Effects of warming and drought stress on the growth characteristics, photosynthetic-transpiration rates, and yield of winter wheat

Qian Li[1], Yang Gao[2*], Abdoul Kader Mounkaila Hamani[1,2], Guangshuai Wang[2], Junming Liu[2], Yuanyuan Fu[1], Xingpeng Wang[1*]

(1. *College of Water Resource and Architecture Engineering, Tarim University, Alar 843300, Xinjiang, China*;
2. *Institute of Farmland Irrigation, Chinese Academy of Agricultural Sciences, Xinxiang 453002, Henan, China*)

Abstract: Climate change has limited crop productivity worldwide. Understanding crop response to global climate changes is vital to maintaining agricultural sustainable development. A two-year experiment was conducted to investigate the effects of warming and drought on crop growth and winter wheat yield production. The results showed that both warming and drought shortened the crop growth period, reduced the leaf area index, and increased winter wheat biomass accumulation. Under sufficient water supply conditions, warming would increase photosynthetic and transpiration rates and water use efficiency, while under water deficit conditions, the opposite was observed. Under warming conditions, the grain yield of the water deficit treatment was 8.9% lower than that of the sufficient water supply treatment. Under non-warming conditions, the grain yield of water deficit treatment was 12.4% lower than that of the sufficient water supply. Under the conditions of water-sufficient supply, the grain yield of the warming treatment was 4.4% lower than that of the non-warming treatment, and under the conditions of water deficit, the grain yield of the warming treatment was 1.3% lower than that of the non-warming treatment. Warming tends to decrease wheat growth and grain yield, but sufficient water supply could improve winter wheat's water use efficiency and reduce the warming limitation on wheat production.

Keywords: winter wheat, warming, leaf area index, photosynthetic rate, yield, biomass
DOI: 10.25165/j.ijabe.20241703.8225

Citation: Li Q, Gao Y, Hamani A K M, Wang G S, Liu J M, Fu Y Y, et al. Effects of warming and drought stress on the growth characteristics, photosynthetic-transpiration rates, and yield of winter wheat. Int J Agric & Biol Eng, 2024; 17(3): 121–129.

1 Introduction

With global warming, drought and temperature rise have become the key constraints for wheat production[1-3]. Previous studies have reported that an increase of 1.0°C in China's annual average temperature, the world wheat yields could lead to a reduction of about 10%[4,5].

By the end of the 21st century, the global annual temperature is projected to increase by 1.8°C-4.0°C[6]. Increased incidence of extreme weather events[7], such as short-term ultra-high temperatures (>33°C) and dry periods[8], are also expected under future climate scenarios[9] and carry significant risks for crop production[7]. However, several studies have shown that rising temperature benefits wheat production[10,11]. Some researchers believe that the appropriate interval of temperature for the heat grain filling stage should be ranged from 18°C to 24°C[12]. A short period before and after flowering with a temperature greater than 30°C results in winter wheat low grain number per spike and grain abortion[13].

In the North China Plain (NCP), with the increase in temperature, the sowing time of winter wheat was delayed, the greening time was advanced, and the crop growth period was shortened[14]. With the increase in temperature, winter wheat's leaf area significantly increased before anthesis, while the leaf area decreased after anthesis[14]. Therefore, under warming conditions, the functional leaves of winter wheat will senescence prematurely, which is not conducive to dry matter accumulation and yield formation[14]. High temperature induces leaf senescence and reduces grain weight by shortening the grain-filling stage[15]. Temperature increase accelerates the whole plant senescence and the grain-filling process, resulting in early ripening[16], leading to significant yield loss[17]. However, some studies reported that warming could accelerate the growth and development of winter wheat shoots, improve the starch synthase activity and the 1000-grain weight, and thus increase wheat yield[10,18,19]. Other studies have shown that each 1°C temperature increase in warming causes wheat flowering to advance by about 10 d, and the time of wheat post-flowering shortens by 4.1 d[20].

The frequency of droughts will significantly increase under climate change, especially in arid/semi-arid regions. Although there are several studies on the effects of water deficit on the water-carbon cycle at different levels of the ecosystem, systematic research on the water-carbon coupling process at different spatial and temporal scales is still scarce. Crops will maintain high water use efficiency (WUE) due to moderate water deficit, while WUE will be decreased under severe drought[21,22]. The stomatal conductance of leaves would be reduced under drought stress to reduce crop water loss and improve transpiration efficiency[23]. Deng

Received date: 2023-03-08 **Accepted date:** 2024-04-08

Biographies: Li Qian, MD, research interest: water-saving irrigation, Email: wsxzazj1314@163.com; **Abdoul Kader Mounkaila Hamani**, PhD, research interest: water-saving irrigation, Email: m_abdoulkader@yahoo.com; **Guangshuai Wang**, PhD, Associate Researcher, research interest: water-saving irrigation, Email: wangguangshuai@caas.cn; **Junming Liu**, PhD, research interest: water-saving irrigation, Email: liujunming0225@163.com; **Yuanyuan Fu**, MD, research interest: water-saving irrigation, Email: fyycaas@gmail.com.

***Corresponding author: Yang Gao**, PhD, Professor, research interest: theory and technology of efficient crop water use, Tel: +86-13849378772, Email: gaoyang@caas.cn; **Xingpeng Wang**, PhD, Professor, research interest: water-saving irrigation. Tel: +86-13999068354, Email: 13999068354@163.com.

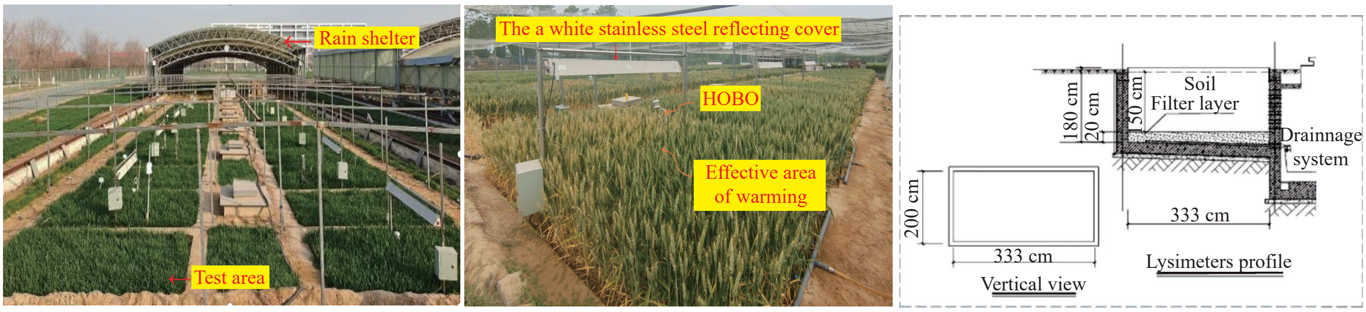
et al.[24] found that the biomass of plant leaves varies with the degree of water deficit, and the biomass allocation of the farmland system has no obvious response to short-term drought[25]. In addition, the frequency and amount of precipitation also affect biomass and accumulation[26]. In addition to directly affecting plant growth[27], the most affected process is related to photosynthesis[28,29]. The direct effects of drought on photosynthesis are caused by stomatal closure[30] and occur earlier, while the indirect effects are caused by the down regulation of photosynthetic metabolism that occurs under long-term or more severe stress[31,32]. Pradhan et al.[33] suggested that drought, high temperature, and their synergistic stress could reduce the grain yield of spring wheat from seedling emergence to the flowering stage. Drought reduces the morphological and physiological traits, photosynthesis, leaf water potential, xylem sap movement, and stomatal closure[34]. To date, there are few investigations on the interaction of warming and drought on wheat growth and yield formation. Therefore, understanding the effects of warming and drought stress on wheat is of key importance for wheat cultivation and decision-making management. It also has important implications for understanding winter wheat's adaptability to the environment under future climate scenarios.

In arid and semi-arid regions, such as the NCP, soil moisture condition plays an important role in crop response to climate changes. However, the regulation of water supply on wheat growth and yield performance under climate change remains unclear. Therefore, it could be hypothesized that warming and drought have a combined influence on crop growth and yield preformation. To improve the ability of crops to cope with climate change, a winter wheat experiment with warming and drought stress was carried out in lysimeters under a rain shelter from 2020-2022. The objectives of this study were to investigate the effects of warming and drought on crop growth, photosynthesis and transpiration rates, and yield of winter wheat.

2 Materials and methods

2.1 Experimental site

The experiment was conducted from October 2020 to May 2022 at the Comprehensive Experimental Station of the Chinese Academy of Agricultural Science (35°14′N, 113°76′E, altitude 74 m), located in Qiliying Town, Xinxiang city, Henan province, China. The lysimeters experiment was conducted under a rain shelter (Figure 1a) to protect the lysimeters against rainfall and effectively reduce the influence of precipitation on the experimental results. The site has a warm temperate continental climate with an annual average temperature of 14°C and annual average precipitation of 580 mm. The lysimeter has an area of 3.33 m×2.00 m and a soil depth of 1.8 m[35]. According to the World Reference Base for Soil Resources (WRB) classification method, the soil of the test site was luvisol (https://www.isric.org/explore/wrb#:~:text=The%20World%20Reference%20Base%20), with a bulk density of 1.45 g/cm^3 and a field capacity (θ_{FC}) of 26% (mass basis).



a. Electronic radiation infrared heater, lysimeters, and rain shelter

b. The height of the warming lamp can be adjusted according to the canopy warming effect reaching 1.5°C-2.0°C and determining the effective area during the wheat growing season, the temperature was measured at 20 cm above the canopy using a HOBO hygrometer

c. Schematic diagram of lysimeter[35]

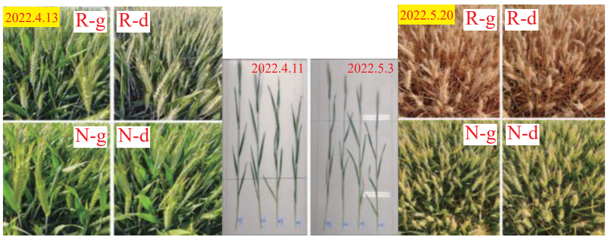
Figure 1 Overview of test site facilities

2.2 Experimental design

Two temperature levels and two irrigation rates were designed in a randomized complete block design experiment. In total, there were four treatments, i.e., R-g: warming of 1.5°C with sufficient water supply, R-d: warming of 1.5°C with deficit water supply, N-g: non-warming with sufficient water supply, N-d: non-warming with deficit water supply. Each treatment was replicated three times. The electric infrared heater (model MRM2420, Kalglo Electronics Co., Inc., PA, USA) was adopted for air warming (Figure 1), which comprised the infrared heater and electronic controller. The infrared heater has a far-infrared heating black-body tube (length of 1.8 m and diameter of 1.8 cm) with a power of 2000 W, an iron bracket, and a white stainless steel reflecting cover (length of 2 m and width of 0.2 m). The bracket was fixed in the soil before sowing, and the far-infrared heating tube was suspended with iron support. The height of the heating tube was adjusted with measurements of an infrared thermometer to ensure the temperature increased by around 1.5°C. The 24 h continuous warming mode was adopted during the winter wheat growing season. The lysimeter plot has an area of 3.33 m×2.00 m. According to the infrared thermometer measurements, the effective warming area was about 2 m^2. No heating treatment was also provided with a lampshade to control and reduce the error of test factors.

Winter wheat (*Triticum aestivum* L.) of Zhoumai-22 (The wheat seeds were purchased from Daneng Agricultural Materials Company in Xinxiang, Henan Province, China) was sown on October 15, 2020, and October 25, 2021, and harvested on May 20, 2021, and May 27, 2022, respectively. The sufficient water treatment with an irrigation rate of 45 mm was performed when the average soil moisture in the 0-60 cm soil layer decreased to 70% of the field water capacity. The water deficit treatment with an irrigation rate of 33 mm was performed when the average soil moisture in the 0-60 cm soil layer decreased to 55% of field water capacity. Soil moisture was measured by the gravimetric method. Soil was taken once at each growth stage and divided into three layers of 60 cm, and 20 cm for each layer. Before sowing, fertilizer was applied to each lysimeter at 255 kg/hm^2 of urea, 998 kg/hm^2 of superphosphate, and 210 kg/hm^2 of calcium sulfate. After sowing, 120 kg/hm² of urea was applied to each lysimeter along with water in the second and third irrigation events. The fertilizer doses were determined based on our previous results. The irrigation method of this experiment was drip irrigation. There were four drip lines in each lysimeter. The drip line had a diameter of 16 mm, an emitter distance of 0.33 m, and a flow rate of 2.2 L/h.

To find out the intuitive differences between treatments, as shown in Figure 2, the left figures were taken at the grain-filling stage of the warming treatment, the middle pictures indicated the difference in plant height between the two observation times, and the right pictures were taken at the mature stage of the warming treatment (the time on the picture is the shooting time).



Note: R-g: warming of 1.5ºC with sufficient water supply. R-d: warming of 1.5ºC with water deficit. N-g: non-warming with sufficient water supply. N-d: non-warming with water deficit.

Figure 2 Growth process of winter wheat under warming and drought stress

3 Measurements

3.1 Winter wheat phenology

According to the order of winter wheat's organ formation, the wheat growth season was divided into 9 stages, i.e., seedling, tillering, overwintering, turning-green, jointing, heading, flowering, grain filling, and maturity, respectively. The corresponding date of these stages was recorded when 50% of wheat plants reached a certain stage.

3.2 Environmental factors

Air temperature and relative humidity of the wheat canopy were measured with the HOBO Temperature/RH Data Logger (MX2301, USA), which was placed 20 cm above the canopy. Soil water content was measured by the gravimetric method. Air temperature in the warming treatments was about 1.3°C-1.5°C higher than the non-warming treatments (Figures 3c and 3d), and the temperature controlled by R treatment is increased by about 1.5°C-2.0°C compared with N treatment. The temperature in the winter wheat season was generally low, and the Vapor Pressure Deficit (VPD) value above the canopy was not significantly different under the conditions of sufficient water supply and water deficit, so it was not included in the analysis.

3.3 Plant height, leaf area index, biomass, and light interception

Plant height and biomass were measured every 10-14 d during

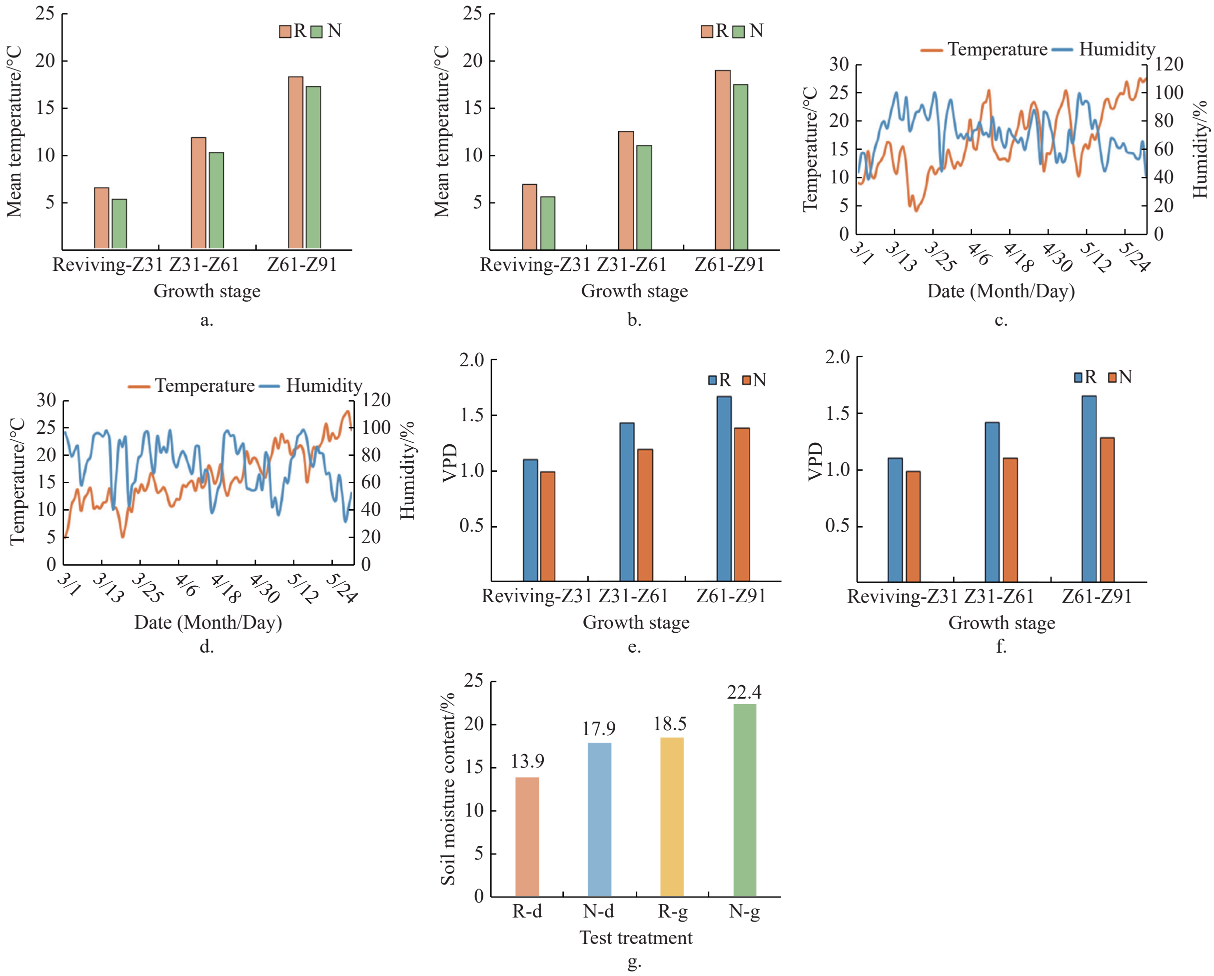


Figure 3 Mean temperature within the wheat canopy in 2020-2021 (a) and 2021-2022 (b). The temperature and humidity measured by a weather station in the growing season of (c) 2020-2021 and (d) 2021-2022. The VPD is measured by a weather station in the growing season of (e) 2020-2021 and (f) 2021-2022. R is a warming treatment. N is not a warming treatment. Z31, Z61, and Z91 indicate jointing, anthesis, and maturity, respectively, (g) The soil water content in different treatments

the two seasons. Wheat plants were divided into stem, leaf, and ear, dried at 105°C for 30 min, then dried at 75°C until constant weight. Leaf area index (LAI) and light interception were measured by SunScan canopy analyzer (ss1, delta-T, UK) at 11:00 a.m., with an interval of 14 d. Light interception of the wheat canopy was calculated with photosynthetically active radiation (PAR) above and below the canopy.

3.4 Photosynthetic and transpiration rates, and SPAD

Leaf photosynthetic rate (Pn) and transpiration rate (Tr) were measured using Li-Cor 6400XT (Li-Cor Bio-sciences, Lincoln, Nebraska, USA) at 9:00-12:00 am (The stomata of wheat leaves are completely open and stable)[36]. With the reference CO_2 of 400 μmol CO_2/mmol and light intensity of 1200 μmol/m^2·s, the WUE was calculated as Pn/Tr. In the first two dates of measurements in 2021 and the first three dates of observations in 2022, the fully developed leaf of wheat was taken for measuring. Thereafter, the flag leaf of winter wheat was sampled for measuring. SPAD was measured with SPAD-502 meter (Minolta Camera Co., Ltd., Osaka, Japan), before flowering, SPAD values were observed once every 14 d, and the interval changed to 5 d after flowering, respectively. Pn, Tr, and SPAD were replicated three times for each treatment.

3.5 Yield and yield components

At harvest, the wheat ears within 1 m^2 of the effective warming area were collected, and then the wheat yield was determined by ear number of 1 m^2, threshing, and weighing. 30 randomly selected wheat spikes were used to determine the number of grains per spike. The thousand-grain weight was measured by weighing 1000 grains (dry weight), three replicates per treatment.

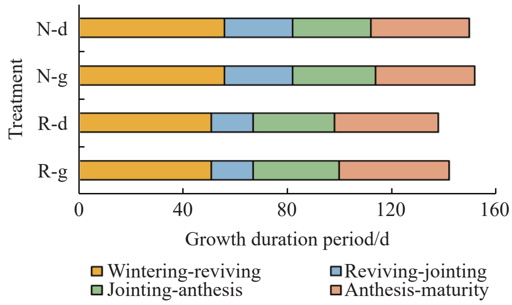
3.6 Statistical analysis

Microsoft Excel 2010 was used for data analysis and mapping, the DPS data processing system V13.5 (http://www.dpsw.cn) was used for statistical analysis to determine the differences between different treatments, and Duncan's multiple comparisons were used for the significance test (p<0.05).

4 Results

4.1 Effects of warming and drought on winter wheat phenology

Figure 3 shows the growing period average temperature of the wheat canopy and the daily average temperature changes under the warming and non-warming treatments. As the temperature sensor of the HOBO MX2301 was installed in a solar radiation shield, the measured canopy temperature (Figure 3) was lower than the designed warming of 1.5°C. Compared with the treatment without warming, the warming treatment advanced the growth period of winter wheat. Increasing temperature advanced jointing, flowering, grain filling, and maturity by 15, 13, 8, and 7 d, respectively (Figure 4). During the whole growth period, the water deficit under the same temperature conditions was 2-4 d earlier than the sufficient water supply treatment, and the warming under the same water conditions was 10-12 d earlier than the non-warming treatment (Figures 2 and 4).

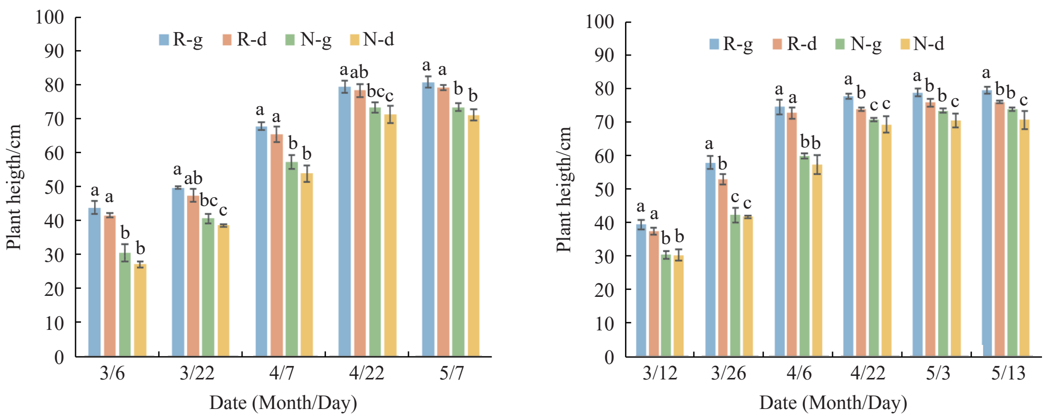


Note: R-g: warming of 1.5°C with sufficient water supply. R-d: warming of 1.5°C with water deficit. N-g: non-warming with sufficient water supply. N-d: non-warming with water deficit.

Figure 4 Effects of temperature increase and drought stress on the growth process of winter wheat in 2021-2022 season

4.2 Effects of warming and drought on plant height, biomass, and SPAD

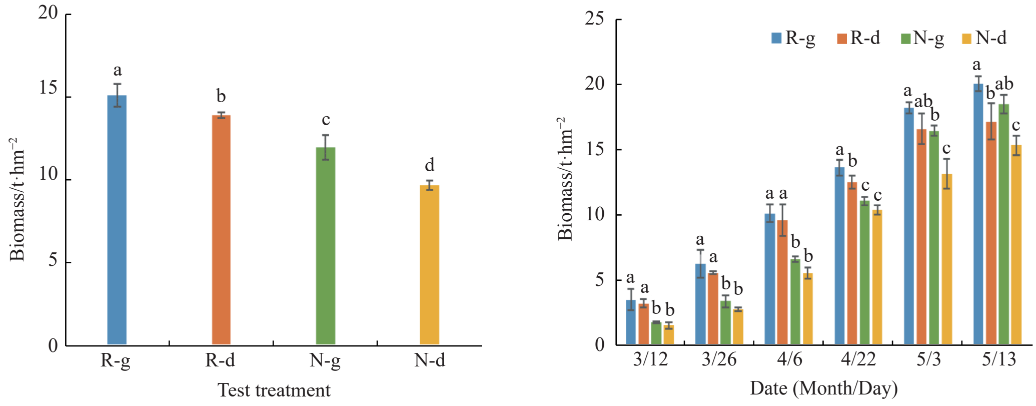
As shown in Figures 5-7, during the growing seasons of 2021 and 2022, the experimental results of plant height, biomass, and SPAD of winter wheat under temperature increase and drought stress were consistent, with significant differences among treatments. Plant height and biomass of wheat in R-g, R-d, N-g, and N-d during the whole growth period showed a decreasing trend (Figure 5). In the two wheat seasons, under the same water conditions, the plant height in R-g was 20.5% and 18.9% higher than that in N-g, and that in the R-d was 23.8% and 15.7% higher than that in N-d. Under the same temperature conditions, the plant height in R-g was 3.5% and 5.2% higher than that in R-d, and that in the N-g was 5.6% and 2.4% higher than that in N-d. The warming increased plant height, while drought limited plant height.



a. 2020-2021 b. 2021-2022

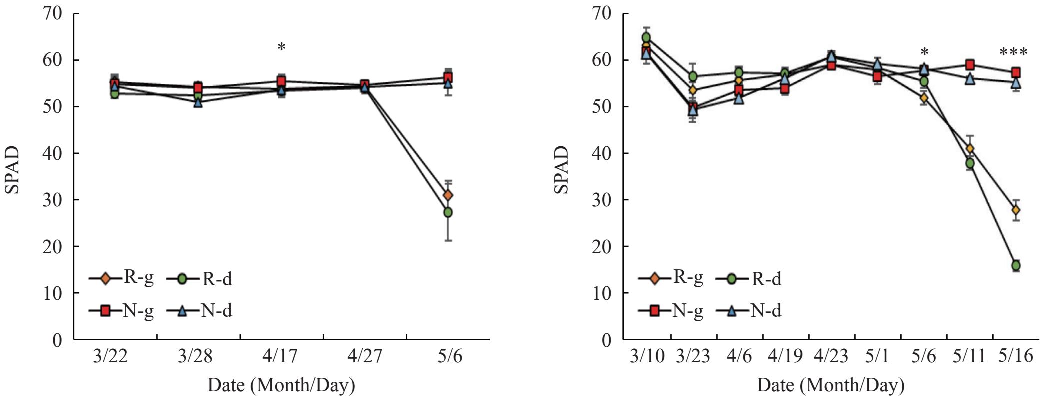
Note: R-g: warming of 1.5°C with sufficient water supply. R-d: warming of 1.5°C with water deficit. N-g: non-warming with sufficient water supply. N-d: non-warming with water deficit. Data was shown with the average value of three replicates. Different letters on top of error bars represent significant differences at p<0.05. The same as below.

Figure 5 Effects of temperature increase and drought stress on plant height of winter wheat



a. 2020-2021 b. 2021-2022

Figure 6 Effects of warming and drought stress on winter wheat biomass



a. 2020-2021 b. 2021-2022

Note: R-g: warming of 1.5°C with sufficient water supply. R-d: warming of 1.5°C with water deficit. N-g: non-warming with sufficient water supply. N-d: non-warming with water deficit. Data was shown with the average value of three replicates. *, **, and *** mean significant at 0.05, 0.01, and 0.001 levels, respectively. The error bars represent the standard errors.

Figure 7 Effects of temperature increase and drought stress on SPAD of winter wheat

In 2021 (Figure 6a), biomass data were available only at harvesting. The results showed that the biomass in the adequate water supply treatment was 8.6% and 23.5% higher than the water deficit treatment under warming and non-warming conditions, respectively. Under sufficient water supply and water deficit conditions, the increasing temperature improved the wheat biomass by 26% and 43.3% compared with the non-warming treatment. In 2022 (Figure 6b), under the same water conditions, the plant biomass of R-g and R-d was 45.7% and 56.4% higher than that of N-g and N-d, respectively. Under the same temperature conditions, the wheat biomass of R-g and N-g was 10.4% and 15.2% higher than that of R-d and N-d, respectively.

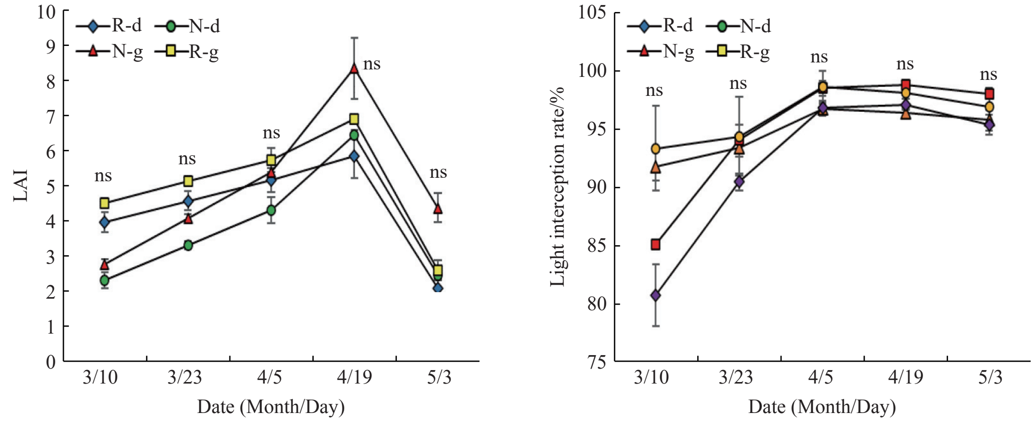
After the wintering stage of winter wheat, the SPAD value in the two-year experiment showed a downward trend (Figure 7). The SPAD value of the flag leaf decreased gradually during the grain-filling stage, and the SPAD value in the temperature-increasing treatment was higher than that in the non-warming treatment. The SPAD value in the warming treatments decreased rapidly at the wheat maturity stage, the value in R-g and R-d was 54.1% and 71.1% lower than that in N-g and N-d, respectively. The SPAD of warming and water deficit treatments decreased faster than that of non-warming and sufficient water supply treatments in the grain filling period, which indicated that temperature increase would advance and shorten the growth period of winter wheat.

4.3 Effects of warming and drought on leaf area index and light interception.

As shown in Figure 8, leaf area index (LAI) and light interception rate increased first and then decreased after the over-wintering stage of winter wheat. Under the same water conditions, the LAI in R-g was 27.6% higher than that in N-g, and the LAI in R-d was 42.2% lower than the value in N-d. Under the same temperature conditions, the LAI of R-g was 55.3% higher than that of R-d, and the LAI of N-g was 44.1% lower than that of N-d. The LAI at the third observation showed different variations between treatments compared with the first two observations (Figure 8a). For the last two data observations, the LAI of R-g was 12.1% and 41.1% lower than that of R-d and N-g, respectively. The LAI of R-d was 5.9% lower than that of N-d, and the LAI of N-g was 29.0% lower than that of N-d. LAI and light interception rate of winter wheat increased first and then decreased after the green stage. N-g showed a greater LAI change trend, while R-d showed a slower LAI change trend. The higher the LAI between different treatments, the higher the light interception rate. (Due to a lack of partial data from the first growing season, only the LAI of the second growing season was provided)

4.4 Effects of warming and drought on the photosynthetic and transpiration rates of winter wheat

In the growing season of 2020-2021 (Figure 9), the Pn of wheat in R-g and N-g was 22.9% and 7.3% higher than the value in R-d and N-d, and the corresponding value of Tr was higher by 39.6% and 7.2%, respectively. In the 2021-2022 season (Figure 10), the observation of photosynthesis and transpiration data under both heating and non-heating treatments was not at the same time (water consumption rate was different between heating and non-heating

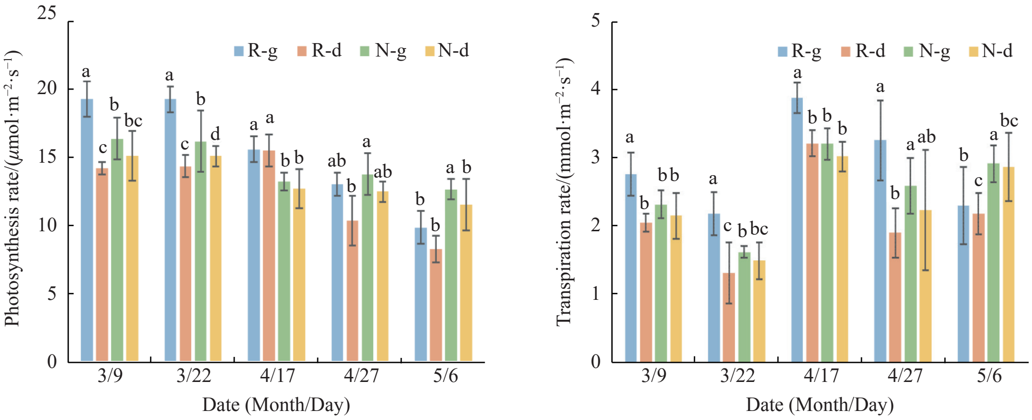


a. 2020-2021 b. 2021-2022

Note: R-g: warming of 1.5°C with sufficient water supply. R-d: warming of 1.5°C with water deficit. N-g: non-warming with sufficient water supply. N-d: non-warming with water deficit. Data are shown with the average value of three replicates. ns means not significant. The error bars represent the standard errors.

Figure 8 Effects of warming and drought stress on LAI and light interception rate of winter wheat

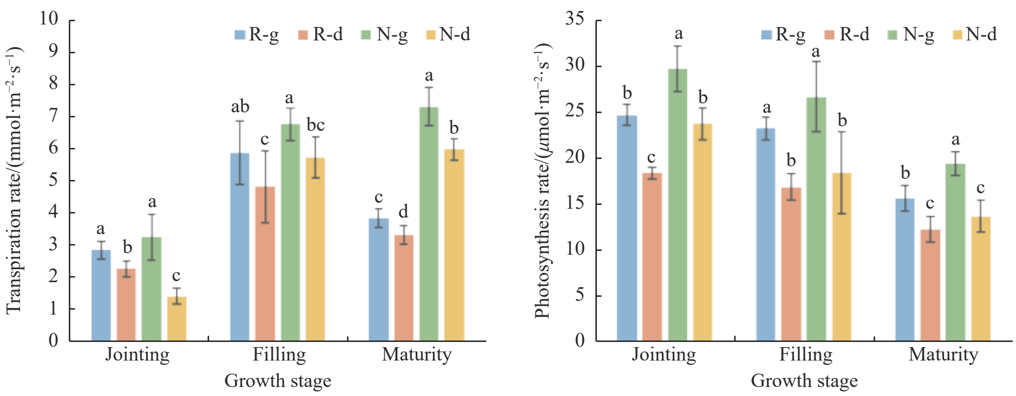
treatments, so irrigation time and observation time were different). Figure 10 shows the differences in photosynthetic and transpiration rates among the four treatments of winter wheat at the jointing, grain filling, and maturity stages. For the net photosynthetic rate (Figure 10a), under the same temperature conditions, the Pn in R-g was 25.6%, 27.3%, and 21.4% higher than the value in R-d, while the Pn in N-g was 20.2%, 31.0%, and 29.3% higher than the value in N-d at the jointing, grain filling, and maturity stages, respectively. Under the same water conditions, the Pn in R-g was 20.4%, 14.8%, and 23.9% lower than the value in N-g, and the Pn in R-d was 29.1%, 9.0%, and 11.5% lower than the value in N-d, respectively. For the transpiration rate (Figure 10b), under the same temperature conditions, the Tr in R-g was 20.2%, 17.8%, and 13.7% higher than the value in R-d, and the Tr in N-g was 54.9%, 11.9%, and 42.5% higher than the value in N-d at the jointing, grain filling, and maturity stages, respectively. Under the same water conditions, the Tr in R-g was 13.9%, 15.3%, and 89.5% lower than the value in N-g, and the Tr in R-d was 0, 18.8%, and 79.8% lower than the value in N-d at the jointing, grain filling, and maturity stages, respectively.



a. Photosynthetic rate at different observation time points b. Transpiration rate at different observation time points

Note: R-g: warming of 1.5°C with sufficient water supply. R-d: warming of 1.5°C with water deficit. N-g: non-warming with sufficient water supply. N-d: non-warming with water deficit. Data was shown with the average value of three replicates. The error bars represent the standard errors. The same as below.

Figure 9 Effects of warming and drought stress on photosynthetic and transpiration rates of winter wheat (2020-2021)



a. Photosynthetic rate at different growth stages b. Transpiration rate at different growth stages

Figure 10 Effects of warming and drought stress on photosynthetic and transpiration rates of winter wheat (2021-2022)

WUE of winter wheat in R-g, R-d, N-g, and N-d, as shown in Figure 11, was 3.72, 3.68, 3.58, and 3.50 μmol/mmol, respectively. The results indicated that moderate warming (increasing 1.5°C-2.0°C in this experiment) increased the WUE of winter wheat, while drought decreased the WUE. Under the same irrigation condition, the WUE of R-g increased by 1.0% compared with N-g, WUE of R-d increased by 4.9% compared with N-d. The WUE of R-g was 1.1% higher than that of R-d under the same temperature, WUE of N-g was 2.2% higher than that of N-d.

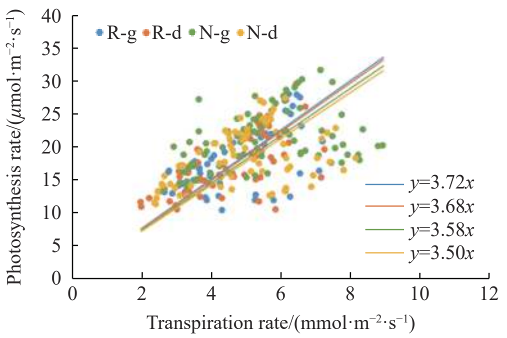


Figure 11 Effects of warming and drought stress on water use efficiency of winter wheat (2021-2022)

4.5 Effects of temperature increase and drought on wheat yield and yield components.

According to the yield data in the 2020-2021 season, Water deficit decreased spike number, the grain number per spike, thousand grain weight and grain yield under increasing temperature and no increasing temperature. Under the condition of full water supply, the spike number, the grain number per spike, thousand-grain weight and grain yield were increased by warming treatment. Under the condition of water deficit, the spike number and grain yield were increased, however the grain number per spike and thousand grain weight were decreased.

According to the yield data in the 2021-2022 season, the warming treatment promoted the grain number per spike of winter wheat and decreased the spike number. The grain number per spike of R-g was 2.5% higher than that of N-g, and the spike number of R-g was lower by 13.9% than N-g. The spike number of R-d was 3.0% lower than that of N-d, and the grain number per panicle of R-d was 10.6% higher than that of N-d. However, the thousand-grain weight and grain yields of R-g were 1.1% and 4.4% lower than the values of N-g, and the thousand-grain weight and grain yield of R-d were 0.8% and 1.3% lower than the values of N-d, respectively. Drought decreased the spike number, grain number per spike, and grain yield while increasing the thousand-grain weight. The spike number, grain number per spike, and grain weight of R-g were 7.3%, 9.2%, and 8.9% higher than R-d, R-g was 3.9% lower than R-d, N-g was 20.9%, 17.8%, and 12.4% higher than N-d, N-g thousand-kernel weight was 5.7% lower than N-d. The spike number, grain number per spike, and grain yield of winter wheat in R-d were decreased by 19.7%, 6.2%, and 12.2% compared with N-g, and the thousand-grain weight of R-d was 5.2% higher than that of N-g.

Combining the data of two winter wheat growing seasons, it was found that under the condition of sufficient water supply, increasing temperature would increase the grain weight of winter wheat. Under the condition of water deficit, the effect of increasing temperature on grain weight of winter wheat was inconsistent.

5 Discussion

Although the heating area is limited in the current experiment, the effective area is enough to show the acceleration of warming on winter wheat phenology. This study showed that increasing temperature in the late overwintering after the winter could resume the growth of winter wheat and shorten the whole growth period (Figures 2 and 4). Previous research confirmed that between 1948 and 2004, the wheat phenological period in China decreased by 6-10 d in winter, mainly due to an increase in daily minimum temperature during the spring[37-40]. This warming reduced the number of days below the wheat suitable temperature for growth and the frequency of cold damage[41,42]. The results of this study showed that the growing season was shortened by about 7 d on average, which was consistent with previous studies[38]. Prasad et al.[33] showed that under temperature increase, wheat plants developed more rapidly, lost more chlorophyll content, and had fewer grains per spike. Du et al.[36] reported that early warming brought forward the phenological stage, and early warming reduced the temperature of each stage before flowering. In addition, the increased temperature was found to accelerate wheat development, thus affecting a briefer duration of a critical period, and decreasing solar radiation capture with adverse consequences for biomass accumulation and grain yield formation[14]. The changes in leaf SPAD significantly affected leaf photosynthesis under temperature increases and drought stress, and there was a significant (p<0.01) positive correlation. This indicated that higher SPAD resulted in higher Pn[43,44]. Thus, the leaf SPAD was significantly reduced at high temperatures during the grain filling and ripening stages, which resulted in a decrease in Pn. In this study, it was found that the SPAD value of wheat leaves under temperature increases increased earlier than that of non-temperature increase treatment during the whole growth period (Figure 7). This is generally due to the effect of heat, which is consistent with the results of Prasad et al.[33] and Du et al.[36]. Heat has a positive effect on growth, but it accelerates development. For example, the SPAD in the warming treatment in the late season decreased rapidly (Figure 7). However, biomass was consistently greater under warming than that under non-warming, suggesting that under warming, higher green leaf area could be acquired in the early season of wheat resulting in more light capture and biomass (Figures 6 and 8).

Porter and Gawith[12] and Wheeler et al.[45] reported that late-maturing genotypes increased yield and transpiration efficiency under water deficit conditions[46,47], and drought stress decreased the thousand-grain weight of winter wheat (Table 1), while Table 2 shows drought stress increased the thousand-grain weight. In addition, increasing temperature and drought stress brought forward the wheat growth and shortened the growth period of winter wheat. There were significant differences in Pn and Tr between the increasing temperature and non-increasing temperature treatments (Figures 9 and 10). Stomatal conductance (Gs) is an important physiological factor regulating plant Pn under water deficit conditions[48,49]. In the present experiment, drought stress significantly reduced Pn and Tr (Figures 9 and 10)[31,32]. Moreover, warming accelerated leaf senescence during the grain-filling stage[50], resulting in yield lose[51]. WUE of the winter wheat increased under moderate warming conditions, while decreased under drought conditions, which was consistent with Dong et al.[21]. The increasing temperature at the flowering stage would affect pollen and thus inhibit fruiting[32]. The increasing temperature before winter would increase the tillering number of winter wheat[52,53]. The current study showed that warming prolonged wheat growth delayed overwintering, and increased stem count and biomass accumulation. At the same time, warming and drought stress reduced the winter wheat yield, which was consistent with Hunt et al.[51] In addition, the wheat yield was reduced under the combined effect of warming and drought stress, which was similar to previous studies[10,20]. Other studies have shown that due to the shortening of flowering initiation time and the reduction of grains per spike, the warming effect for stem elongation was negative[17]. Ye et al.[11] also reported that increasing temperature at the tillering stage increased effective tiller number and wheat yield, which was inconsistent with our results, possibly due to the differences between treatments, experimental design, wheat varieties tested, and the experimental environment. Under the condition of temperature increases and water control in a controlled environment, the high temperature reduces wheat yield due to the reduction of green leaf area, effective tiller number per plant, grain weight, grain number per panicle, and harvest index[33,54,55]. In addition, air warming will cause premature senescence of wheat leaves, which is not conducive to dry matter accumulation and yield formation[14]. The results of this experiment showed that increasing temperature (global warming) will reduce winter wheat yield (Table 2), which was consistent with previous studies[10,20].

Table 1 Effects of warming and drought stress on winter wheat yield and yield components in the 2020-2021 season

Treatment	Spike number/ $\times10^4$ hm^{-2}	Grain number per spike	Thousand kernel weight/g	Grain yield/ kg·hm^{-2}
R-g	525.26±6.44^a	44.95±0.16^a	49.74±0.95^a	9951.13±253.65^a
R-d	502.51±5.82^b	41.12±0.73^b	45.32±0.69^b	9035.14±272.11^c
N-g	512.65±3.77^a	43.51±0.33^a	47.21±1.11^a	9522.92±205.77^b
N-d	492.89±7.21^b	41.36±0.18^b	46.11±0.54^b	8750.34±215.31^b

Note: R-g: warming of 1.5°C with sufficient water supply. R-d: warming of 1.5°C with water deficit. N-g: non-warming with sufficient water supply. N-d: non-warming with water deficit. Data was shown with the average value±standard error of three replicates. Different letters in each column represent significant differences at $p<0.05$. The same as below.

Table 2 Effects of warming and drought stress on winter wheat yield and yield components in the 2021-2022 season

Treatment	Spike number/ $\times10^4$ hm^{-2}	Grain number per spike	Thousand-grain weight/g	Grain yield/ kg·hm^{-2}
R-g	458.23±10.0^b	44.60±1.99^a	51.98±1.14^b	8464.73±313.05^a
R-d	427.21±5.57^d	40.83±1.04^a	54.08±0.74^a	7774.12±292.16^b
N-g	532.60±4.73^a	43.50±2.69^a	51.42±0.34^b	8852.86±53.55^a
N-d	440.55±6.66^c	36.90±2.01^b	54.53±1.24^a	7873.40±351.13^b

6 Conclusions

The present research studied the growth characteristics, photosynthetic rate, and transpiration rate of winter wheat under warming and drought stress to provide a clear understanding of crop productivity under climate warming. The results showed that warming and drought stress could shorten the growth period of winter wheat, and homotropic effects of temperature increase and drought stress on plant height, leaf area, and biomass of winter wheat. In addition, warming and drought stress affected the chlorophyll content and stomatal conductance of winter wheat, which affected wheat photosynthetic capacity and further reduced wheat's productivity. In general, warming and drought stress their interaction can reduce the yield of winter wheat, compared with the non-warming treatment, the spike number and grain yield decreased, the grain number per spike increased, and the water use efficiency increased under the warming treatment. Compared with the sufficient water supply treatment, the water deficit reduced the spike number, grain number per spike, and grain yield of winter wheat. The photosynthetic rate was decreased by the warming and drought stress, which is not conducive to the accumulation of dry matter and the productivity of crops. Therefore, further research should focus on the effects of climate change on crop photosynthesis and its regulatory measures, which would provide basic knowledge for maintaining crop productivity under global climate change.

Acknowledgements

This research was financially supported by the National Natural Science Foundation of China (Grant No. 51879267), the China Agriculture Research System of MOF and MARA (Grant No. CARS-03-19), and the Agricultural Science and Technology Innovation Program (ASTIP).

[References]

[1] Abdelrahman M, Burritt D J, Gupta A, Tsujimoto H, Tran L S P. Heat stress effects on source-sink relationships and metabolome dynamics in wheat. J. Exp. Bot., 2020; 71: 543–554.
[2] Ye Z, Qiu X, Chen J, Cammarano D, Ge Z, Ruane A C, et al. Impacts of 1.5°C and 2.0°C global warming above preindustrial on potential winter wheat production of China. Eur. J. Agron., 2020; 120: 126–149.
[3] Zheng C, Zhang J, Chen J, Chen C, Tian Y, Deng A, et al. Nighttime warming increases winter-sown wheat yield across major Chinese cropping regions. Field Crops Res., 2017; 214: 202–210.
[4] You L, Rosegrant M W, Wood S, Sun D. Impact of growing season temperature on wheat productivity in China. Agric. For. Meteorol., 2009; 149: 1009–1014.
[5] Asseng S, Ewert F, Martre P, Rötter R P, Lobell D B, Cammarano, D, et al. Rising temperatures reduce global wheat production. Nat. Clim. Chang., 2015; 5: 143–147.
[6] Bita C E, Gerats T. Plant tolerance to high temperature in a changing environment: scientific fundamentals and production of heat stress-tolerant crops. Front. Plant Sci., 2013; 4: 273.
[7] Zheng B, Chenu K, Dreccer M F, Chapman S C. Breeding for the future: what are the potential impacts of future frost and heat events on sowing and flowering time requirements for Australian bread wheat (*Triticum aestivum*) varieties? Glob. Chang. Biol., 2012; 18: 2899–2914.
[8] Li Y, Ye W, Wang M, Yan X. Climate change and drought: a risk assessment of crop-yield impacts. Clim. Res., 2009; 39(1): 31–46.
[9] Trnka M, Olesen J E, Kersebaum K C, Skjelvåg A O, Eitzinger J, Seguin B, et al. Agroclimatic conditions in Europe under climate change. Glob. Chang. Biol., 2011; 17(7): 2298–2318.
[10] Fang S, Cammarano D, Zhou G, Tan K, Ren S. Effects of increased day and night temperature with supplemental infrared heating on winter wheat growth in North China. Eur. J. Agron., 2015; 64: 67–77.
[11] Ye J, Gao Z, Wu X H, Lu Z Y, Li C D, Wang X B, et al. Impact of increased temperature on spring wheat yield in northern China. Food Energy Secur., 2021; 10: e283.
[12] Porter J R, Gawith M. Temperatures and the growth and development of wheat: a review. Eur. J. Agron., 1999; 10: 23–36.
[13] Ferris R, Ellis R, Wheeler T, Hadley P. Effect of high temperature stress at anthesis on grain yield and biomass of field-grown crops of wheat. Ann. Bot., 1998; 82: 631–639.
[14] García G A, Dreccer M F, Miralles D J, Serrago R A. High night temperatures during grain number determination reduce wheat and barley grain yield: a field study. Glob. Chang. Biol., 2015; 21: 4153–4164.
[15] Dias A, Lidon F. Evaluation of grain filling rate and duration in bread and durum wheat, under heat stress after anthesis. J. Agron. Crop. Sci., 2009; 195: 137–147.
[16] Farooq M, Bramley H, Palta J A, Siddique, K. H. Heat stress in wheat during reproductive and grain-grain filling phases. Crit. Rev. Plant Sci., 2011; 30(6): 491–507.
[17] Barnabas B, Jager K, Feher A. The effect of drought and heat stress on reproductive processes in cereals. Plant Cell Environ., 2008; 31: 11–38.
[18] Liu L, Hu C, Olesen J E, Ju Z, Yang P, Zhang Y. Warming and nitrogen fertilization effects on winter wheat yields in northern China varied between four years. Field Crops Res., 2013; 151: 56–64.
[19] Zhao C, Piao S, Huang Y, Wang X, Ciais P, Huang M, et al. Field warming

experiments shed light on the wheat yield response to temperature in China. Nat. Commun., 2016; 7: 13530.
[20] He D, Fang S, Liang H, Wang E, Wu D. Contrasting yield responses of winter and spring wheat to temperature rise in China. Environ. Res. Lett., 2020; 15: 124038.
[21] Dong G, Guo J X, Chen J Q, Sun G, Gao S, Hu L J, et al. Effects of spring drought on carbon sequestration, evapotranspiration and water use efficiency in the Songnen meadow stepp.in northeast China. Ecohydrology, 2011; 4(2): 211–224.
[22] Reichstein M, Tenhunen J D, Roupsard O, Ourcival J M, Rambal S. Severe drought effects on ecosystem CO_2 and H_2O fluxes at three Mediterranean evergreen sites: revision of current hypotheses? Glob. Chang. Biol., 2002; 8(10): 999–1017.
[23] Edwards C E, Ewers B E, McClung C R, Lou P, Weinig C. Quantitative variation in water-use efficiency across water regimes and its relationship with circadian, vegetative, reproductive, and leaf gas-exchange traits. Molecular Plant, 2012; 5(3): 653–668.
[24] Deng J M, Wang G X, Morris E C, Wei X P, Li D X, Chen B M, et al. Plant mass: Density relationship along a moisture gradient in North-West China. J. Ecol., 2006; 94(5): 953–958.
[25] Poorter H, Niklas K J, Reich P B, Oleksyn J, Poot P, Mommer L. Biomass allocation to leaves, stems and roots: Meta-analyses of interspecific variation and environmental control. New Phytol., 2012; 193(1): 30–50.
[26] Wu Z T, Dijstra P, Koch G W, Penuelas J, Hungate B A. Responses of terrestrial ecosystems to temperature and precipitation change: A meta-analysis of experimental manipulation. Glob. Chang. Biol., 2011; 17(2): 927–942.
[27] Skirycz A, Inzé D. More from less: plant growth under limited water. Curr. Opin. Biotechnol., 2010; 21(2): 197–203.
[28] Chaves M M, Flexas J, Pinheiro C. Photosynthesis under drought and salt stress: regulation mechanisms from whole plant to cell. Ann. Bot., 2009; 103(4): 551–560.
[29] Sharkey T D. Effects of moderate heat stress on photosynthesis: importance of thylakoid reactions, rubisco deactivation, reactive oxygen species, and thermotolerance provided by isoprene. Plant Cell Environ., 2005; 28(3): 269–277.
[30] Flexas J, Diaz-Espejo A, Berry J A, Cifre J, Galmés J, Kaldenhoff R, et al Analysis of leakage in IRGA's leaf chambers of open gas exchange systems: quantification and its effects in photosynthesis parameterization. J. Exp. Bot., 2007; 58(6): 1533–1543.
[31] Lawler D W, Cornic G. Photosynthetic carbon assimilation and associated metabolism in relation to water deficits in higher plants. Plant Cell Environ., 2002; 25(2): 275–294.
[32] Salvucci M E, Crafts-Brandner S J. Inhibition of photosynthesis by heat stress: the activation state of Rubisco as a limiting factor in photosynthesis. Physiol. Plant., 2004; 120(2): 179–186.
[33] Prasad P V V, Pisipati S R, Ristic Z, Bukovnik U, Fritz A K. Impact of nighttime temperature on physiology and growth of spring wheat. Crop Sci., 2008; 48: 2372–2380.
[34] Bhusal N, Lee M, Han A R, Han A, Kim H S. Responses to drought stress in Prunus sargentii and Larix kaempferi seedlings using morphological and physiological parameters. For. Ecol. Manag., 2020; 465: 11809.
[35] Huang C, Gao Y, Qin A Z, Liu Z G, Zhao B, Ning D F, et al. Effects of waterlogging at different stages and durations on maize growth and grain yields. Agr. Water. Manage., 2022; 261: 107334.
[36] Hu Q, Weiss A, Feng S, Baenziger P S. Earlier winter wheat heading dates and warmer spring in the US Great Plains. Agric. For. Meteorol., 2005; 135(1-4): 284–290.
[37] Piao S, Ciais P, Huang Y, Shen Z, Peng S, Li J, et al. The impacts of climate change on water resources and agriculture in China. Nature., 2010; 467: 43–51.
[38] Qian S A, Fu Y, Pan F F. Climate change tendency and grassland vegetation response during the growth season in Three-River Source Region. Sci. China Earth Sci., 2010; 53(10): 1506–1512.
[39] Qian C, Yan Z W, Fu C B. Climatic changes in the twenty-four solar terms during 1960-2008. China. Sci. Bull., 2012; 57: 276–286.
[40] Dai L Q, Li C Q, Yao S R, Zhang W Z. Variation analysis of freezing injury on winter wheat under climate warming in Hebei Province. Chin. J. Agrometeorol., 2010; 31(3): 467–471.
[41] Ross M S, Ruiz P L, Sah J P, Hanan E J. Chilling damage in a changing climate in coastal landscapes of the subtropical zone: a case study from south Florida. Glob. Chang. Biol., 2009; 15(7): 1817–1832.
[42] Du X, Gao Z, Sun X N, Bian D H, Ren J H, Yan P, et al. Increasing temperature during early spring increases winter wheat grain yield by advancing phenology and mitigating leaf senescence. Sci. Total Environ., 2021; 812: 152557.
[43] Long S P, Osborne C P, Humphries S W. Photosynthesis, rising atmospheric CO_2 concentration and climate change. In: Bremeyer, A., Hall, D. O., Melillo, J. (Eds.), Scope 56: Global Change. Wiley, Chichester, UK. 1997.
[44] Arcus V L, Prentice E J, Hobbs J K, Mulholland A J, Van der Kamp M W, Pudney C R, et al. On the temperature dependence of enzyme catalyzed rates. Biochemistry, 2016; 55: 1681–1688.
[45] Wheeler T R, Craufurd P Q, Ellis R H, Porter J R, Vara Prasad P V. Temperature variability and the yield of annual crops. Agric. Ecosyst. Environ., 2000; 82(1-3): 159–167.
[46] Verma V, Foulkes M J, Worland A J, Sylvester-Bradley R, Caligari P D S, Snape J W. Mapping quantitative trait loci for flag leaf senescence as a yield determinant in winter wheat under optimal and drought-stressed environments. Euphytica., 2004; 135: 255–263.
[47] Haussmann B, Mahalakshmi V, Reddy B, Seetharama N, Hash C, Geiger H. QTL mapping of stay-green in two sorghum recombinant inbred populations. Theor. Appl. Genet., 2002; 106: 133–142.
[48] Medrano H, Escalona J M, Bota J, Gulías J, Flexas J. Regulation of photosynthesis of C3 plants in response to progressive drought: stomatal conductance as a reference parameter. Ann. Bot., 2002; 89: 895–905.
[49] Bhusal N, Bhusal S J, Yoon T M. Impact of drought stress on photosynthetic response, leaf water potential, and stem sap flow in two cultivars of bi-leader apple trees (*Malus* × *domestica* Borkh.). Sci. Hortic., 2019; 246: 535–543.
[50] Liu B, Liu F, Tian L, Cao W, Zhu Y, Asseng S. Post-heading heat stress and yield impact in winter wheat of China. Glob. Chang. Biol., 2014; 20: 372–381.
[51] Hunt J R, Hayman P T, Richards R A, Passioura J B. Opportunities to reduce heat damage in rain-fed wheat crops based on plant breeding and agronomic management. Field Crops Res., 2018; 224: 126–138.
[52] Simmons S R. Growth, development, and physiology. In: Wheat and Wheat Improvement, 13. American Society of Agronomy, Madison. Skirycz, A., Inzé, D., 2010. More from less: plant growth under limited water. Curr. Opin. Biotechnol., 1987; 21(2): 197–203 .
[53] Singh S N. Climate change and crops. Springer-Verlag, Berlin, Heidelberg, Berlin, Germany, 2009.
[54] Gibson L R, Paulsen G M. Yield components of wheat grown under high temperature stress during reproductive growth. Crop Sci., 1999; 39: 1841–1846.
[55] Rahman M A, Chikushi J, Yoshida S, Karim A. Growth and yield components of wheat genotypes exposed to high temperature stress under control environment. Bangladesh J. Agric. Rec., 2009; 34(3): 361–372.