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Effects of Water Stress on Photosynthesis, Yield, and Water Use Efficiency in Winter Wheat

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Abstract: Drought has become one of the major constraints to agricultural development, particularly in areas that lack water. Studying the effects of different water stresses on the photosynthesis, growth, yield, water use efficiency (WUE) and irrigation water productivity (IWP) of winter wheat will provide data for the development of scientific irrigation strategies for water-saving agricultural methods. According to the size of the field water capacity, four different water stress levels were set, i.e., 30–40% (severe stress), 40–50% (moderate stress), 50–60% (mild stress) and 60–80% (well-watered) of field water capacity, controlling the amount of irrigation through an automatic irrigation system. The results showed that the seasonal changes in photosynthetic parameters, such as net photosynthetic rate (Pn), intercellular carbon concentration (Ci), stomatal conductance (Gs) and transpiration (E), significantly decreased under moderate and severe stress. As a result, the height, biomass and grain size of winter wheat decreased significantly, which led to low WUE and IWP. The Pn of the mild stress group only slightly decreased compared to that of the well-watered group, and was actually higher during the flowering and grain-filling stages, resulting in increases in dry biomass and 1000 grain weight of 2.07% and 1.95%, respectively. Higher WUE and IWP were attributed to higher yields and less water use. Thus, mild stress (60–80% field water capacity) resulted in the optimal use of water resources without a significant reduction in yield in the North China Plain (NCP). Therefore, mild stress can be considered a suitable environment for winter wheat growth in arid areas.

Keywords: winter wheat; photosynthesis; yield; water use efficiency; irrigation water productivity

1. Introduction

Wheat is one of the three main food crops globally [1]. The North China Plain is the main wheat-planting area in China, although drought often occurs there [2]. Drought has become an important environmental factor restricting agricultural development in this region [3,4]. If drought occurs during the wheat growth period, it has a great impact on the wheat yield and can easily result in a food security crisis [5]. Irrigation has become the main method used to alleviate drought. However, water resources are scarce on the North China Plain. Improper irrigation not only wastes water resources, but also damages crop growth [6]. Therefore, it is necessary to study proper irrigation techniques, improve water use efficiency (WUE) and irrigation water productivity (IWP), and increase production.

Drought has an effect on the physiological parameters of vegetation, such as chlorophyll content, photosynthetic parameters, biomass and yield [7–10]. To date, many scholars have studied how the soil water content or the relative water content of leaves affects crop photosynthesis and yield [11–13]. Studies have shown that drought causes stomatal restriction or non-stomatal restriction during photosynthesis, or both [14,15]. Drought causes a reduction of the intercellular CO_2 concentration through stomatal restriction, resulting in limiting photosynthesis [16]. Non-stomatal limitations can be defined as an inhibition of Rubisco or short ATP, a decrease in photosynthetic pigment content, or a photosynthetic system reducing the activity of enzymes involved in light cooperation to suppress crop photosynthesis [17,18]. Drought reduces the duration of photosynthesis of wheat during the flowering stage. In the flag leaf stage, a water shortage reduces the assimilation rate. Furthermore, drought accelerates the decomposition of assimilation during senescence [19]. Therefore, drought affects the growth of wheat differently at different growth stages. By restricting photosynthesis, drought affects the height, biomass and yield of winter wheat.

WUE is related to the ability of a plant to absorb concentrations of carbon and to limit water loss by controlling stomatal closure [10,20,21]. WUE is also closely related to the net photosynthetic rate (Pn) and transpiration rate (E), and is influenced by soil water content [22,23]. Katerji [7] and Mashilo [24] showed that water stress reduces WUE, but Liu [21] found that WUE tends to increase with mild water stress. Therefore, it is crucial to study the effect of water stress on WUE. Irrigation water productivity (IWP) is associated with yield and irrigation volume [25]. It is necessary to understand the relationship between yield and irrigation. Improving WUE and IWP, while ensuring good yields in arid regions, is an important issue that needs to be addressed.

In this study, four different water stress gradients were established, by controlling the amount of irrigation, so as to explore how different levels of water stress affect the growth, WUE and IPW of winter wheat. The purpose of this study was (1) to analyze the effects of different water stresses on the photosynthesis, height and biomass of winter wheat, and (2) to explore the influence of different water stresses on the relationship between yield and WUE and IWP. The results of this study could help farmers to make the best use of limited water resources in areas that suffer water shortages, improve WUE, increase yield, and provide strong theoretical support for water-saving agricultural methods.

2. Materials and Methods

2.1. Study Site Description

This experiment was conducted in the Fangshan Comprehensive Experimental Station of Beijing Normal University (39°35′ N and 115°42.5′ E) in northern Xiapodian Village, Doudian, Fangshan District, Beijing, China (Figure 1). The experimental station is located in the plain area of Fangshan District, which belongs to the warm temperate semi-humid monsoon continental climate zone. The annual average temperature is 11.6 °C, the lowest temperature is in January (monthly average temperature = −5.6 °C) and the highest temperature is in July (monthly average temperature = 26 °C). The average annual precipitation is 602.5 mm and the seasonal distribution of precipitation is uneven; there is less precipitation in winter and spring, accounting for 1.6% and 10.1% of the annual precipitation, respectively. The frost-free period is 191 days. According to the international classification standards of soil type, the soil type of the area is loam (14.5% clay, 40.8% silt and 44.7% sand). The soil bulk density and field capacity of the study area were 1.39 g/cm^3 and 25%, respectively. The soil organic matter content was 10.36 g/kg, and the total nitrogen and total phosphorus contents were 0.95 g/kg and 0.28 g/kg, respectively.

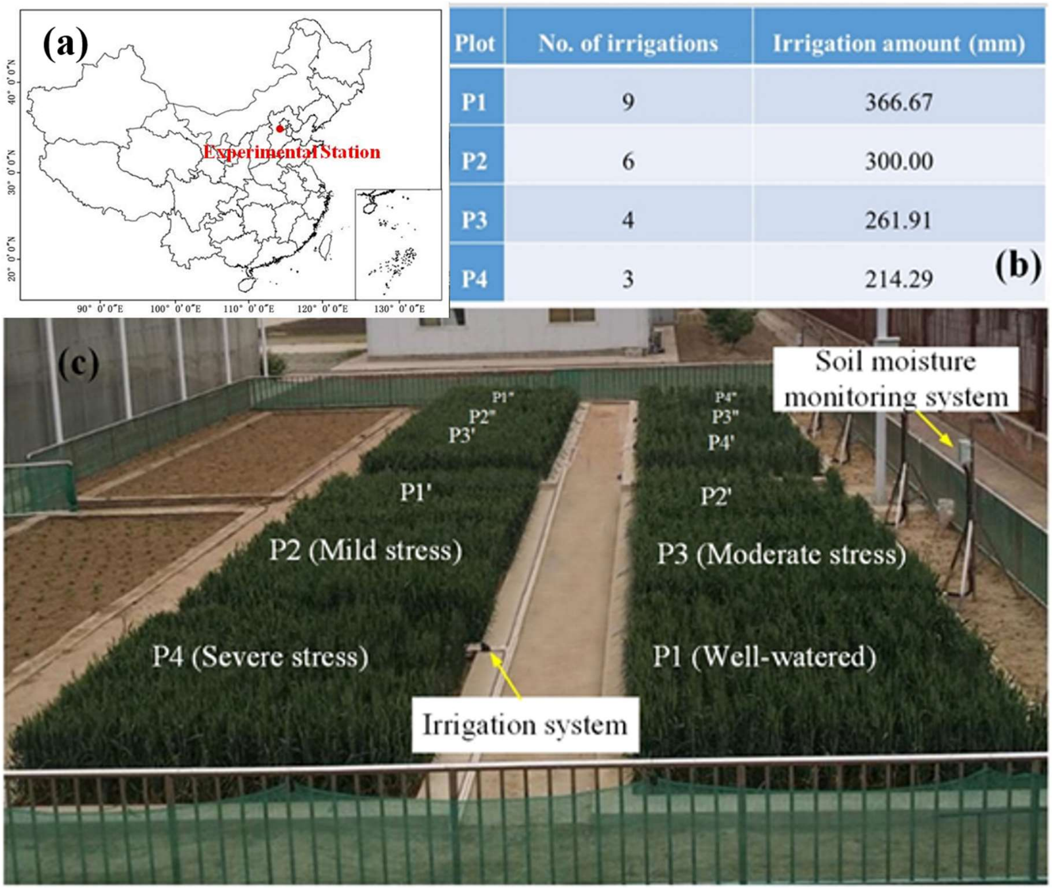

Figure 1. (**a**) Location of the experimental field. (**b**) Number of irrigators and amount of irrigation used for the different water treatments during the growing season. (**c**) Experimental field of winter wheat under different water treatments. P1: well-watered; P2: mild stress; P3: moderate stress; P4: severe stress. Px′ and Px″ are the replications of Px.

2.2. Experimental Design and Treatments

The winter wheat planted in this experiment was Jinnong 7. The winter wheat was planted on 10 October 2018 and harvested on 10 June 2019. Before planting, organic fertilizer (chicken manure) was applied to each plot at 4000 kg/hm^2. Diammonium phosphate (N, 18%; P_2O_5, 46%) at 1000 kg/hm^2, and urea $(NH_2)_2CO$ (N, 46%) at 1000 kg/hm^2, were applied on 5 March 2019. Each plot was planted with 15 rows of winter wheat, with rows spaced 20 cm apart and a planting density of 350 seeds per square meter.

Water stress was applied by setting four levels of moisture treatment, randomized completely with three replications. The experiment was carried out in twelve 3 × 4-m plots. To prevent water penetration between different plots, 1-m-high concrete walls were used between plots to block water flow and eliminate the interference of water penetration between plots. According to the field water capacity, the experimental fields were controlled at 60–80% (well-watered, P1), 50–60% (mild stress, P2), 40–50% (moderate stress, P3) and 30–40% (severe stress, P4) of the field water capacity. Gradient irrigation was used to create different water stress levels. To more accurately control the soil moisture, an advanced automatic irrigation system was used during the experiment. The automatic irrigation system monitors the soil water content in the water pool through a single-chip microcomputer. When the water content is lower than the lower limit of the set threshold, the single-chip microcomputer opens a solenoid valve through a relay and begins automatic irrigation. When the water content is higher than the upper limit of the set threshold, the microcontroller closes the solenoid valve through the relay, ending irrigation. To ensure the emergence rate of winter wheat, plots were irrigated identically on 20 November 2018 and

5 March 2019, with irrigation amounts of 100 mm and 95.24 mm, respectively. The amount of irrigation was controlled from 4 April 2019. Plot P1 was irrigated nine times with a cumulative irrigation of 366.67 mm, P2 six times with a cumulative irrigation of 300.00 mm, P3 four times with a cumulative irrigation of 261.91 mm, and P4 three times with a cumulative irrigation of 214.29 mm (Figure 2).

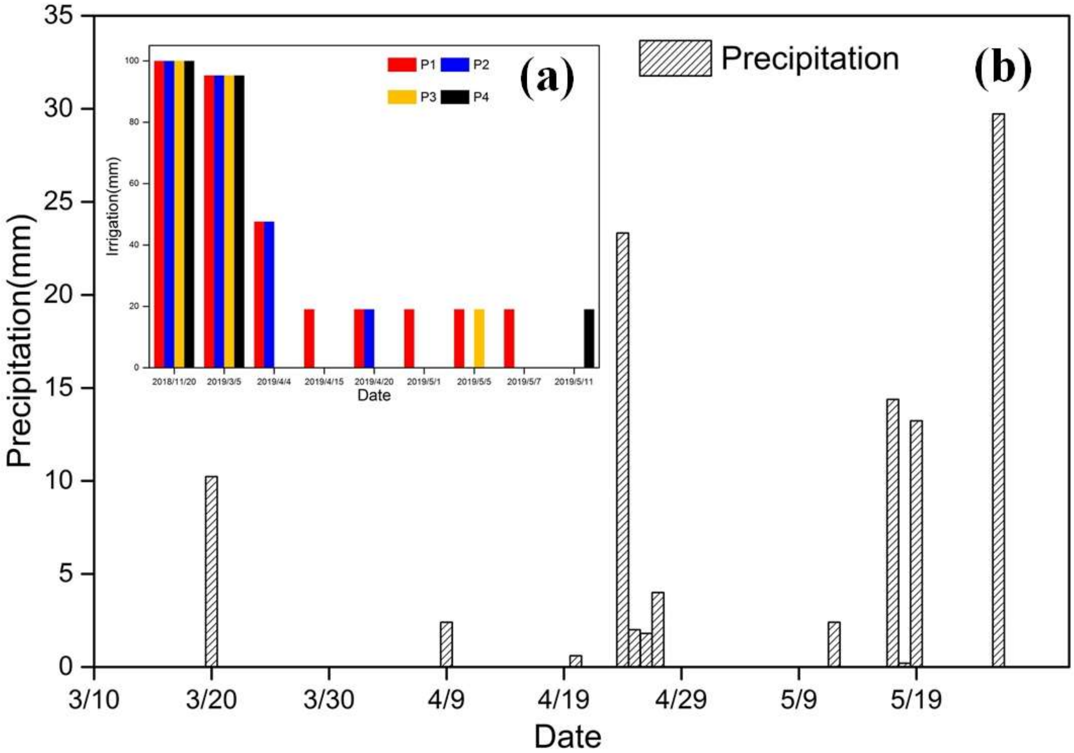

Figure 2. (**a**) Precipitation during the winter wheat growing season and (**b**) irrigation under different water treatments.

2.3. Soil Moisture

Soil moisture data were collected by the automatic soil moisture monitoring system Hydra Probe (Stevens, Portland, Oregon, USA). The system was composed of data collectors and soil moisture sensors. The sensors were installed at depths of 10, 20 and 50 cm below the surface in every plot. The collectors collected data through an SDI-12 bus at intervals of 5 min. Meanwhile, the data were sent to the server through GPRS, and users were able to view and download the data through browsers.

2.4. Photosynthetic Parameters

On clear, cloudless days, measurements were taken in the experimental plots using the portable photosynthesis measurement system Li-6800 (LI-COR, Lincoln, Nebraska, USA), from 08:00 to 18:00. The environment in the leaf chamber was not controlled during the measurement. There was no control of the CO_2 concentration, photosynthetic active radiation (PAR), or temperature in the leaf chamber. The gas was exchanged through the connection between the buffer bottle and the air inlet of the main engine. The CO_2 concentration, PAR and air temperature (T_{air}) were the true values of the environment. The flow setpoint was set at 500 μmol s^{-1} and the fan speed was set at 10,000 rpm.

In each experimental plot, 10 individual plants with good growth and no diseases or pests were selected. The photosynthetic parameters were measured using one leaf from each plant. Measurements were taken every 3 to 9 days, depending on the weather. Winter wheat phenology was evaluated according to the BBCH (Biologische Bundesanstalt, Bundessortenamt and Chemical industry) scale [26]. We conducted experiments on 22 April, 1 May, 6 May, 9 May, 16 May, 21 May and 29 May in 2019, from the green returning stage to the maturity stage. The observed indicators included net photosynthetic rate

(Pn), transpiration rate (E), stomatal conductance (Gs), intercellular CO_2 concentration (Ci), PAR, T_{air}, leaf temperature (T_{leaf}), etc.

2.5. Wheat Growth and Yield

A total of 10 individual plants was selected from each plot and their heights were measured using a tape measure. The 10 plants were cut close to the ground, placed in an envelope, and quickly weighed to give the fresh biomass of winter wheat. They were placed into an incubator at 105 °C for 30 min to de-enzyme, and the temperature of the incubator was adjusted to 85 °C for drying until the weight remained constant. Finally, the plants were weighed for the dry weight of the aboveground biomass. We calculated the difference between the two consecutive measurements of height and dry biomass weight, giving the height difference and dry weight difference, which were used for analysis. On 10 June, 1 m^2 of winter wheat was harvested from each plot. After drying, the grain, straw, spike and 1000 grain weights were measured

2.6. WUE and IWP

ET was calculated as follows.

$$ET = P + I - D - R - \triangle SW \tag{1}$$

where ET (mm) is evapotranspiration, P (mm) is rainfall, I (mm) is the amount of irrigation water, D (mm) is the downward drainage beneath the crop root zone and R (mm) is surface runoff, which was ignored in this study. $\triangle$SW refers to changes in soil moisture content at different levels (0–80 cm) from planting to harvesting [27].

The WUE was calculated as follows.

$$WUE = Y/ET \tag{2}$$

where WUE is the water use efficiency and Y (kg m^{-2}) is the grain yield [21].

Irrigation water productivity (IWP) was calculated as follows.

$$IWP = Y/I \tag{3}$$

2.7. Statistical Analysis

Data were collated in Microsoft Excel 2013, and one-way ANOVA tests were performed using Statistical Product and Service Solutions 21 (SPSS21). Differences between means were analyzed using the least-significant difference (LSD) test at 5% probability level. Graphs were created using OriginPro 8.

3. Results

3.1. Seasonal Variations of Environmental Variables

Soil moisture data were recorded from sowing to harvesting. The values were calculated using the average of soil moisture at 10, 20 and 50 cm depths. Figure 3 shows the changes of soil moisture under different water treatments, from the green returning to the maturity stage. On 4 April, because the P1 and P2 plots reached the lower limit of soil moisture, the automatic irrigation equipment irrigated the plots and their soil moisture levels rose. However, P3 and P4 had not reached the lower limit of soil moisture, so no irrigation was carried out and the soil moisture continued to decrease. It can be seen from Figure 3 that after irrigation, the soil moisture rose, and irrigation was performed when the soil moisture fell to the lower limit. The cumulative irrigation amounts of P1, P2, P3 and P4 were 366.67, 300, 261.91 and 214.29 mm, respectively, which led to the establishment of different water stresses.

In the experiment, the soil moisture in each plot was roughly within the set range, and most of the time P1 > P2 > P3 > P4, indicating that the water control experiment was successful.

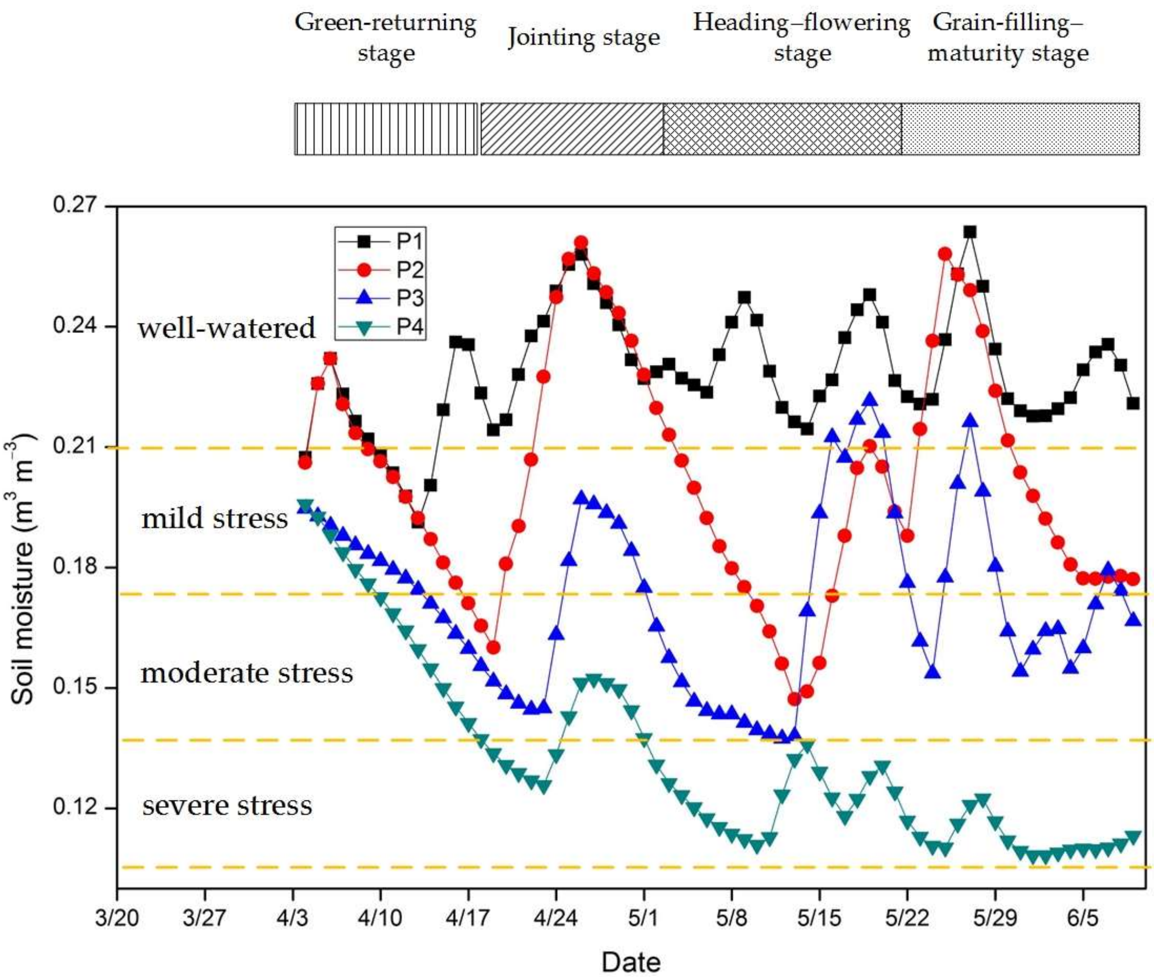

Figure 3. The variations of soil moisture during the experiment under different water treatments. P1: well-watered; P2: mild stress; P3: moderate stress; P4: severe stress. The values were calculated using the average of soil moisture at 10, 20 and 50 cm depths. The dashed yellow lines indicate the range of different water treatments. The phenological phases were identified according to the BBCH (Biologische Bundesanstalt, Bundessortenamt and Chemical industry) scale.

The two main meteorological variables (i.e., PAR and T_{air}) were observed from the jointing to the maturity stage. As shown in Figure 4a, we saw that both PAR and T_{air} showed a rising trend in fluctuation. They both rose sharply during the jointing stage. The T_{air} showed a trough at the early heading–flowering stage (May 6), and the trough of PAR appeared at the late heading–flowering stage (May 16). Then, they rose until the maturity stage. The ranges of T_{air} and PAR were 26.18–37.17 °C and 822.47–1685.91 µmol m^{-2} s^{-1}, respectively. There was no significant difference in the Tleaf of winter wheat from the jointing stage to the heading stage under different water stress levels. As the water stress continued, the Tleaf values were in the order of P4 > P3 > P2 > P1 (Figure 4b).

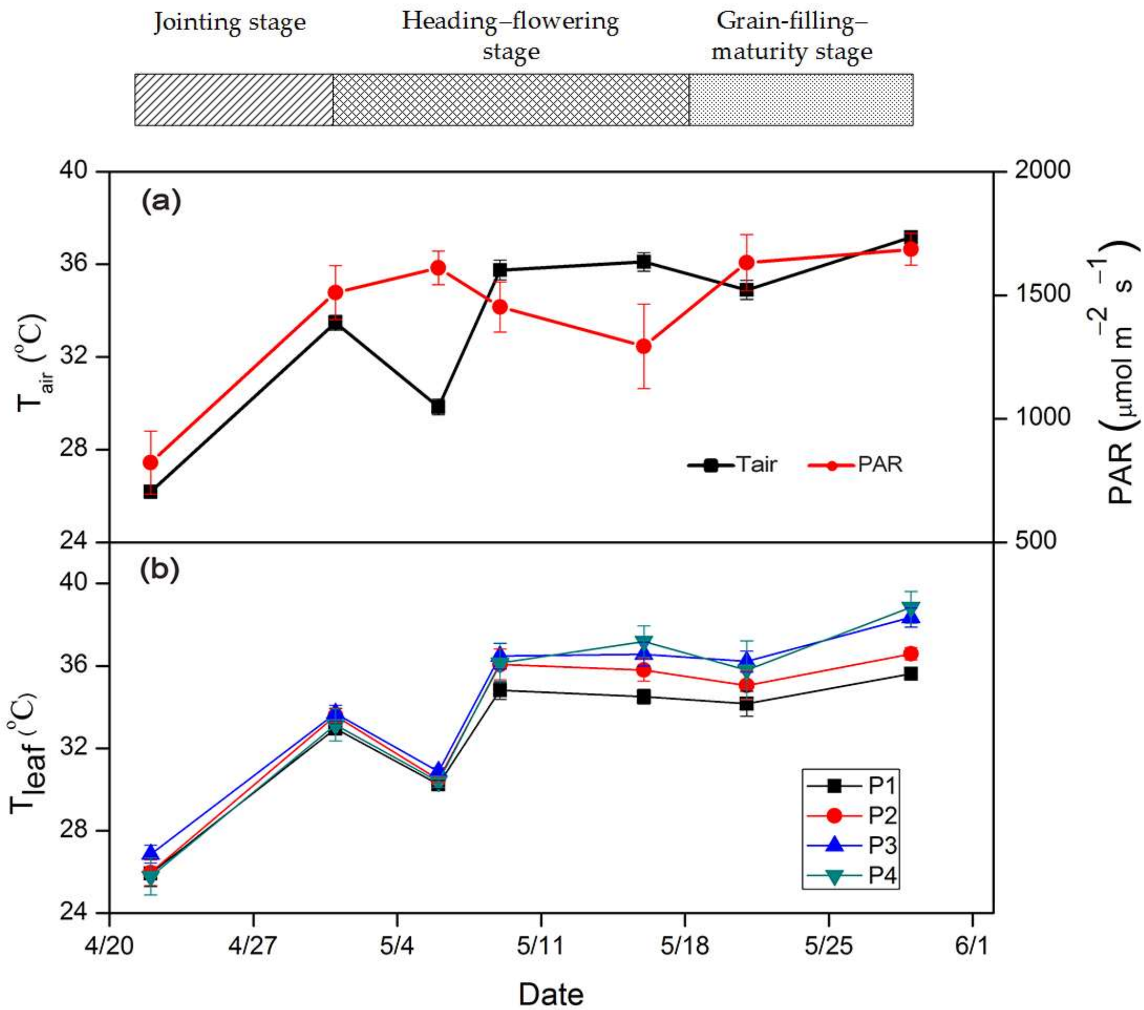

Figure 4. Seasonal variation in mean air temperature (T_{air}), mean photosynthetically active radiation (PAR) (**a**) and leaf temperature (T_{leaf}) (**b**) of winter wheat under different treatments. P1: well-watered; P2: mild stress; P3: moderate stress; P4: severe stress. Bars indicate the standard deviation (SD) of the mean. The phenological phases were identified according to the BBCH scale.

3.2. Seasonal Changes of Photosynthetic Parameters

3.2.1. Stomatal Conductance

Gs is the degree of stomatal opening; stomata are windows for gas exchange in leaves that control vegetation photosynthesis and transpiration. Gs decreased significantly with the duration of water stress (Figure 5). The changes of the Gs values of P1 and P2 were similar to one another, but different to P3 and P4. The mean value of Gs at different growth stages ranked as follows: P1 > P2 > P3 > P4. Compared to P1, the mean Gs values of P2, P3 and P4 decreased by 26.48%, 49.55% and 60.91%, respectively. The Gs values of P1 and P2 began to decline during the jointing stage, with those of P1 and P2 reaching a minimum value at the heading–flowering stage, with values of 0.35 and 0.22 mol $m^{-2}s^{-1}$, respectively. The values then began to increase, peaking on 16 May at the late heading–flowering stage and then falling again. A second trough then appeared at the grain-filling stage, finally increasing to a maximum size of 0.50 and 0.37 mol $m^{-2}s^{-1}$, respectively. The Gs of P3 began to rapidly decrease from the jointing stage to the heading stage, and then slightly increased. After 21 May, the Gs of P3 plummeted to its lowest value of 0.11 mol $m^{-2}s^{-1}$. The Gs of P4 rapidly decreased from the jointing stage to the heading stage, then leveled off, and then slowly decreased from the heading–flowering stage to its minimum value of 0.06 mol $m^{-2}s^{-1}$.

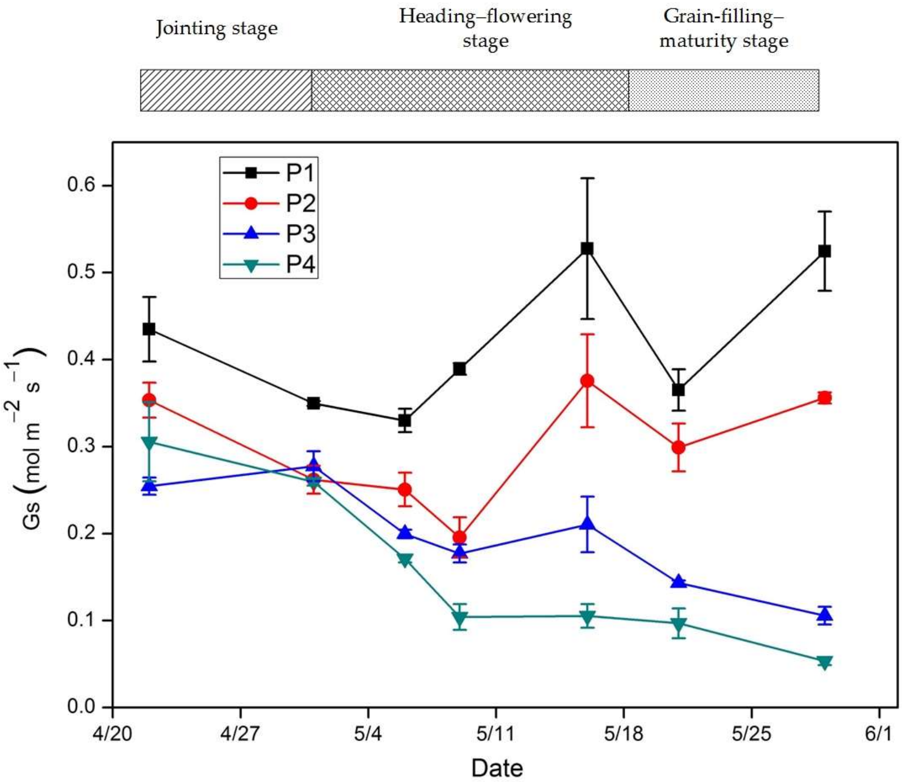

Figure 5. Seasonal changes in stomatal conductance (Gs) of winter wheat under different treatments. P1: well-watered; P2: mild stress; P3: moderate stress; P4: severe stress. Bars indicate the standard deviation (SD) of the mean. The phenological phases were identified according to the BBCH scale.

3.2.2. Intercellular CO_2

Intercellular carbon concentration (Ci) is closely related to photosynthesis, which is affected by Gs directly. The Ci and GS were significantly positively correlated (r = 0.825**, $p < 0.01$, Table 1). The Ci showed downward trends under different degrees of water stress (Figure 6). Drought reduced the Ci of winter wheat, with the mean Ci values in the order of P1 (264.92 µmol mol^{-1}) > P2 (238.35 µmol mol^{-1}) > P3 (223.15 µmol mol^{-1}) > P4 (211.66 µmol mol^{-1}). Compared to that of P1, the mean Ci values of P2, P3 and P4 decreased by 10.03%, 15.77% and 20.10%, respectively. The Ci change trends associated with the four different water stress treatments were basically the same. In contrast to the Ci of P1, which reached a minimum value at the end of the jointing stage, those of P2, P3 and P4 reached their minimum values at the heading stage. All then gradually increased, and reached peaks during the flowering stage at 289.70, 261.37, 235.80 and 195.37 mol^{-1}, for P1–P4, respectively. Subsequently, except for P3, the other three treatments first decreased and then increased.

Table 1. Pearson correlation between stomatal conductance (Gs), intercellular carbon concentration (Ci), net photosynthetic rate (Pn) and transpiration rate (E) of winter wheat under different water treatments.

Photosynthetic Parameters	Correlation Coefficient			
	Gs	Ci	Pn	E
Gs	1			
Ci	0.825 **	1		
Pn	0.791 **	0.446 *	1	
E	0.687 **	0.444 *	0.588 **	1

** $p < 0.01$. * $p < 0.05$.

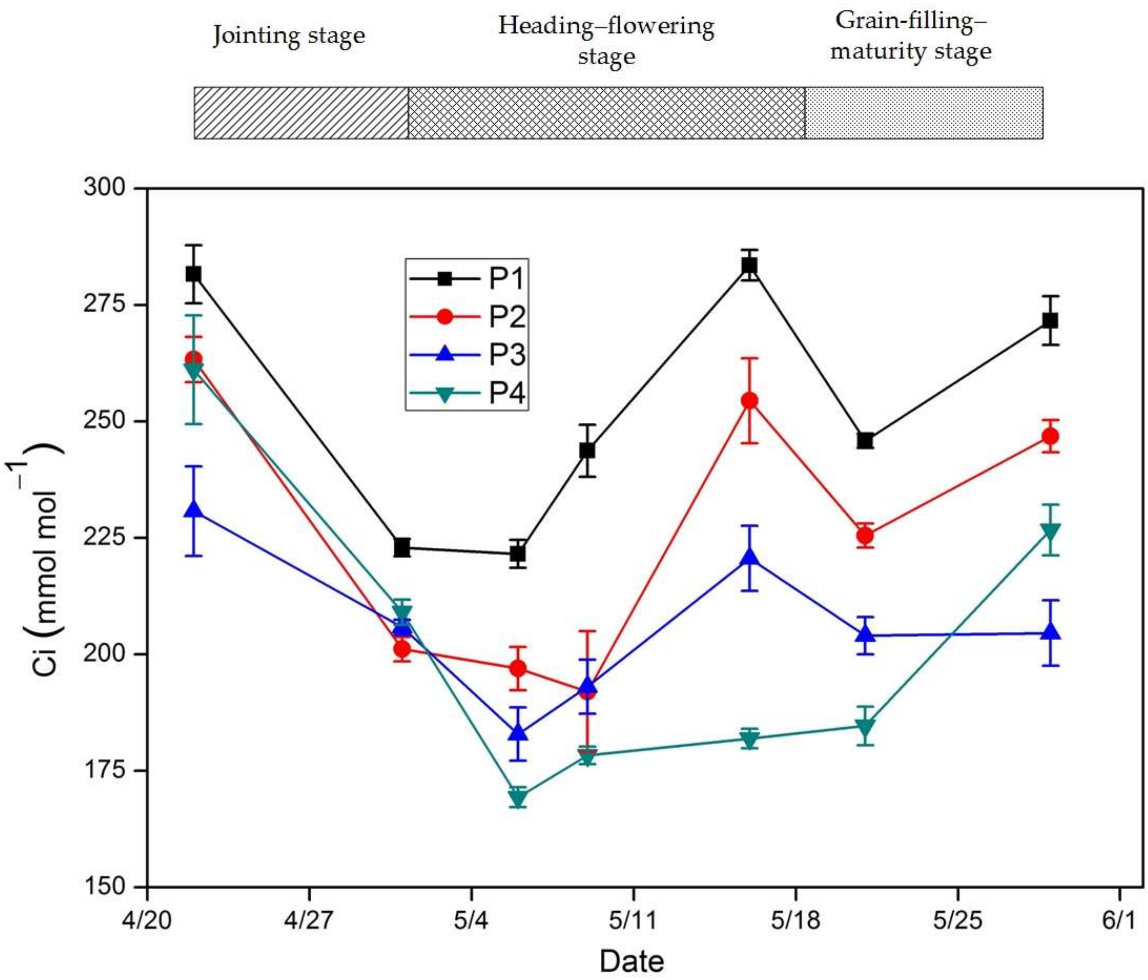

Figure 6. Seasonal changes in intercellular carbon concentration (Ci) of winter wheat under different treatments. P1: well-watered; P2: mild stress; P3: moderate stress; P4: severe stress. Bars indicate the standard deviation (SD) of the mean. The phenological phases were identified according to the BBCH scale.

3.2.3. Net Photosynthetic Rate

Pn is an important index by which to measure vegetation photosynthesis. Gs influences Pn by controlling Ci. Thus, the trend of Pn was similar to that of Gs. We found that the Pn presented a positive correlation with the Gs (r = 0.791**, $p < 0.01$, Table 1) and Ci (r = 0.446*, $p < 0.05$, Table 1).

Pn decreased to different degrees due to water stress, particularly under moderate and severe stress (Figure 7). Compared to that of the well-watered group, the mean Pn values of the mild, moderate and severe stress treatments decreased by 2.80%, 21.46% and 35.93%, respectively. The maximum values of Pn occurred at the heading stage for the well-watered and mild stress treatments, and were 24.31 and 23.07 µmol $m^{-2}s^{-1}$, respectively. The date of the maximum Pn under moderate and severe stress was earlier, at the end of the jointing stage, and the maximum values were 21.66 and 21.07 µmol $m^{-2}s^{-1}$, respectively. The Pn values of P1 and P2 slowly increased during the jointing stage, reached peaks at the heading stage, and then sharply decreasing. The Pn of P1 increased on 16 May and leveled off during the grain-filling–maturity stage. For P2, the Pn showed a significant increase at the middle of the heading–flowering stage, and its value was even higher than that of P1. The change trends of Pn for P3 and P4 were basically the same, increasing during the jointing stage, reaching the maximum value at the end of the jointing stage, and then decreasing suddenly at the heading stage. The Pn then stabilized and decreased after 16 May. For P4, the Pn slightly increased at the middle of the heading–flowering stage, and then fell again after the flowering stage.

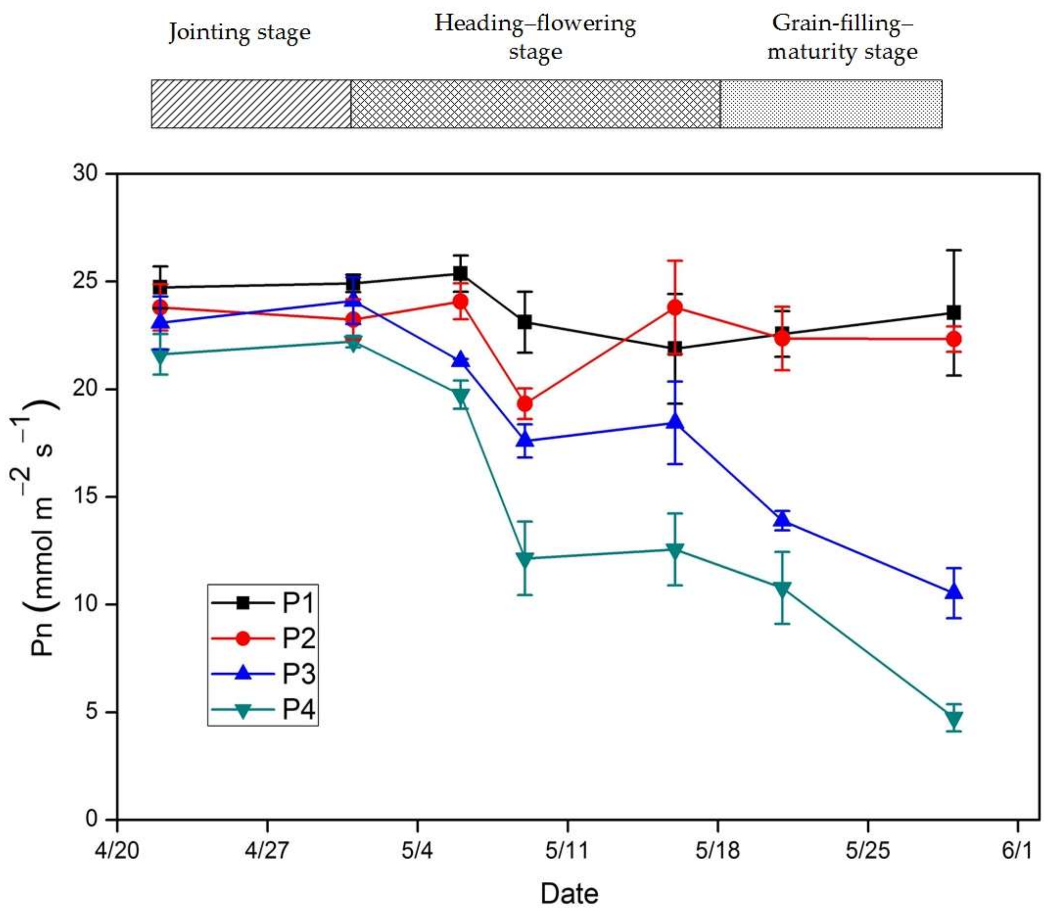

Figure 7. Seasonal changes in net photosynthetic rate (Pn) of winter wheat under different treatments. P1: well-watered; P2: mild stress; P3: moderate stress; P4: severe stress. Bars indicate the standard deviation (SD) of the mean. The phenological phases were identified according to the BBCH scale.

3.2.4. Transpiration Rate

The E value's decrease became more pronounced as water stress intensified (Figure 8). The change trend of E was similar to that of Ci, showing a positive correlation (r = 0.687**, $p < 0.01$, Table 1). At the seasonal scale, the mean values of E were in the order P1 > P2 > P3 > P4. Compared to P1, the mean values of P2, P3 and P4 decreased by 12.53%, 33.30% and 51.33%, respectively. The E under different water stresses reached a peak at the end of the jointing stage. The second peak values of P1 and P3 appeared during the heading–flowering stage, at 11.95 and 8.32 mmol $m^{-2}s^{-1}$, respectively. Subsequently, P1 decreased and then increased, while P3 continued to decrease. P2 continued to increase after reaching a trough at the heading stage, while P4 sharply decreased after its peak, slowly declining at the middle of the heading–flowering stage, and slightly increasing during the grain-filling stage, before finally falling to its lowest value.

3.3. Height and Biomass

Water stress affected the growth of winter wheat at various growth stages (Table 2). From Figure 9a, we can see that there was a significant positive correlation between Pn and height difference ($R^2 = 0.3806$, $p < 0.05$), indicating that the height of winter wheat was affected by photosynthesis. The maximum heights of the well-watered group and the mild, moderate and severe stress groups were 84.58, 69.38, 64.91 and 56.02 cm, respectively. Compared to the well-watered group, the winter wheat heights significantly decreased during each growth stage by 17.97%, 23.26% and 33.77%, respectively. The heights of the winter wheat increased by more than 20 cm within 22 days. The height of the winter wheat under the well-watered irrigation regime increased by nearly 40 cm. The height differences between the well-watered irrigation group and the mild, moderate and severe stress groups were more obvious, reaching 20.08, 29.80 and 27.01 cm, respectively, at the heading stage. Subsequently, the height of each plot slowly increased and stabilized slightly.

In addition, the measured data showed that different water stress levels caused different changes in the aboveground biomass of the winter wheat. We found a significant positive correlation between Pn and dry weight difference (Figure 9b). Thus, the change trend of height was similar to that of Pn. During the entire experimental period, the fresh weight under the well-watered regime was significantly higher than that under the moderate and severe stress treatments. However, on 26 April (jointing stage), 6 May (heading stage), 21 May (grain-filling stage) and 29 May (maturity stage), the fresh weights of the well-watered irrigation and mild water stress wheats were not different; in particular, on 6 May (heading stage) and 21 May (grain-filling stage), the fresh weights of mild stress were even higher than those of the well-watered group. The dry weight of the aboveground biomass was similar to the fresh weight. From the jointing to the maturity stage, the dry weight without water stress was significantly higher than that of the moderate and severe water stress groups. However, the effect of mild stress on the dry weight of the aboveground biomass was not significant, and did not result in a dry weight reduction. Most of the time, the dry weights of the mild stress winter wheat were higher than well-watered winter wheat. From the beginning of the observations to the heading stage, the fresh weight under each water stress level rapidly increased; however, at the middle of the heading–flowering stage, the fresh weight of each block showed a downward trend. Subsequently, the fresh weights of the well-watered, mild stress and moderate stress winter wheat groups continued to slightly increase, while the fresh weight of the severe stress winter wheat continued to decrease. During the entire observational period, the dry weights under different water gradients showed increasing trends, except for the decreases seen in the well-watered, mild stress and moderate stress wheat groups at the middle of the heading–flowering stage, and the severe stress wheat at the end of the growing season.

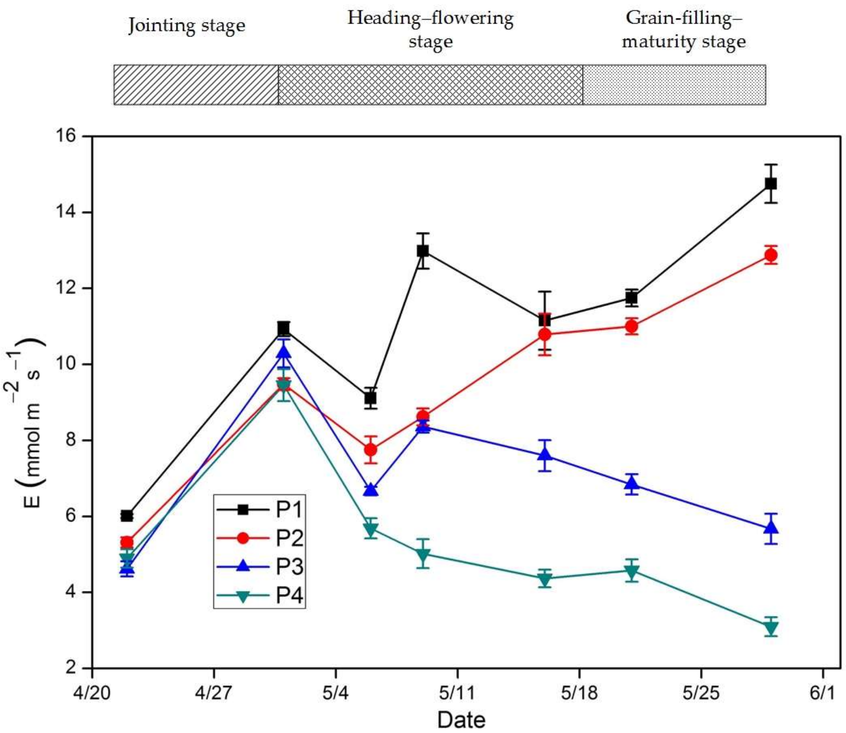

Figure 8. Seasonal changes in transpiration rate (E) of winter wheat under different treatments. P1: well-watered; P2: mild stress; P3: moderate stress; P4: severe stress. Bars indicate the standard deviation (SD) of the mean. The phenological phases were identified according to the BBCH scale.

Table 2. The height and biomass of winter wheat under different water treatments.

Growth Stage	Date	Height (cm)				Fresh Weight (g)				Dry Weight (g)			
		P1	**P2**	**P3**	**P4**	**P1**	**P2**	**P3**	**P4**	**P1**	**P2**	**P3**	**P4**
Jointing stage	4/14	42.62 ± 1.90a	36.27 ± 2.04b	30.06 ± 1.14c	27.87 ± 0.76c	2.41 ± 0.16a	1.84 ± 0.32b	0.76 ± 0.25c	0.90 ± 0.19c	0.38 ± 0.05a	0.31 ± 0.07a	0.14 ± 0.04b	0.15 ± 0.05b
	4/22	59.82 ± 2.67a	50.7 ± 1.07b	43.46 ± 2.51c	44.23 ± 2.19bc	6.47 ± 0.34a	5.69 ± 0.43b	4.86 ± 0.52c	5.36 ± 0.38b	1.22 ± 0.23a	1.28 ± 0.25a	0.81 ± 0.29c	0.95 ± 0.16b
	4/26	63.47 ± 3.65a	53.69 ± 2.89b	44.2 ± 1.97c	45.21 ± 1.7c	6.97 ± 0.44a	6.05 ± 0.29b	5.37 ± 0.46c	6.17 ± 0.38b	1.27 ± 0.14a	1.27 ± 0.25a	0.95 ± 0.16c	1.09 ± 0.14b
	5/1	70.38 ± 2.59a	59.02 ± 2.48b	50.89 ± 1.94c	49.29 ± 1.21c	8.49 ± 0.53a	7.16 ± 0.48b	6.35 ± 0.66c	6.96 ± 0.43bc	1.39 ± 0.19a	1.30 ± 0.23a	1.25 ± 0.28a	1.39 ± 0.16a
Heading–flowering stage	5/6	80.78 ± 3.78a	60.7 ± 1.44b	50.98 ± 2.43c	53.77 ± 2.06bc	9.96 ± 0.17b	10.78 ± 0.29a	8.50 ± 0.23c	7.31 ± 0.23d	2.11 ± 0.22a	2.29 ± 0.26a	1.82 ± 0.19b	1.72 ± 0.17b
	5/9	81.14 ± 3.92a	67 ± 2.42b	54.8 ± 3.04c	54.83 ± 1.87c	9.11 ± 0.63a	7.16 ± 0.67b	7.10 ± 0.78b	6.64 ± 0.59b	1.97 ± 0.17a	1.76 ± 0.20a	1.70 ± 0.21a	1.81 ± 0.19a
	5/16	83.33 ± 1.77a	69.36 ± 1.95b	57.12 ± 1.19c	55.62 ± 1.52c	10.07 ± 0.47a	9.44 ± 0.69b	7.93 ± 0.72c	6.51 ± 0.65d	2.32 ± 0.19a	2.56 ± 0.24a	1.99 ± 0.19b	1.99 ± 0.20b
Grain-filling–maturity stage	5/21	84 ± 5.29a	69.25 ± 0.48b	57.22 ± 1.6c	55.63 ± 1.61c	9.71 ± 0.39a	9.99 ± 0.71a	8.42 ± 0.67a	4.98 ± 0.38b	2.77 ± 0.13ab	3.08 ± 0.26a	2.52 ± 0.21b	1.79 ± 0.13c
	5/29	84.58 ± 3.95a	69.38 ± 3.48b	64.91 ± 2.74b	56.02 ± 1.09c	10.35 ± 0.66a	10.00 ± 0.73a	8.66 ± 0.46b	4.50 ± 0.56c	3.38 ± 0.19a	3.45 ± 0.23a	3.15 ± 0.18a	1.87 ± 0.14b

Each value represents a mean of 10 plants. Values are shown as mean ± standard error (SE) of mean. Values on particular days with the same letter under different treatments are not significantly different at the level of $p < 0.05$ according to the LSD (least-significant difference) test.

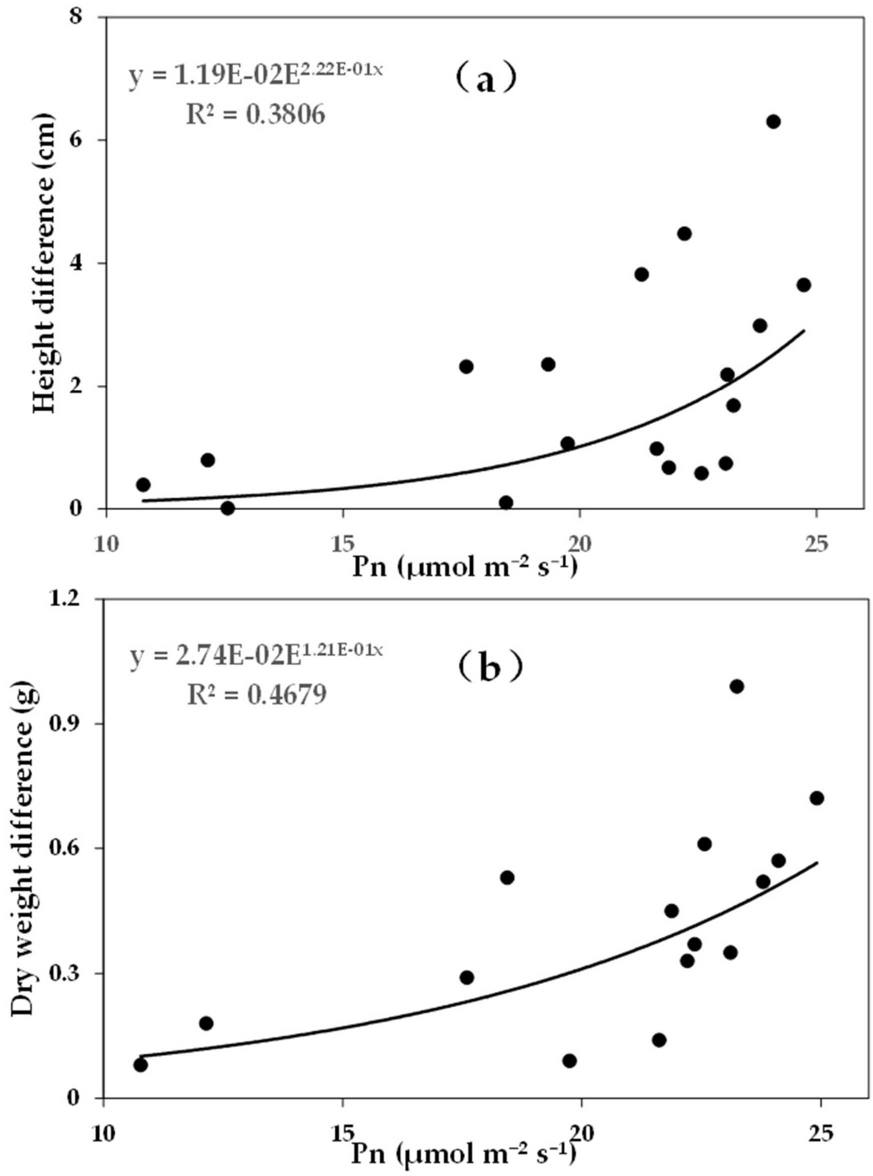

Figure 9. Relationship between net photosynthetic rate (Pn) and height difference (**a**), and dry weight difference (**b**) of winter wheat under different water treatments.

3.4. Yield and Yield Components

The grain weight, spike and 1000 grain weights decreased significantly under moderate and severe stress, but did not change significantly under mild stress (Figure 10a,c,d). Compared to well-watered winter wheat, the grain weights of the mild, moderate and severe water stress wheats decreased by 7.27%, 32.73% and 43.64%, respectively. The mild, moderate and severe stress winter wheat treatments saw spike weights reduced by 5.38%, 20.43% and 38.17%, respectively. The effect of severe stress on the 1000 grain weight of winter wheat resulted in a significant decrease of 23.22%. Moderate stress reduced the 1000 grain weight by only 14.28%, while mild stress increased the 1000 grain weight of winter wheat by 1.95%. Water stress had a significant effect on the straw weight of winter wheat (Figure 10b). Compared to the well-watered plants, the straw weights under mild, moderate and severe water stress decreased by 45.55%, 46.35% and 54.05%, respectively.

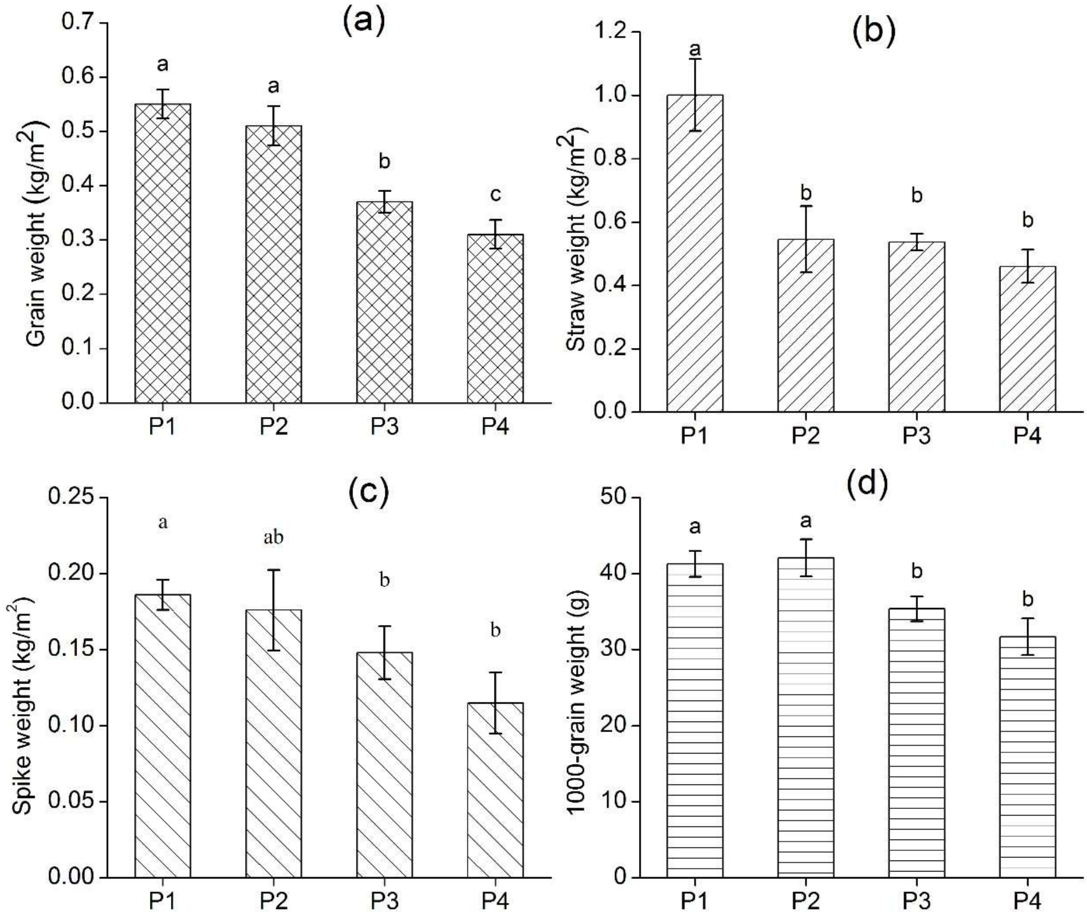

Figure 10. Yield and the yield components (**a**) grain, (**b**) straw, (**c**) spike and (**d**) 1000 grain weight of winter wheat under different treatments. P1: well-watered; P2: mild stress; P3: moderate stress; P4: severe stress. Bars show ± standard deviation (SD). Values with the same letter under different treatments are not significantly different at the level of $p < 0.05$ according to the LSD test.

3.5. WUE and IWP

Different water stress gradients had different effects on the WUE and IWP. It can be seen in Table 3 that the WUE and IWP under moderate and severe stress significantly decreased, while those under mild stress increased. Compared to well-watered plants, the WUE values of the moderate and severe water stress wheats decreased by 15.70% and 19.91%, respectively, while the WUE of the mild stress plants increased by 7.87%. The IWP values recorded for the moderate and severe stress winter wheat treatments decreased by 7.12% and 4.78%, respectively, while that of the mildly stressed wheat increased by 13.46%.

Table 3. Irrigation level, evapotranspiration (ET), water use efficiency (WUE) and irrigation water productivity (IWP) in winter wheat under different water treatments.

Plot	Irrigation Amount (mm)	ET (mm)	WUE (kg/hm^2/mm)	IWP (kg/hm^2/mm)
P1	366.67	484.60 ± 18.19a	11.40 ± 0.67a	15.01 ± 0.43b
P2	300.00	417.03 ± 4.95b	12.25 ± 0.52a	17.03 ± 0.67a
P3	261.91	381.35 ± 15.36b	9.61 ± 0.51b	13.94 ± 0.28b
P4	214.29	336.73 ± 3.69c	9.10 ± 0.30b	14.29 ± 0.41b

Values are shown as mean ± standard error (SE) of mean. Values in the same column with the same letter under different treatments are not significantly different at the level of $p < 0.05$ according to the LSD test.

4. Discussion

Drought will become more frequent and severe in the future [28]. It is crucial to understand the responses of plant gas exchange, yield, WUE and IWP to drought.

It is well known that water stress can inhibit gas exchange characteristics, and as a result affect the photosynthetic capacity of plants [29]. The current study showed that water deficit conditions significantly reduced winter wheat Pn, E, Ci and Gs values. This finding was consistent with those of Ma [30] and Liu [21]. When water stress occurs, the photosynthesis of winter wheat may be affected by both stomatal and non-stomatal effects. In our study, photosynthesis was mainly limited by stomatal conductance, because the stomatal conductance decreased under water stress (Figure 5). Controlling water loss through stomatal closure has been considered as an early response of plants to water stress [28,31]. As water stress continues, the stomata remain closed for longer during the day. This leads to a reduction in carbon assimilation rate and water loss, which results in the maintenance of carbon assimilation at the expense of low water availability. The stomatal closure may also result in an increased susceptibility to photodamage. Stomata are the gates whereby carbon–water exchange takes place [32]. Closing the stomata helps to reduce water loss caused by transpiration, which can be adjusted by signals sent from the roots in drying soil. Decreases in transpiration result in increased Tleaf (Figure 4b). Stomatal limitation is generally considered to be a major factor in the weakening of photosynthesis under water stress [33,34]. This is attributed to the decreases in Ci (Figure 6) and Pn (Figure 7), thereby suppressing overall photosynthesis. In the case of water deficit, the reduction of leaf RWC (relative water content) and water potential causes the stomata to close, leading to a decrease in the effectiveness of CO_2, and results in a decrease in Pn. In our study, positive correlations between Gs and Ci (0.825**; Table 1), Pn (0.791**; Table 1) and E (0.687**; Table 1) were observed, suggesting that Ci, Pn, and E were significantly influenced by stomatal regulation in winter wheat. Similar results have been found in winter wheat under water stress. This indicates that stomatal closure is a response to water stress. Stomatal closure and decreased photosynthesis are common responses of plants to water stress [35]. Interestingly, in this study, stomatal closure was not significantly affected by mild stress, resulting in no obvious reduction in photosynthesis. The variation in photosynthesis may be attributed to the changes of photosynthetic machinery, leaf area, temperature, chlorophyll content and leaf relative water content. During the jointing stage, Gs and Ci both showed downward trends, while Pn increased, which may have been caused by the increasing temperature and chlorophyll content. The increase in Pn in the different water stress plots on 9 May was due to the increase in soil water content due to irrigation.

We found that water stress significantly reduced the height of winter wheat. This result was consistent with Taiz and Zeiger [36], and Samarah [37]. The positive correlation between Pn and height difference shown in Figure 9 suggests that height was influenced by Pn in winter wheat. The decrease in winter wheat height was mainly caused by photosynthesis and decreased osmotic potential. The decrease in photosynthesis affected the growth and development of the winter wheat, resulting in a height decrease. Here, we found that the phonological phase that had the greatest impact on the height of winter wheat was the jointing stage, which was consistent with it being the period of active mitotic cell division. Water stress during the jointing stage is likely to inhibit the full development of plant organs, which depend on the degree of cell division that occurs during this phenological stage.

The fresh and dry weights of the aboveground biomass significantly decreased under both moderate and severe drought stress, because the decrease in photosynthesis caused by the water deficit affected the development of the leaves, which were unable to fully extend. The photosynthetic effective radiation intercepted by winter wheat decreased, resulting in a reduction in plant height and material accumulation, which led to a decrease in biomass. Compared to well-watered plants, the fresh and dry weights of the biomass of the wheats under mild water stress slightly decreased in most observations, and they were higher during the late growth period than those of the well-watered irrigation plants, which was consistent with the variation trend of the net photosynthetic rate (Figure 7). In our study, we observed that there was a significant positive correlation between Pn and height difference (Figure 9a) and dry weight difference (Figure 9b), suggesting that the growth of winter wheat was affected by photosynthesis. Compared with the control, water stress reduced the growth and biomass of wheat (Table 2). These findings are in line with published data [38], which report a decrease in wheat growth and biomass under water stress conditions. The decrease in biomass under water stress may have been due to changes in nutritional status.

Compared to the control, the straw weights of winter wheat decreased by 45.55%, 46.35% and 54.05% under mild, moderate and severe water stress, respectively (Figure 10b). The results were consistent with Martyniak [39] and Katerji [7], who found that straw yields were significantly affected by water treatments. In our study, we observed that the heights decreased significantly under mild, moderate and severe water stress, which shows that the decrease in straw yield under water stress is usually attributable to reduced plant height. Similar research has found this in winter wheat under water stress [37]. The 1000 grain weights of winter wheat under moderate and severe stress significantly decreased by 23.22% and 14.28%, respectively, while mild drought increased the 1000 grain weight of winter wheat by 1.95% (Figure 10d). The reduction of the 1000 grain weight can be attributed to the shorter grain-filling times under moderate and severe water stress, which leads to a lower dry matter accumulation or a reduced rate and duration of starch accumulation in the endosperm. Thus, the seeds were smaller under moderate and severe water stress. As a result, the 1000 grain weights were low. Samarah [4] reported that the developed grains under water stress had lower grain weights and faster grain water losses than well-irrigated plants. In our study, grain yield was significantly reduced under moderate and severe water stress. Previous studies have shown that the decrease in total grain production under water stress is due to the decrease in grain yield per unit area, such as grain weight per spike [40], grain number per spike [41], spike number per square meter [42] and tiller number per plant [4]. In our study, water stress may have reduced grain yield via the 1000 grain weight. Moderate and severe water stress reduced leaf photosynthesis severely, shortened the duration of photosynthesis, promoted the senescence of flag leaves significantly, rapidly degraded the internal structure of plants, and affected the transport of photosynthetic products to grains. As a result, the yield of winter wheat was significantly reduced under moderate and severe water stress. It is interesting that the grain, spike and 1000 grain weights did not decrease significantly under mild water stress (Figure 10a,c,d). This was due to the fact that the capacity for photosynthesis did not weaken under mild water stress. Winter wheat can maintain a high Pn during the growth stages under mild water stress, which contributes to full grain-filling. As a result, the yield of winter wheat under mild stress was not significantly affected. The same results have been found by others for winter wheat, which indicates that photosynthesis is an important factor affecting grain yield [3]. Different degrees of water stress affect the transport and distribution of winter wheat dry matter, which in turn affects yield. A certain degree of water stress can promote the transport of assimilates and improve the crop harvest index. In our study, mild water stress did not significantly affect winter wheat yield. Some studies have shown that the application of mild stress during the jointing stage can even increase the yield [43].

WUE represents the ultimate performance of crop yield and water consumption, and it determines the water saving capacity and water productivity of crops. Many previous studies have found that the WUE of various plant species is improved under water stress [44]. During water stress, stomatal closure leads to decreased leaf conductance, photosynthesis and transpiration. Due to the sensitive response of leaf conductance to reduced leaf water potential, the more conservative use of water results in higher WUE in water-deficient plants, which may be a mechanism for improving resource utilization efficiency [21]. WUE is an important physiological adaptation mechanism that can improve crop productivity under conditions of water scarcity [24]. An increase in WUE under mild stress was observed in this study (Table 3). This is because the yield was not significantly reduced, while plants consumed less water. We found that the WUE decreased significantly under moderate and severe stress, which was due to the decreased yields. From the perspective of the physiological mechanism, we can see that the WUE under mild stress was higher than that of well-watered plants, which may be due to water-stressed wheat exhibiting greater wildness, and the fact that wilting always occurs when the saturation deficit is high. As a result, wheat absorbs material only when there is insufficient saturation. Therefore, each carbon molecule it fixes loses less water. The highest IWP was observed under mild water stress, which is consistent with Oweis [45], confirming that the irrigation was most effective in this treatment.

5. Conclusions

It was found that different water stresses had different effects on the growth of winter wheat. Compared to the well-watered group, moderate and severe stress significantly reduced the Pn, E, Ci, Gs, height, fresh biomass weight, dry biomass weight, straw weight, spike weight, grain weight, 1000 grain weight, WUE and IWP of winter wheat. Under mild stress, only the height and straw weight significantly decreased, while the Pn, E, Ci, Gs, fresh biomass, grain and spike weight slightly decreased. The dry biomass, 1000 grain weight, WUE and IWP values under mild stress were higher than they were for well-watered winter wheat. Therefore, in areas with a water shortage, mild stress can be considered the most suitable environment for winter wheat growth, to maintain the yield and maximize the utilization of water resources.

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