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Response of Photosynthesis in Wheat (*Triticum aestivum* L.) Cultivars to Moderate Heat Stress at Meiosis and Anthesis Stages

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Abstract: High temperature has seriously impacted the production of wheat in many countries. We examined four wheat cultivars (PBW343, Berkurt, Janz, and Attila) under heat stress (35/25 °C) and control treatments (23/15 °C) for 3 days at the meiosis and anthesis stages to evaluate the response and recovery of the four cultivars to heat stress and the relationship between photosynthetic parameters related to heat tolerance. Photosynthetic activity in all cultivars declined in plants that were treated at 35 °C, even for only 1 d compared with control plants. However, the differences among the four cultivars were obvious in net photosynthetic rate (*Pn*). At meiosis, the reduction of *Pn* in Berkut and PBW343 was lower and could nearly fully recover after 3 d of recovery and showed higher heat tolerance characteristics. The highest reduction in *Pn* occurred in Janz, which did not recover completely after 3 d of recovery. The same trend was observed at the anthesis stage, but *Pn* in all cultivars could not fully recover. Taking transpiration rate (*Tr*), stomatal conductance (*gs*), intercellular CO_2 concentration (*Ci*), and limitation of stomatal conductance (*Ls*) into account, results suggested the decline in *Pn* under heat stress was mainly caused by non-stomatal restriction. In parallel with the decline in *Pn*, the maximum photochemical efficiency (*Fv*/*Fm*) decreased. In addition, both the maximum rate of net photosynthesis (*Pmax*) and the light saturation point declined after heat stress in all cultivars. However, the relevant photosynthetic parameters of PBW343 and Berkut recovered more quickly at both the meiotic and flowering stages. In summary, there were significant differences in the adaptability of different cultivars to high temperatures, with Berkut and PBW343 being more adaptable to heat stress than Janz and Attila. These may be used as valuable resources for further studies in breeding to understand the physiological mechanisms of heat sensitivity. This paper provides detailed information on the ecophysiological responses of wheat under heat stress.

Keywords: breeding; heat stress; net photosynthetic rate; maximum photochemical efficiency; maximum rate of net photosynthesis; *Triticum aestivum* L.

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1. Introduction

Wheat is one of the most important cereal crops in the world and is cultivated in more than 20% of the world's arable land. The optimum temperature for the growth and development of wheat is 17–25 °C [1]. However, most wheat-growing regions often experience transient heat stress, especially during the meiosis and anthesis stages. Heat stress during meiosis and anthesis has a seriously negative impact on wheat production [2,3]. The projections of increases in global temperature indicate that the annual average temperature will rise 1.5 °C to 6.0 °C by 2100 [4]. At the same time, extreme weather events have become more frequent, which caused decreases in crop yields in recent years [5]. As the global environment deteriorates and the climate warms, the risk of heat stress during the reproductive period of wheat will also increase [6,7]. Globally, a one-degree increase in temperature is projected to reduce wheat production by 5.7% [8,9]. To mitigate and adapt the consequence of climate change on wheat production, scientists are working on developing heat-tolerant wheat germplasm resources. In order to adapt new crop varieties to future climates, we need to get information on how crops cope with high temperatures and how to improve their heat tolerance [10,11]. Photosynthesis, as the ultimate source of energy for crop yield formation, and photosynthesis in wheat leaves during the meiosis and anthesis stages directly affects wheat grain weight, which is a fundamental factor in determining wheat yield [12]. Therefore, it is necessary to study the outcome of high stress on photosynthetic function and chlorophyll fluorescence of wheat leaves during the meiosis and anthesis stages to screen heat-tolerant cultivars during wheat breeding.

The harvest index of wheat is approximately 0.45, which is difficult to improve [13]. Genetic improvement of photosynthetic characteristics is a critical measure to improve wheat yield. Different cultivars have differences in adaptability to high temperatures. Studies have shown that the genetic variations of photosynthetic rates among different wheat cultivars under heat stress were related to the loss of chlorophyll [14,15]. It is generally believed that the disruption of photochemistry in the light reaction and the reduction of Rubisco activity in the dark reaction were the main reasons that caused the decrease in heat-induced photosynthesis [16–18]. In addition, chlorophyll fluorescence is a useful indicator to detect the genotypic differences under heat stress. Research has shown that the decrease in photosynthesis resulted from the inhibition of photosystem II (PSII) activity, which also led to a decrease in the variable chlorophyll fluorescence. The sensitivity of PSII to heat stress has become an important indicator of the resistance of wheat and other crops to high-temperature photosynthesis [19,20].

Wheat plants are more easily damaged by heat stress in the reproductive stage than in the asexual reproductive stage. Environmental conditions at floral development and anthesis can affect the expression of gametes and seed-set rate space [21]. Therefore, this study aimed to examine the photosynthetic characteristics and chlorophyll fluorescence parameters of four wheat varieties under heat stress conditions so that suitable heat-tolerant wheat varieties could be screened. In verifying the above-mentioned presumption, four wheat cultivars were treated at 35 °C for three days at meiosis and anthesis stages, respectively, in a greenhouse experiment, and the impacts of heat stress on *Pn*, *Tr*, *gs*, *Ci*, *Ls*, carboxylation efficiency (CE), photosynthetic light response (PLR), chlorophyll content, and Fv/Fm of four wheat cultivars were studied so as to find out the photosynthetic tolerance of wheat cultivars. This will be beneficial to improve photosynthetic performance in flag leaves during wheat breeding and to increase the yield.

2. Materials and Methods

2.1. Experimental Design

This experiment was carried out in a controlled temperature environment glasshouse at the University of Sydney, Narrabri campus. The plant material consisted of four wheat cultivars (PBW343, Berkut, Janz, and Attila). All seeds were obtained from the I.A. Watson Plant Breeding Institute, Narrabri, NSW. A pot trial was conducted under greenhouse conditions with natural light. Seeds were sown in plastic pots. Each pot with a top diameter of 16.5 cm, a bottom diameter of 12.0 cm, and a height of 19.5 cm was filled with Osmocote Professional Premium Potting Mix and fertilized with Osmocote® (The Scotts Company, Marysville, MI, USA)(N:P:K = 19.4:1.6:5), a slow release fertilizer. Seedlings were thinned to one plant per pot when plants reached three fully developed leaves approximately 14 days after sowing. The temperature of the greenhouse was set at 23/15 °C (day/night) with 50% humidity during plant growth.

The controlled temperature environment glasshouse was divided into many cabinets, and three cabinets were used in this experiment. The temperature of each cabinet can be controlled using air conditioners. When most of the wheat culm leaves in each pot reached the meiosis stage, the plants were subjected to a 3-day heat stress treatment (35 °C/22 °C;

day/night) and then moved to normal temperatures (23 °C/15 °C; day/night) for recovery; when most of the culms in each pot reached flowering, the plants were again subjected to a 3-day heat stress treatment (35 °C/22 °C; day/night). After the heat stress treatment, all wheat pots were moved back to the greenhouse and kept growing until maturity. Wheat grown continuously at 23 °C/15 °C was used as a control. Optimal agronomic pest and disease control and weeding were applied to all wheat pot plants as required by local wheat production. Since tolerance to high temperatures was the only stress variable to be evaluated, each wheat pot plant in the experiment was irrigated. The amount of irrigation for each potted plant was obtained based on differences in daily weights to compensate for water losses due to evaporation, and the soil moisture content of all pots was kept close to field capacity throughout the experiment to ensure water was not a limiting factor.

2.2. Measurement Items and Methods

2.2.1. Measurement of Photosynthetic Parameters

During the meiosis and anthesis stages of wheat, the rate of net photosynthesis (Pn, μmol(CO_2)·m^{-2}·s^{-1}), stomatal conductance (gs, mmol(H_2O)·m^{-2}·s^{-1}), intercellular CO_2 concentration (Ci, μmol·mol^{-1}), and the rate of transpiration (Tr, mmol(H_2O)·m^{-2}·s^{-1}), and carboxylation efficiency (CE) of the middle part of the flag leaf on the main stem of the plant in wheat pots for each treatment were measured using the portable photosynthesis system (Li-6800, LI-COR, USA). A sunny day was chosen for the measurements from 9:30 to 11:30 a.m. The light intensity during the measurements was 1000 μmol·m^{-2}·s^{-1}, and the temperature was kept at the condition inside the growth chambers where the plants were placed. The limitation of stomatal conductance (Ls) was measured by the equation [22]:

$$Ls = 1 - Ci/Ca, \tag{1}$$

where Ls is the limitation of stomatal conductance, Ci is the intercellular CO_2 concentration, Ca is the ambient CO_2 concentration.

2.2.2. Measurement of Carboxylation Efficiency and Photosynthetic Light Response Curve

Using the Li-6800 portable photosynthesis meter, at the level of an exogenous CO_2 cylinder and artificial light (600 μmol/(m^2·s)), determining the Pn of wheat leaves at concentration gradients below 250 μmol·mol^{-1} CO_2 and the measurement time and plant site were the same as the photosynthetic parameters, and the carboxylation efficiency (CE) was found from the initial slope of the Pn-CO_2 concentration curve.

The photosynthetic light response (PLR) curves were determined using a Li-6800 m. The flag leaf was illuminated at a PPFD of 1600 μmol·m^{-2}·s^{-1} for 20–30 min until a steady state was reached. Then Pn was measured at 14 levels of PPFD (2000, 1800, 1600, 1400, 1200,1000, 800, 600, 400, 200, 100, 50, 30, and 0 μmol·m^{-2}·s^{-1}), respectively. CO_2 concentration was 390 μmol·mol^{-1}. A nonrectangular hyperbola equation was used to fit this response curve. For each PLR curve, coefficients of the NRH equation were fitted by the nonlinear least-square method. The NRH equation was as follows [23,24]:

$$P_n = \frac{\alpha \cdot I + P_{max} - \sqrt{(\alpha \cdot I + P_{max})^2 - 4\theta \cdot \alpha \cdot I \cdot P_{max}}}{2\theta} - R_d(\theta \neq 0) \tag{2}$$

where I is photosynthetically photon flux density (PPFD, μmol·m^{-2}·s^{-1}); θ is the convexity of the PLR curve; α is the apparent quantum yield (AQY); $Pmax$ is the maximum net photosynthetic rate (μmol·m^{-2}·s^{-1}); Rd is the dark respiration (μmol·m^{-2}·s^{-1}).

2.2.3. Measurement of Chlorophyll Content and Chlorophyll Fluorescence Traits

During the meiosis and anthesis stages of the experiment, sunny days were selected for the measurements, starting from 9:30 a.m., respectively. The relative chlorophyll content

(SPAD value) of the middle part of the flag leaves on the main stem was determined by a chlorophyll meter (SPAD-502, Konica Minolta, Japan).

During the meiosis and anthesis stages of the experiment, the chlorophyll fluorescence parameters were taken by a Li-6800 fluorescence detector. The tested leaves were dark-adapted with a leaf clip for half an hour before measurement and then irradiated with a weak modulated measuring light to determine initial chlorophyll fluorescence (*Fo*). A saturating light pulse of 12,000 $\mu mol \cdot m^{-2} \cdot s^{-1}$ was then applied for 1s to measure the maximum chlorophyll fluorescence (*Fm*). Variable chlorophyll fluorescence (*Fv*) is the difference between *Fo* and *Fm*. The maximum photochemical efficiency (Fv/Fm) is calculated by:

$$Fv/Fm = (Fm - Fo)/Fm, \tag{3}$$

For the above indicators, three pots with similar plant growth were selected for each measurement as three repetitions.

2.3. Data Analysis

Excel 2010 was used for data analysis and graphing. Photosynthetic parameters, photosynthetic light response (PLR) curve, chlorophyll content, and fluorescence traits of wheat plants were analyzed using SPSS 26.0 software on Duncan's multiple range for analysis of variance of data means of repeated measurements, with differences in means at the 5% or 1% level ($p < 0.05$ or $p < 0.01$) considered to be statistically significantly different.

3. Results

3.1. Net Photosynthetic Rate (Pn) and Photosynthetic Parameters

The effects of heat stress on the net photosynthetic rate of four wheat cultivars at meiosis and anthesis are shown in Figure 1. The results indicated that the net photosynthetic rate (*Pn*) of four wheat cultivars under heat stress decreased gradually at both the meiosis and anthesis stages. Moreover, during heat stress, the *Pn* in Janz and Attila decreased more significantly compared to the control than in PBW343 and Berkut. At the meiosis stage, the *Pn* was significantly lower ($p < 0.05$) in Janz (14.14%) and Attila (12.88%) compared to controls. In contrast, PBW343 showed a higher degree of heat resistance with only a slight decrease in *Pn* (6.76%). Furthermore, after the plants had recovered for 3 days, the *Pn* of PBW343 gradually returned to normal values (Figure 1a), followed by Berkut (Figure 1b), while the *Pn* of Janz and Attila did not fully return to normal values (Figure 1c,d).

Figure 1 shows that the *Pn* of the four wheat cultivars decreased more at anthesis than at meiosis and that their *Pn* could not fully return to normal values after 5 days of incubation at restored normal temperatures, in which Janz had the greatest decline in *Pn* under heat stress, while Berkut had the highest *Pn* rate after 5 days of recovery. However, there was no remarkable difference between the *Pn* rates of Berkut and PBW343 after 5 days of recovery (Figure 1a,b). On the first day of restoration to normal temperature, the *Pn* of Janz and Attila decreased further and then increased slightly. Thus, 3 days after the plants were transferred to normal temperature, the *Pn* of Berkut reached 95.47% of the control level, but Janz and Attila only partially recovered to 89.81% and 91.43% of the control level, respectively.

For the four wheat cultivars under heat stress, the changes of *Pn* were usually accompanied by the changes of *gs*, *Ci*, *Tr*, and *Ls*. Since the trends of these four photosynthetic parameters in four cultivars showed nearly the same trends during the meiosis and anthesis stages, the four photosynthetic parameters of PBW343 at meiosis were selected to be analyzed (Table 1). During heat stress, the *Ci* presented no significant changes compared with the control, while *Tr* and *gs* increased significantly. On the first day of recovery, *gs* sharply decreased in stressed plants. Accompanied by the decrease of *gs*, *Ci* decreased significantly ($p < 0.05$). On the other hand, the *Ls* value was lower than the control during the heat stress treatment but significantly increased in PBW343 when the plants were moved to normal temperature for recovery. However, the *Ls* values were not significantly different on the third day after recovery compared to the first and second days ($p < 0.05$).

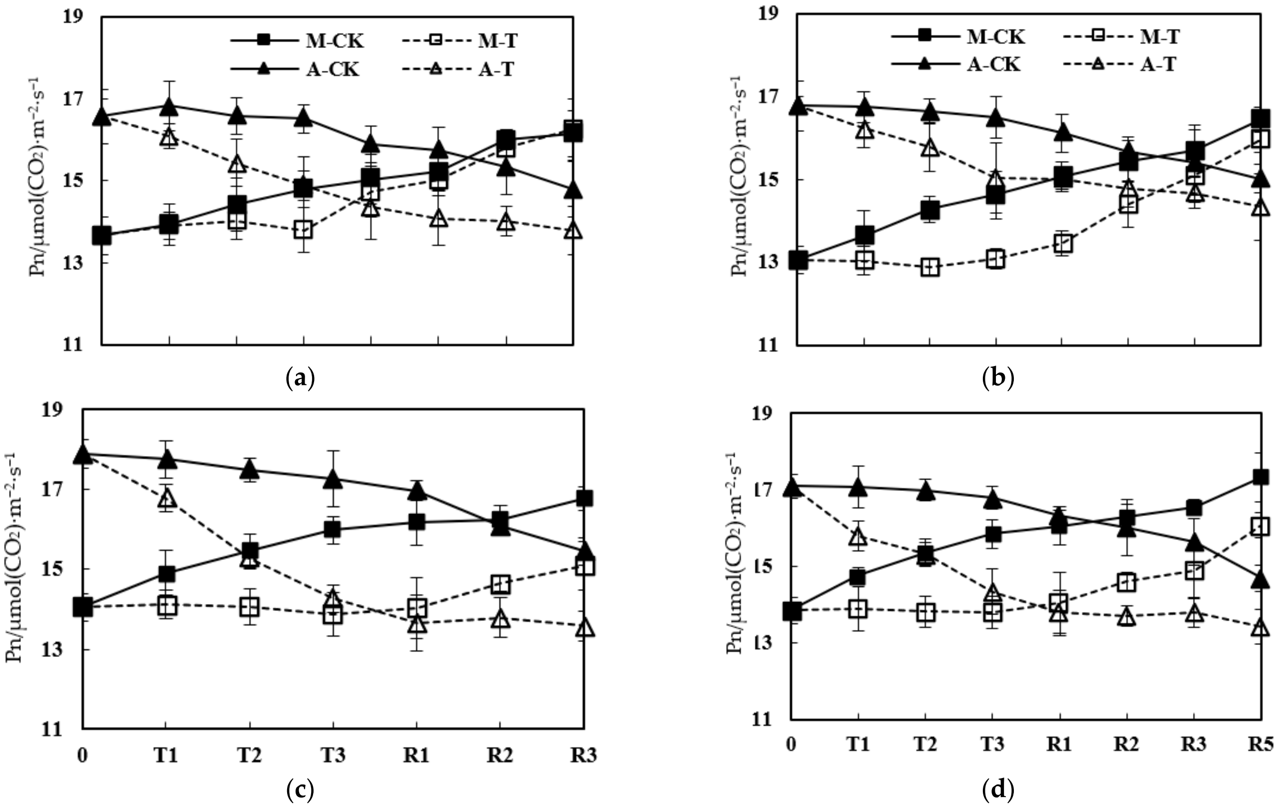


Figure 1. Changes of the *Pn* during heat stress and recovery at different stages in four wheat cultivars. M-CK means the values of controls at meiosis; M-T means the values of plants under heat stress at meiosis; A-CK means the values of controls at anthesis; A-T means the values of plants under heat stress at anthesis. Panel (**a**): PBW343; Panel (**b**): Berlut; Panel (**c**): Janz; Panel (**d**): Attila. T1-T3 are the number of days the plants were under heat stress, and R1-R5 are the number of days the plants were in recovery.

Table 1. Changes of *gs*, *Ci*, *Tr*, and *Ls* in PBW343 during heat stress and recovery at the meiosis stage.

Parameter	Treatment	Days after Treatment				Days after Recovery		
		0	T1	T2	T3	R1	R2	R3
					d			
g_s	CK	0.45 ± 0.003^a	0.47 ± 0.005^b	0.46 ± 0.003^b	0.51 ± 0.004^b	0.51 ± 0.002^a	0.51 ± 0.003^a	0.53 ± 0.001^a
	T	0.45 ± 0.003^a	0.63 ± 0.003^a	0.73 ± 0.004^a	0.73 ± 0.004^a	0.32 ± 0.003^b	0.45 ± 0.003^b	0.50 ± 0.002^a
C_i	CK	242 ± 2.2^a	247 ± 2.5^a	254 ± 2.9^a	248 ± 2.6^a	256 ± 1.4^a	251 ± 1.7^a	240 ± 2.2^a
	T	242 ± 2.2^a	254 ± 2.5^a	252 ± 2.6^a	253 ± 2.1^a	219 ± 1.2^b	234 ± 1.9^b	235 ± 3.8^a
Tr	CK	2.80 ± 0.022^a	2.78 ± 0.002^b	2.89 ± 0.022^b	3.04 ± 0.003^b	3.35 ± 0.041^a	2.98 ± 0.021^a	2.82 ± 0.021^a
	T	2.80 ± 0.022^a	3.31 ± 0.003^a	4.22 ± 0.056^a	4.20 ± 0.004^a	3.57 ± 0.036^a	2.97 ± 0.021^a	2.51 ± 0.029^a
L_s	CK	0.19 ± 0.005^a	0.176 ± 0.003^a	0.15 ± 0.002^a	0.17 ± 0.002^a	0.15 ± 0.002^b	0.16 ± 0.003^b	0.19 ± 0.002^a
	T	0.19 ± 0.005^a	0.153 ± 0.002^a	0.16 ± 0.003^a	0.16 ± 0.002^a	0.27 ± 0.003^a	0.22 ± 0.002^a	0.21 ± 0.003^a

CK: controls; T: heat stress treatment. Units of *gs*, *Ci*, *Tr*, and *Ls* in the Abbreviations Table. Four photosynthetic parameters are significantly different between days after treatment and days after recovery ($p \leq 0.05$) when followed by different lowercase letters. T1, T2, T3: after 1 d, 2 d, and 3 d heat stress; R1, R2, R3: after 1 d, 2 d, and 3 d recovery. The same as below.

As for different cultivars, the change value of each photosynthetic parameter in cultivar Janz was the highest. Moreover, the decreased degree of these parameters at meiosis was lower than at anthesis. The results mentioned above reflected that different cultivars had marked differences in the adjustability to heat stress. Results suggested that the decrease in *Pn* under high temperature within 3 d was mainly caused by non-stomatal restriction, but stomatal restriction may be one of the limiting factors that induced a continued decline in *Pn* during the recovery period.

3.2. Carboxylation Efficiency (CE) and PLR Curve

Heat stress inhibited the carboxylation efficiency (CE) of wheat leaves, but the decrease extent was different among the four wheat cultivars (Table 2). At the meiosis stage, Attila showed a significant decrease after 3 days of exposure to heat stress, followed by Janz, but there was no difference between them, and they only recovered to 83% of control values after 3 days of recovery (Table 2). On the other hand, PBW343 and Berkut showed a slight decrease after three days of heat stress treatment and almost a complete return to normal values after 3 d of recovery. At the anthesis stage, the same trend in carboxylation efficiency (CE) was observed in the wheat leaves as in meiosis. CE in Janz and Attila still decreased by 25.38% and 17.54% compared to their controls after 3 days of recovery, while PBW343 and Berkut almost completely recovered to normal values (Table 2).

Table 2. Changes of carboxylation efficiency (CE) in the four wheat cultivars during heat stress and recovery at different stages.

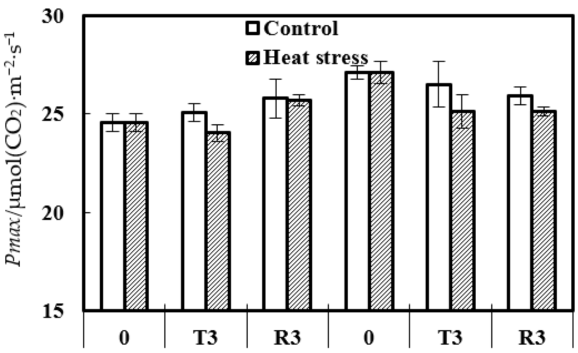
Cultivars	Treatment	Meiosis			Anthesis		
		0	T3	R3	0	T3	R3
PBW 343	CK	0.0516 ± 0.0002 [a]	0.0561 ± 0.0002 [a]	0.0605 ± 0.0003 [a]	0.0610 ± 0.0008 [a]	0.0586 ± 0.0002 [a]	0.0573 ± 0.0003 [a]
	T	0.0516 ± 0.0002 [a]	0.0526 ± 0.0001 [a]	0.0584 ± 0.0001 [a]	0.061 ± 0.0008 [a]	0.0525 ± 0.0002 [a]	0.0525 ± 0.0004 [a]
Berkut	CK	0.0499 ± 0.0003 [a]	0.0564 ± 0.0001 [a]	0.0611 ± 0.0003 [a]	0.0622 ± 0.0002 [a]	0.0586 ± 0.0003 [a]	0.0565 ± 0.0002 [a]
	T	0.0499 ± 0.0003 [a]	0.0519 ± 0.0003 [a]	0.0583 ± 0.0003 [a]	0.0622 ± 0.0002 [a]	0.0546 ± 0.0003 [a]	0.0538 ± 0.0002 [a]
Janz	CK	0.0528 ± 0.0002 [a]	0.0574 ± 0.0003 [a]	0.0627 ± 0.0002 [a]	0.0654 ± 0.0004 [a]	0.0624 ± 0.0003 [a]	0.0599 ± 0.0003 [a]
	T	0.0528 ± 0.0002 [a]	0.0458 ± 0.0006 [b]	0.0522 ± 0.0006 [b]	0.0654 ± 0.0004 [a]	0.0445 ± 0.0004 [b]	0.0447 ± 0.0006 [b]
Attila	CK	0.0583 ± 0.0002 [a]	0.0609 ± 0.0003 [a]	0.0645 ± 0.0004 [a]	0.0649 ± 0.0003 [a]	0.0629 ± 0.0003 [a]	0.0587 ± 0.0002 [a]
	T	0.0583 ± 0.0002 [a]	0.0483 ± 0.0002 [b]	0.0535 ± 0.0004 [b]	0.0649 ± 0.0003 [a]	0.0487 ± 0.0002 [b]	0.0484 ± 0.0003 [b]

Note: Lowercase letters in the table represent significant differences between treatments ($p < 0.05$).

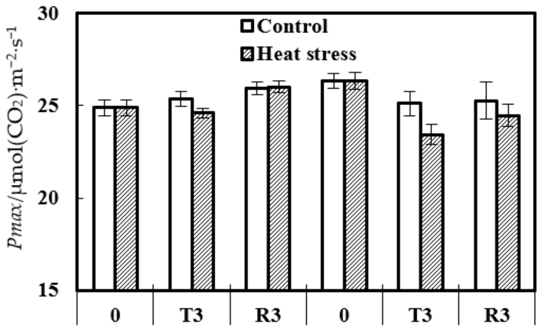
In this experiment, PLR curve was used to analyze the photosynthetic activities of wheat. The results showed the maximum rate of net photosynthesis (*Pmax*) in flag leaves of the four wheat cultivars were altered by heat stress at both meiosis and anthesis (Figure 2). During the meiosis and anthesis stages, *Pmax* of all four cultivars declined after 3 days of heat stress in all four cultivars. Although *Pmax* in Janz and Attila were higher than PBW343 and Berkut at normal temperature, the decrease was greater under heat stress (Figure 2).

As far as the different stages were concerned, all four wheat cultivars showed lower decreases in *Pmax* at the meiosis stage than at the anthesis stage. In particular, PBW343 and Berkut showed an almost complete return to normal *Pmax* after 3 days of meiotic recovery (Figure 2a,b). However, at the anthesis stage, the *Pmax* was only partially recovered in all four wheat cultivars, with Attila in particular showing the lowest recovery (Figure 2d).

Heat stress had a significant effect on the light saturation point (LSP) of the flag leaves of the four wheat cultivars during meiosis and anthesis (Figure 3).



(**a**)



(**b**)

Figure 2. *Cont.*

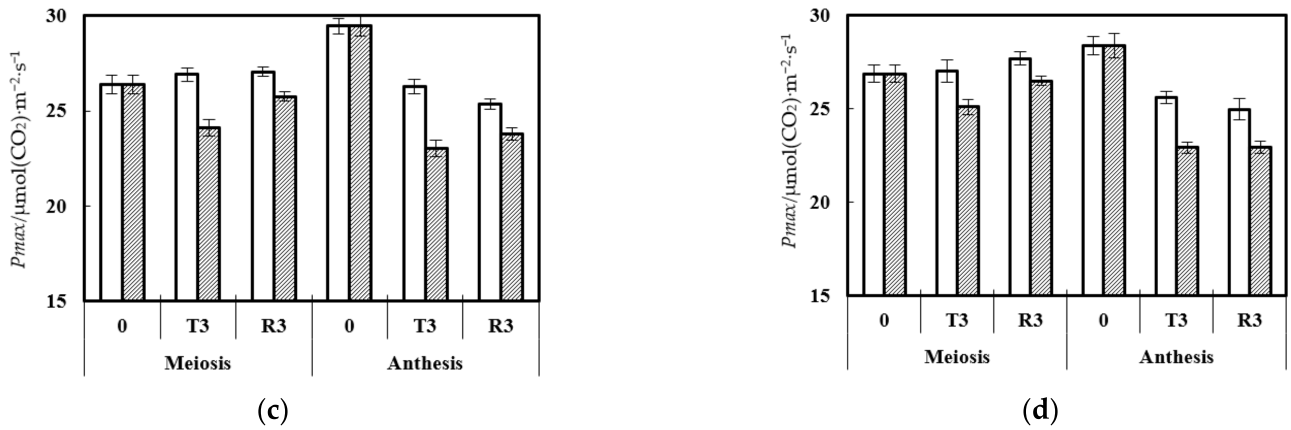


Figure 2. The *Pmax* during heat stress and recovery at different stages in the four wheat cultivars. Panel (**a**): PBW343; Panel (**b**): Berkut; Panel (**c**): Janz; Panel (**d**): Attila. T3 is the number of days the plants were under heat stress, and R3 is the number of days the plants were in recovery.

After 3 days of heat stress treatment, the light saturation points in the four cultivars decreased significantly at both the meiosis stage and the anthesis stage, and they could not fully return to normal after 3 days of recovery (Figure 3). At the meiosis stage, the LSP in PBW343 and Berkut were less impacted by heat stress compared with Janz and Attila. However, the LSP could partly recover after plants were maintained at normal temperature for 3 days. A similar trend was observed at the anthesis stage, while the four cultivars showed a greater decrease in LSP and a poorer recovery than at the meiosis stage, especially Janz and Attila.

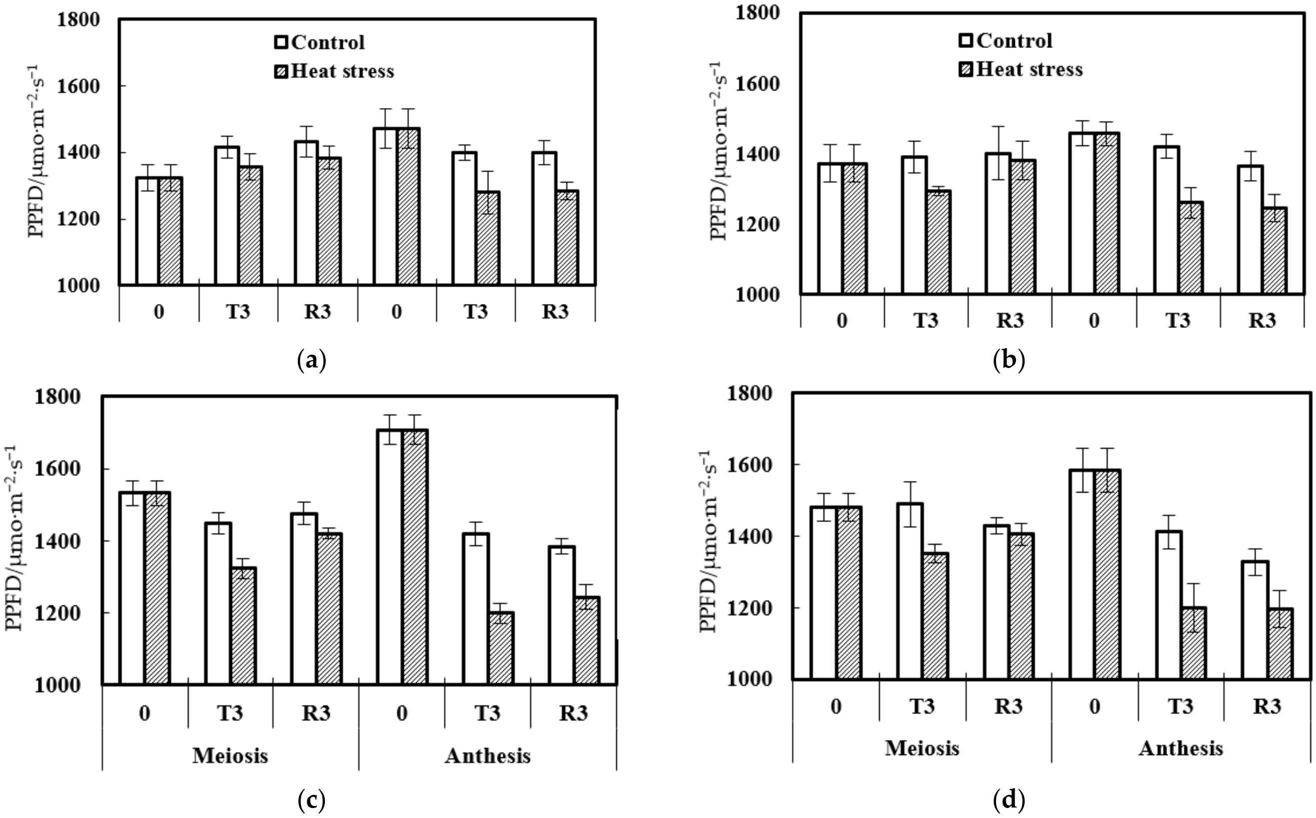


Figure 3. Light saturation point (LSP) during heat stress and recovery at different stages in the four wheat cultivars. Panel (**a**): PBW343; Panel (**b**): Berkut; Panel (**c**): Janz; Panel (**d**): Attila. T3 is the number of days the plants were under heat stress, and R3 is the number of days the plants were in recovery.

3.3. Chlorophyll Content and Chlorophyll Fluorescence Traits

At the meiosis stage, the chlorophyll content (SPAD value) of the four wheat cultivars increased with growth time. After heat stress treatment, the chlorophyll content of all four wheat cultivars decreased, with the chlorophyll content of Janz significantly different from the control and the other three wheat cultivars not remarkably different from the control (Table 3). After 3 days of recovery, the SPAD values of all four wheat cultivars were lower than those of the control but not significantly different. However, heat stress greatly reduced the chlorophyll content of the four wheat cultivars during the anthesis stage ($p < 0.05$). After 3 days of recovery, the chlorophyll content of the four wheat cultivars did not fully recover to the control values and remained markedly lower than the control (Table 3).

Table 3. Changes of relative chlorophyll content during heat stress and recovery at different stages.

Cultivars	Treatment	Meiosis			Anthesis		
		0	T3	R3	0	T3	R3
PBW 343	CK	42.78 ± 0.076 [a]	44.24 ± 0.043 [a]	45.19 ± 0.065 [a]	46.85 ± 0.041 [a]	46.94 ± 0.043 [a]	45.34 ± 0.043 [a]
	T	42.78 ± 0.076 [a]	42.98 ± 0.033 [a]	44.62 ± 0.024 [a]	46.85 ± 0.041 [a]	42.28 ± 0.024 [b]	41.96 ± 0.033 [b]
Berkut	CK	44.70 ± 0.041 [a]	45.16 ± 0.029 [a]	46.13 ± 0.047 [a]	47.89 ± 0.074 [a]	46.87 ± 0.024 [a]	45.98 ± 0.024 [a]
	T	44.70 ± 0.041 [a]	43.56 ± 0.042 [a]	45.03 ± 0.024 [a]	47.89 ± 0.074 [a]	43.09 ± 0.049 [b]	42.68 ± 0.024 [b]
Janz	CK	44.23 ± 0.024 [a]	45.67 ± 0.024 [a]	47.03 ± 0.024 [a]	47.76 ± 0.049 [a]	46.57 ± 0.024 [a]	44.67 ± 0.024 [a]
	T	44.23 ± 0.024 [a]	43.33 ± 0.024 [b]	45.67 ± 0.024 [a]	47.76 ± 0.049 [a]	41.09 ± 0.049 [b]	40.63 ± 0.024 [b]
Attila	CK	44.90 ± 0.041 [a]	45.45 ± 0.050 [a]	46.89 ± 0.033 [a]	47.43 ± 0.111 [a]	46.91 ± 0.042 [a]	45.16 ± 0.033 [a]
	T	44.90 ± 0.041 [a]	44.04 ± 0.033 [a]	45.98 ± 0.024 [a]	47.43 ± 0.111 [a]	41.34 ± 0.033 [b]	41.07 ± 0.024 [b]

Note: Lowercase letters in the table represent significant differences between treatments ($p < 0.05$).

The experimental results showed that heat stress modified the chlorophyll fluorescence emission in the four wheat cultivars. Under heat stress treatment, the Fv/Fm declined gradually in the stressed plants, while their Fv/Fm gradually increased as the recovery period progressed (Tables 4 and 5). However, the decline at anthesis was more extensive than at meiosis. At the meiosis stage, after 3 days of stress, the maximum decrease was seen in Janz (23.52% lower than the control value), followed by Attila, Berkut, and PBW343 (Table 4). At the anthesis stage, the reduction of Fv/Fm was less in PBW343 in comparison with the other three cultivars. Janz still declined significantly, resulting in a heat stress inhibition of 26.01% (Table 5).

Table 4. Changes of Fv/Fm in the four wheat cultivars during heat stress and recovery at the meiosis stage.

Cultivars	Treatment	Days after Treatment				Days after Recovery		
		0	1	2	3	1	2	3
					d			
PBW343	CK	0.79 ± 0.017 [a]	0.78 ± 0.021 [a]	0.79 ± 0.012 [a]	0.80 ± 0.042 [a]	0.79 ± 0.025 [a]	0.81 ± 0.012 [a]	0.81 ± 0.012 [a]
	T	0.79 ± 0.017 [a]	0.77 ± 0.022 [a]	0.75 ± 0.019 [a]	0.73 ± 0.017 [b]	0.80 ± 0.022 [a]	0.80 ± 0.022 [a]	0.82 ± 0.019 [a]
Berkut	CK	0.78 ± 0.022 [a]	0.78 ± 0.024 [a]	0.79 ± 0.017 [a]	0.79 ± 0.017 [a]	0.80 ± 0.017 [a]	0.81 ± 0.012 [a]	0.81 ± 0.008 [a]
	T	0.78 ± 0.022 [a]	0.75 ± 0.012 [a]	0.73 ± 0.017 [b]	0.71 ± 0.009 [b]	0.77 ± 0.022 [b]	0.79 ± 0.017 [a]	0.81 ± 0.009 [a]
Janz	CK	0.79 ± 0.031 [a]	0.74 ± 0.009 [b]	0.79 ± 0.025 [a]	0.80 ± 0.017 [a]	0.81 ± 0.022 [a]	0.81 ± 0.017 [a]	0.81 ± 0.012 [a]
	T	0.79 ± 0.031 [a]	0.73 ± 0.012 [a]	0.65 ± 0.014 [b]	0.61 ± 0.029 [b]	0.66 ± 0.017 [b]	0.71 ± 0.017 [b]	0.80 ± 0.009 [a]
Attila	CK	0.79 ± 0.025 [a]	0.79 ± 0.017 [b]	0.79 ± 0.017 [a]	0.80 ± 0.017 [a]	0.81 ± 0.017 [a]	0.82 ± 0.022 [a]	0.82 ± 0.012 [a]
	T	0.79 ± 0.025 [a]	0.69 ± 0.033 [a]	0.64 ± 0.009 [b]	0.60 ± 0.022 [b]	0.68 ± 0.021 [b]	0.75 ± 0.017 [b]	0.81 ± 0.025 [a]

Note: Lowercase letters in the table represent significant differences between treatments ($p < 0.05$).

In addition, all cultivars recovered fully in terms of Fv/Fm after 3 d of recovery at the meiosis stage, but PBW343 recovered more rapidly compared to the other cultivars (Table 4). Conversely, there were still marked differences between Janz, Attila, and their controls ($p < 0.05$) at the anthesis stage after 3 days of recovery (Table 5).

Table 5. Changes of Fv/Fm in the four wheat cultivars during heat stress and recovery at the anthesis stage.

Cultivars	Treatment	Days after Treatment				Days after Recovery		
		0	1	2	3	1	2	3
		d						
PBW343	CK	0.83 ± 0.003 [a]	0.83 ± 0.012 [a]	0.83 ± 0.002 [a]	0.82 ± 0.004 [a]	0.82 ± 0.001 [a]	0.82 ± 0.002 [a]	0.82 ± 0.002 [a]
	T	0.83 ± 0.003 [a]	0.78 ± 0.004 [b]	0.72 ± 0.003 [b]	0.71 ± 0.003 [b]	0.78 ± 0.004 [b]	0.80 ± 0.003 [a]	0.80 ± 0.004 [a]
Berkut	CK	0.82 ± 0.004 [a]	0.82 ± 0.003 [a]	0.82 ± 0.003 [a]	0.82 ± 0.001 [a]	0.82 ± 0.002 [a]	0.82 ± 0.005 [a]	0.81 ± 0.002 [a]
	T	0.82 ± 0.004 [a]	0.78 ± 0.004 [b]	0.73 ± 0.002 [b]	0.71 ± 0.002 [b]	0.77 ± 0.004 [b]	0.78 ± 0.019 [b]	0.80 ± 0.004 [a]
Janz	CK	0.83 ± 0.003 [a]	0.82 ± 0.004 [a]	0.82 ± 0.006 [a]	0.82 ± 0.002 [a]	0.82 ± 0.002 [a]	0.81 ± 0.004 [a]	0.80 ± 0.003 [a]
	T	0.83 ± 0.003 [a]	0.75 ± 0.002 [b]	0.70 ± 0.005 [b]	0.60 ± 0.013 [b]	0.67 ± 0.002 [b]	0.71 ± 0.002 [b]	0.74 ± 0.004 [b]
Attila	CK	0.82 ± 0.002 [a]	0.82 ± 0.002 [a]	0.82 ± 0.004 [a]	0.82 ± 0.003 [a]	0.81 ± 0.002 [a]	0.81 ± 0.003 [a]	0.81 ± 0.002 [a]
	T	0.82 ± 0.002 [a]	0.76 ± 0.001 [b]	0.70 ± 0.006 [b]	0.67 ± 0.004 [b]	0.70 ± 0.001 [b]	0.73 ± 0.001 [b]	0.75 ± 0.003 [b]

Note: Lowercase letters in the table represent significant differences between treatments ($p < 0.05$).

4. Discussion

4.1. Heat Stress Affected the Pn and Photosynthetic Parameters of Wheat

The experimental results revealed heat stress reduced photosynthesis, affected pollination, and then eventually decreased the grain yield of wheat. This experiment aimed to explore the differences among variable wheat cultivars when they were exposed to moderately high temperatures, such as 35 °C at different stages, in order to breed heat-tolerant wheat cultivars. Heat stress at both meiosis and anthesis caused a great adverse impact on the net photosynthetic rate of wheat plants, but the four wheat cultivars were affected differently, with PBW343 and Berkut being less affected and able to recover more quickly compared to Janz and Attila (Figure 1). Studies have shown that varieties in the net rate of CO_2 assimilation reflected the changes in stomatal conductance and/or mesophyll photosynthetic capacity [25,26]. Hu and Ding [27] reported that though both meiosis and anthesis were sensitive to heat stress, anthesis was the most sensitive stage during the whole growth period. In our study, anthesis was more sensitive to high temperature than meiosis in the four wheat cultivars, and *Pn* in plants that encountered heat stress episodes at the anthesis stage declined more and were slower to recover (Figure 1). However, in terms of the four wheat cultivars, *Pn* in PBW343 and Berkut recovered quickly compared to Janz and Attila at both stages, and PBW343 could even recover completely after 3 d of recovery at a normal temperature at the meiosis stage. At the meiosis and anthesis stages, the four wheat cultivars showed progress in their *gs*, *Ci*, and *Tr*, and a reduction in *Ls* at 35 °C heat stress (Table 1). The increase of *gs, Ci*, and *Tr* indicated that the decrease in CO_2 assimilation during heat stress was not mainly caused by stomatal closure [28–30]. Our data are supported by Ji et al. [31].

On the basis of the above analysis, our experiments also showed that the photosynthesis of PBW343 and Berkut were more resistant to high temperatures. In addition, the ability of plants to modulate leaf temperature by increasing transpiration is critical under heat stress. The enhancement in *Tr* is the natural reaction of high temperature, which is a factor associated with controlling stomatal opening. In our experiment, PBW343 and Berkut showed higher *Tr* and *Gs* than Janz and Attila (Table 1). It meant that heat-resistance wheat varieties showed a lower heat sensitivity index and better canopy cooling, which promoted higher yield under high-temperature stress [32].

4.2. Carboxylation Efficiency (CE) and PLR Curve in Response to Heat Stress

Heat stress significantly affected carboxylation efficiency (CE). CE decreased in four cultivars under heat stress. The values of CE in Janz and Attlia were higher in the controls, but the decrease was much greater than PBW343 and Berkut under the stress episodes (Table 2). High temperatures inhibited electron transport and reduced the efficiency of CO_2 diffusion from the stomata to the carboxylation site, which was closely related to the decrease in photosynthetic efficiency [33–35]. In our experiment, PBW343 and Berkut showed a slight decrease after three days of heat stress treatment and almost a complete return after 3 d of recovery, which indicated that PBW343 and Berkut wheat were more efficient in carboxylation. Some researchers reported that the concentration of CO_2 between plant leaf cells increased while promoting a significant increase in carboxylation efficiency (CE) [36,37]. The increase in carboxylation reaction efficiency showed that the storage of photosynthetic substances was accelerated, promoting reproductive growth, promoting photosynthesis in wheat plants, improving the transport of photosynthetic substances in the body, and promoting the synthesis and transport of organic compounds [38,39].

Pmax for many plants at light saturation highly depends on temperature [40,41]. Similarly, for the wheat cultivars, light-saturated photosynthesis declined at 35 °C (Figure 2). Under heat stress, the decrease of light saturation was an outcome of the decreased carboxylase activity in regard to oxygenase activity, resulting in a concomitant reduction of ATP and NADPH demand. Though values of *Pmax* in Janz and Attila were higher than PBW343 and Berkut in controls, they declined sharply, and the reduction extents were much greater under heat stress, particularly at the anthesis stage. The light saturation point (LSP) of plants describes the amount of light that is beyond the capability of the chloroplast to absorb, which means the rate of photosynthesis can no longer rise. In our case, the light saturation point in plants that were exposed to heat stress all declined compared to controls at both stages (Figure 3), which meant the adaptation of plants to light intensity was reduced by environmental stress. The result of this study was consistent with research on other plants [42]. In addition, for different cultivars, the reduction extent of PBW343 and Berkut was lower, while the recovery ability was better than that of Janz and Attila, especially at the meiosis stage.

4.3. Heat Stress Reduced Chlorophyll Content and Chlorophyll Fluorescence Traits

Chlorophyll fluorescence analysis showed that exposure to 35 °C depressed photosynthesis by inducing the photoinhibition of PSII in view of a significant decline in Fv/Fm observed in plants under stress. Though some researchers reported the Fv/Fm did not change significantly when plants were under 35 °C, a substantial decrease in Fv/Fm (Table 4) was observed in the four cultivars in this case. In addition, Fv/Fm in all cultivars that were exposed to 35 °C for 3 d at the meiosis stage could nearly attain a control level after 3 d of recovery, which suggested that the PSII of these wheat cultivars did not lose their activity in this condition. Fv/Fm also showed more sensitivity to heat stress at the anthesis stage than at the meiosis stage. Dew et al. [43] found that wheat cultivars with high Fv/Fm under heat stress maintained high photosynthesis and dry matter. In our case, the decrease in values of Fv/Fm ranged from 12% to 26% after 3 d of heat stress compared to the controls, depending on cultivars. PBW343 and Berkut showed higher Fv/Fm than Janz and Attila (Table 4), accompanied by higher chlorophyll, gs, and *Tr* when plants were exposed to 35 °C (Table 2), which meant PBW343 and Berkut were more heat tolerant than Janz and Attila. The findings suggested the importance of photosynthesis traits in plant breeding, especially under high-temperature conditions.

5. Conclusions

This paper provides detailed information on the ecophysiological responses of wheat plants under heat stress conditions. Photosynthetic activity in four wheat cultivars decreased in plants exposed to 35 °C even for 1 d compared with controls. However, the reduction of *Pn* in Berkut and PBW343 was lower and could nearly fully recover after 3 d of recovery at the meiosis stage. In parallel with the decrease of *Pn*, Fv/Fm also declined. In addition, both the *Pmax* and the light saturation point declined after 3 d of heat stress in the four cultivars. However, the extent of the decrease of all these traits in PBW343 and Berkut was lower than in Janz and Attila, and the recovery was rapid at both the meiosis and anthesis stages. The data showed that different cultivars had remarkable differences in the adaptability to high temperatures; Berkut and PBW343 were more adaptable to heat stress than Janz and Attila.

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Abbreviations

Term	Unit	Description
Pn	μmol(CO_2) m^{-2} s^{-1}	rate of net photosynthesis
Tr	mmol(H_2O) m^{-2} s^{-1}	rate of transpiration
Ci	μmol mol^{-1}	intercellular CO_2 concentrations
gs	mmol(H_2O) m^{-2} s^{-1}	stomatal conductance
L_s		limitation of stomatal conductance
CE		carboxylation efficiency
P_{max}		maximum rate of net photosynthesis
F_v/F_m		maximum photochemical efficiency
PLR		photosynthetic light response
LSP	μmol m^{-2} s^{-1}	light saturation point
PPFD	$\mu mol \cdot m^{-2} \cdot s^{-1}$	photosynthetically photon flux density
CK		controls
T		heat stress treatment

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