*/*Fm* in 'Tampico' (**a**) and 'Hypnotica Tropical Breeze' (**b**) after high-temperature stress. Lowercase letters indicate the significance of different treatment times at the same temperature (Waller−Duncan test, $p < 0.05$), and capital letters indicate significant differences in different treatment temperatures for the same treatment days (Waller−Duncan test, $p < 0.05$). * and ** are significantly different at the 0.05 and 0.01 probability levels (*t*-test).

3.6. Photosynthetic Parameters

Under the control conditions, there was no significant difference in *Pn* between 'Tampico' and 'Hypnotica Tropical Breeze' (Figure 10a,b). Temperature stress resulted in a significant decrease in *Pn* in both groups compared with the control. Under the 2−d 40/35 °C treatment, the *Pn* of the two varieties reached the minimum and were 3.00-fold and 6.25-fold less than those of the control ($p < 0.05$). After the 7−d recovery, the *Pn* of 'Tampico' was significantly higher, i.e., 2.02-fold ($p < 0.01$), but was still significantly lower than that of the control ($p < 0.05$); the *Pn* of 'Hypnotica Tropical Breeze' was significantly higher, i.e., 1.62-fold, than before the recovery ($p < 0.01$).

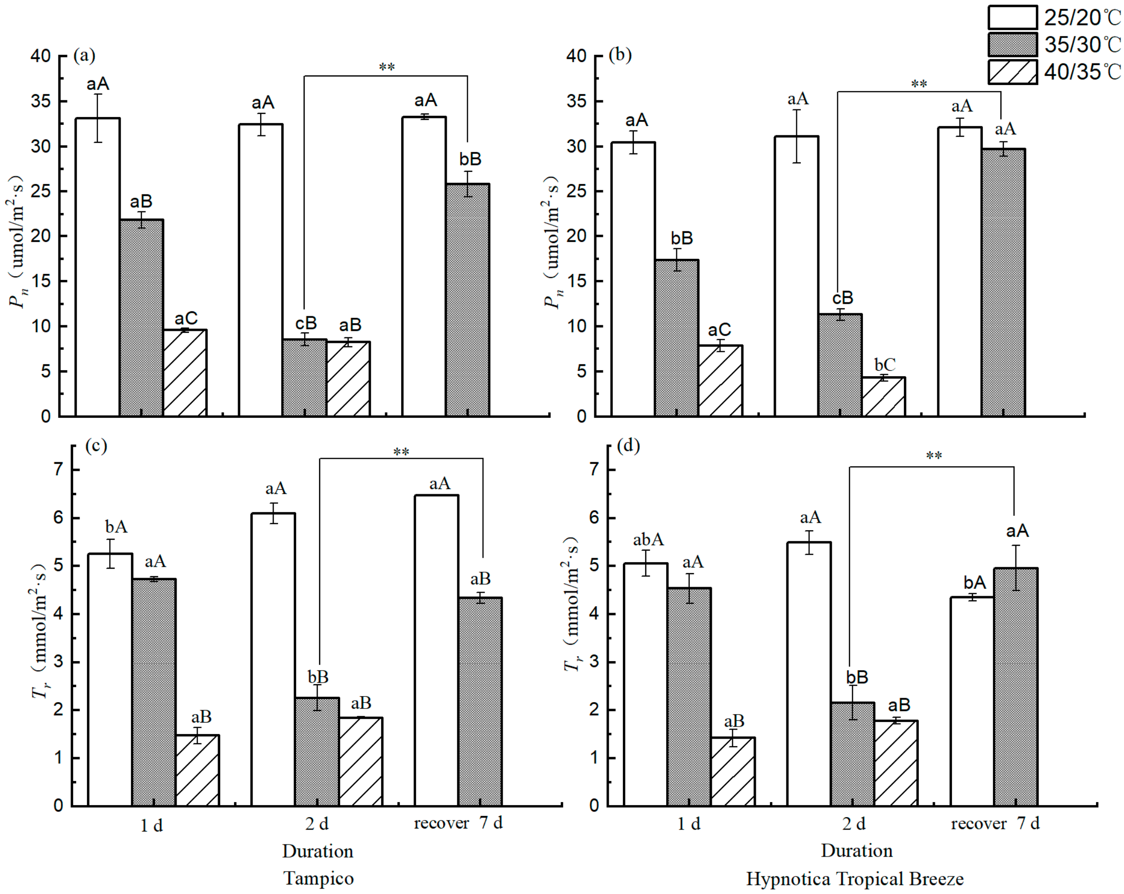

Figure 10. Change of photosynthetic parameters *Pn* and *Tr* of 'Tampico' (**a**,**c**) and 'Hypnotica Tropical Breeze' (**b**,**d**) after high-temperature stress. Lowercase letters indicate the significance of different treatment times at the same temperature (Waller−Duncan test, $p < 0.05$), and capital letters indicate significant differences in different treatment temperatures for the same treatment days (Waller−Duncan test, $p < 0.05$). ** is significantly different at the 0.01 probability levels (*t*–test).

Under the control conditions, the *Tr* of the two dahlia varieties was 5.94 mmol·m^{-2}·s^{-1} and 4.97 mmol·m^{-2}·s^{-1}, showing an extremely significant difference ($p < 0.01$), and the *Tr* of 'Tampico' was larger than that of 'Hypnotica Tropical Breeze' during the same period (Figure 10c,d). With the exception of the 1−d 35/30 °C treatment, the *Tr* decreased significantly compared with the control, and the *Tr* reached a minimum under the 1−d 40/35 °C treatment. The *Tr* of 'Tampico' and 'Hypnotica Tropical Breeze' was 75.25% and 71.41% lower than that of the control, respectively ($p < 0.05$). After the 7−d recovery, the *Tr* of 'Tampico' significantly increased by 92.61% ($p < 0.01$) compared with that before recovery but was still significantly lower than that of the control ($p < 0.05$); the *Tr* of 'Hypnotica Tropical Breeze' was extremely significantly increased 1.30-fold compared with that before recovery ($p < 0.01$).

4. Discussion

High-temperature stress can easily lead to symptoms such as water loss, wilting, and scorching of leaves in the aerial parts of plants. Determining the stress of plants through plant morphological changes is the most commonly used evaluation method [35]. In this study, two dahlia varieties, 'Tampico' and 'Hypnotica Tropical Breeze', were treated with high temperatures to observe and determine the morphological and physiological changes in the two varieties under high-temperature stress. The two dahlia varieties showed mature leaf edge withering, whole leaf wilting, blackening of flower buds, and growth halting after high-temperature stress. However, there were differences in the heat injury index of the two varieties, with the heat injury index of 'Tampico' generally lower than that of 'Hypnotica Tropical Breeze'. By the 7−d recovery after the high-temperature stress of the 2−d 35/30 °C treatment, the two varieties had recovered back to a normal condition. However, under the 2−d 40/35 °C treatment, almost all of the original leaves were dead in 'Tampico', but a very small number of new leaves were growing, whereas all of the aerial parts of the 'Hypnotica Tropical Breeze' plants had died and did not recover, which preliminarily shows that the heat resistance of 'Tampico' is stronger than that of 'Hypnotica Tropical Breeze'.

The size and number of stomata are closely related to leaf transpiration and photosynthesis [33]. By opening and closing the stomata, leaf transpiration can be adjusted, thereby adjusting the temperature of the leaves. On the first day of temperature treatment, the stomatal opening of 'Tampico' increased with increasing temperature, while on the second day, the stomatal opening first decreased and then increased with increasing temperature and was lower than that on the first day (except for the control), possibly because dahlias can reduce leaf temperature by increasing stomatal opening after short-term high-temperature stress, but with the increase in heat stress duration and intensity, leaf cells are damaged, stomata are closed, and leaf water is lost, resulting in a significant reduction in water potential; transpiration is limited, and *Tr* continuously decreased with increasing temperature. The stomatal opening of 'Hypnotica Tropical Breeze' was consistent with that of 'Tampico' on the second day from the beginning of the high-temperature treatment, indicating that the 35/30 °C treatment exceeded the suitable growth temperature range. Nazdar T. et al. [21] showed that stomatal density is positively correlated with plant heat tolerance. The stomatal density of 'Tampico' showed a first decrease and then increase with increasing temperature, at which time its *Tr* and *Pn* also showed the same trend; when the treatment temperature reached 40/35 °C, the stomatal density of 'Tampico' was significantly elevated ($p < 0.05$) after 2 d of treatment. The stomatal density of 'Hypnotica Tropical Breeze' was not significantly different before and after treatment. This phenomenon may be caused by the following two aspects: the first is caused by the difference in heat tolerance of plants themselves. 'Hypnotica Tropical Breeze' has limited ability to adapt to high temperatures, and the leaves are damaged under high temperatures, which affects the normal function of stomata, and it is not possible to regulate stomatal density according to the temperature change [36]. Secondly, photosynthesis pigments were destroyed in the early stage of high-temperature stress, which led to limited photosynthesis and the coupling of photosynthesis and transpiration, resulting in a decrease in *Tr* and stomatal density of 'Tampico'. With the increase of temperature stress time in the later stage, photosynthesis and transpiration appear to be decoupled, and Dahlia reduces the damage caused by high-temperature stress through the increase of *Tr* in order to reduce the temperature of the leaves. The combined effect makes 'Hypnotica Tropical Breeze' limited in its ability to adapt to high temperatures. Dahlia reduced the damage caused by high temperature stress by increasing *Tr* to lower leaf temperature, which increased *Tr* and stomatal density under the combined effect. The stomatal opening, stomatal density, and *Tr* of 'Tampico' were all larger than those of 'Hypnotica Tropical Breeze' during the same period, indicating that 'Tampico' has stronger stomatal regulation ability, transpiration ability, and heat resistance, which is consistent with the findings of Zhang et al. [14] in tomato. Transpiration changes the water potential in plants, and the larger the *Tr* is, the greater the water loss from the leaves. However, after the temperature stress, the *Tr* decreased continuously, and the water potential also decreased, which is consistent with the findings of rice under high-temperature stress [37]. A possible reason for this finding is that the cell membrane structure of dahlia leaves is destroyed during high-temperature treatment, and the selective permeability and active absorption capacity are lost, which leads to a large amount of water loss from the leaves. It may also be due to the production of osmoregulatory substances by dahlias to withstand heat stress, resulting in a reduction in cellular osmotic potential.

The photosynthetic pigment content not only determines the strength of photosynthetic ability but also reflects the adaptation of plants to the environment. During high-temperature stress, the photosynthetic ability and photosynthetic pigment content of the leaves are reduced, water is rapidly lost, and the cell membrane structure is damaged [38], which in turn affects the mechanism of photosynthesis. In this study, the photosynthetic pigment contents, *Pn*, and *Tr* of 'Tampico' were higher than those of 'Hypnotica Tropical Breeze' during the same period, indicating that dahlia varieties with strong heat tolerance have stronger photosynthetic ability. In the two dahlia varieties, the trend of Chl content was similar to that of *Pn*, *Tr*, and *Fm* under high-temperature stress, i.e., a decline, which is consistent with the findings of Xiao F et al. [39]. After the 7−d recovery, the photosynthetic pigment content and Fv/Fm were not significantly different from those of the control, possibly because high-temperature stress leads to the accumulation of reactive oxygen species in plant cells, resulting in the formation of PSII photoinhibition [40], while Chl can alleviate cellular oxidative damage [41]. In addition to being auxiliary pigments for photosynthesis, Car are important nonenzymatic antioxidants in plants [42]. The content of Car in the two dahlia varieties first decreased and then increased, indicating that with increasing high-temperature stress, the antioxidant function of Car in dahlias was enhanced and the effect of supplementing photosynthetic pigments was weakened, causing the synthesis of Car in dahlias to increase and consumption to decrease. Under high-temperature stress, the *Pn* and Fv/Fm of the two dahlia varieties decreased significantly ($p < 0.05$) compared with the control, which is consistent with the findings in wheat [43], possibly because the high-temperature stress causes the destruction of the chloroplast structure and the degradation of photosynthetic pigments, which affects the absorption of light energy by PSI and PSII; PSII is more susceptible to temperature [44], causing oxidation of the PSII reaction center proteins [45], thereby weakening photosynthesis and resulting in a decrease in Fv/Fm [46]. At the same time, high temperatures can cause the enhancement of plant respiration and accelerate the consumption of substrates, which in turn causes a decrease in *Pn* [47]. Under high-temperature stress, F_0 increased and *Fm* decreased. The increase in F_0 and the decrease in *Fm* of 'Tampico' were respectively smaller than those of 'Hypnotica Tropical Breeze', which is consistent with the findings of Vuletí et al. [48], indicating that the increase in F_0 and the decrease in *Fm* can be used as reference indicators to judge the heat resistance of dahlias. This study further demonstrated that there were differences in the heat tolerance of the two dahlia varieties.

5. Conclusions

The heat resistance of 'Tampico' is stronger than that of 'Hypnotica Tropical Breeze'. 'Tampico' has a higher photosynthetic pigment content and stronger stomatal regulation ability and transpiration ability under high-temperature stress, which are potential protective mechanisms of heat-tolerant dahlia varieties against high-temperature stress.

The two dahlia varieties recovered to normal after the 7−d recovery period following the high-temperature stress of the 2−d 35/30 °C treatment, and the high-temperature stress of the 2−d 40/35 °C treatment caused irreversible fatal damage to the 'Hypnotica Tropical Breeze'. The two dahlia varieties can be used in gardens in areas where the average summer temperature is lower than 35 °C; in areas where the average temperature exceeds 35 °C, heat-resistant varieties should be selected, or shading and cooling treatments should be performed to prevent irreversible damage caused by high temperatures.

Author Contributions: D.-Y.X. and D.-F.C. designed and supervised the project. J.-J.L. performed laboratory experiments and wrote the paper. Y.-C.Z. designed figures, tables, and data analyses. S.-C.N. and L.-H.H. have helped in sampling and analyzing the results. W.-B.Y. prepared the plant materials. All authors have read and agreed to the published version of the manuscript.

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