Thermal acclimation of photosynthesis to experimental warming is season-dependent for winter wheat (*Triticum aestivum* L.)

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A B S T R A C T

Temperate plants may show different photosynthetic acclimation capacities, involving varying physiological processes/mechanisms, during different seasons in response to global warming because of seasonal climate variation. Thus, we conducted field warming experiments for winter wheat in its four seasonal periods. These experiments allowed us to examine the thermal acclimation of photosynthesis and the underlying processes/mechanisms (RuBP-carboxylation, RuBP-regeneration, stomatal conductance and the balance between respiration and photosynthesis) to both seasonality and warming effects as well as the interaction between them. We found winter wheat displayed nonlinear acclimation to the seasonal temperature change, and significant acclimation to experimental warming in the four seasons. However, the acclimation capability in response to experimental warming was lower in January than November/April/May. Importantly, the underlying physiological processes/mechanisms to warming effects vary among seasonal periods: RuBP carboxylation contributed to the acclimation of photosynthesis in November and April, while the balance between respiration and photosynthesis caused the major change in January, and lower stomatal conductance played the most important role in May. These results could give insights into the decrease in productivity and increase of biomass accumulation and could help to predict acclimation capability and underlying processes to global warming. In addition, photosynthetic parameters reported here could be used to incorporate seasonal dynamics of thermal acclimation into physiological-process-based ecosystem models.

1. Introduction

The effects of increased temperature on photosynthesis have been intensely discussed in the context of global warming (Medlyn et al., 2002; Campbell et al., 2007; Gunderson et al., 2010; Ow et al., 2010; Crous et al., 2013). A temperature rise of 2–7 °C may exceed the regular temperature fluctuation experienced by plant species, thereby reducing their photosynthetic rate, carbon gain and survival (Sage et al., 2008). Previous studies have illustrated that acclimation ability, defined as the adjustment of photosynthetic temperature response to shifting growth temperatures, could represent the capability of species to cope with global temperature change (Hikosaka et al., 1999; Medlyn et al., 2002; Atkin et al., 2006; Campbell et al., 2007; Gunderson et al., 2010; Ow et al., 2008, 2010; Gorsuch et al., 2010). Recently, field experimental warming has been employed to develop temperature response curves of photosynthesis and its featured parameters, which provide critical insight into the acclimation potentials of different species in response to global warming (Gunderson et al., 2010; Crous et al., 2013; Drake et al., 2015; Sendall et al., 2015).

Species rarely grow in a constant environment; thus, they must be

equipped to deal with environmental variability such as growth temperature fluctuation (Janzen, 1967). Theoretical studies have proposed that responses to within- and among-year fluctuation in ambient environment can be highly informative both in predicting the potential consequences of global climate change and in elucidating the processes of acclimation/plasticity and genetic evolution (Bradshaw and Holzapfel, 2006; Skelly et al., 2007; Diffenbaugh and Field, 2013; Botero et al., 2015). Temperate species are ideal organisms to illustrate the connections of acclimation to seasonal temperature change and global warming, because they experience seasonal variations in growth temperature, in excess of the predicted 2–7 °C due to global warming (IPCC, 2013). Thus, temperate species have been proposed to have a higher acclimation potential than boreal or tropical species, which grow under relatively constant temperature regimes (Dillaway and Kruger, 2010; Sendall et al., 2015). In addition, species located in the cooler portion of their temperature range may have a higher acclimation capability to global warming than those already growing in the warmer/upper limit of their range (Ghannoum and Way, 2011; Gunderson et al., 2010).

In the current study, we hypothesize that the warming acclimation capabilities of temperate species vary seasonally, with higher capacity in winter/spring/fall and the lower in summer. Global warming causes increased growing temperatures during the fall, winter and spring, but these higher temperatures may remain within the typical life-history temperature variation of a temperate species. If temperate species already have a mechanism to acclimate to seasonal or life-history temperature variation, they can likely show greater acclimation capability for fall/winter/spring. While species may show less acclimation ability to warming during the summer, because the new temperatures could exceed its regular growth temperature limit. Previous studies focused on measuring thermal acclimation of plants to warming at a single time (Ow et al., 2008; Gorsuch et al., 2010; Drake et al., 2015; Sendall et al., 2015; Li et al., 2016; Reich et al., 2016). We believe examining acclimation of photosynthesis and respiration toward experimental warming through a plant's entire life history will comprehensively illustrate species' response to warming, including the identification of vulnerable periods, the evaluation of underlying processes and the explanation of integrative growth and production.

Although researchers have started to investigate the temperature responses of photosynthesis (A_n_T) to examine the acclimation capabilities in field warming experiments, the underlying processes and mechanisms are not well illustrated especially for different seasons. Increasing energy of activation for Rubisco carboxylation (Gutteridge and Gatenby, 1995; Yamori et al., 2005; Weston et al., 2007) and RuBP regeneration (Armond et al., 1978; Badger et al., 1982; Yamasaki et al., 2002), decreasing the biochemical balance/ratio between respiration and photosynthesis (Sage and Kubien, 2007; Lin et al., 2012) and increasing stomatal regulation of CO_2 diffusion (Kirschbaum and Farquhar, 1984; Hikosaka et al., 2006; Warren and Dreyer, 2006) have been found to contribute to an upward shift of optimal temperature in the A_n_T relationship, which is indispensable in understanding acclimation ability.

In addition, we speculate that the underlying processes and mechanisms of acclimation to warming differ by season. There are two potential effects which may result in such differences among seasons. First, underlying processes may be subject to different temperature sensitivities, which may cause them to play different roles in seasonal acclimation to warming. For example, RuBP regeneration is more likely to limit photosynthesis at the lower end and higher end of temperature (Hikosaka et al., 2006); suggesting that this process will be more important in winter and summer. Second, in addition to temperature variability, seasons display differences in other environmental factors, such as relative humidity and light intensity. These factors may cause confounding effects on thermal acclimation processes despite an equal temperature increase (Ghannoum et al., 2010; Albert et al., 2011), resulting in different acclimation mechanisms responsible for warming.

For example, high relative humidity in summer may result in the high acclimation capacity of stomatal processes. Although there are pioneer studies that have begun to examine the acclimation of photosynthesis to global warming during different seasons (Campbell et al., 2007; Gunderson et al., 2010), to our knowledge, the effects of the interaction between season and warming on acclimation processes have not been thoroughly examined. We believe that connections may exist between the temperature responses under seasonal acclimation and those under global warming. In a practical view, it is the temperature sensitivity parameters of the underlying processes and mechanisms, not the A_n_T relationships themselves, that are used to model the acclimation dynamics in productivity, physiology and biogeochemical models (Medlyn et al., 2002; Hanson et al., 2005; Kattge and Knorr, 2007; Zhu et al., 2010; Smith and Dukes, 2013; Zhou et al., 2015; Yamori et al., 2016). Thus, a thorough investigation of the thermal acclimation of these underlying processes and mechanisms which respond to seasonal and experimental warming is crucial for the accurate modeling of acclimation to global warming in future biogeochemical models.

Increasing global temperatures may impact the role of agricultural systems on carbon balance as a major ecosystem, as well as food productivity for humans. Crop productivity depends heavily on photosynthesis and respiration rates under ambient growth temperatures. Winter wheat (*Triticum aestivum* L.), one of the most important temperate crops, has a growth period covering late fall, winter, spring and early summer, which encompasses great variation in temperature. Recent studies have proposed that warming will decrease the productivity of winter wheat (Asseng et al., 2015; Tack et al., 2015; Zhao et al., 2016), as well as other crops (Ruiz-Vera et al., 2015), but will increase biomass (Hou et al., 2012). A possible explanation could be that warming increases vegetative growth without increasing productive growth. With such economic value and life history traits, winter wheat is an ideal organism to study photosynthetic acclimation to warming across multiple seasons. In the current study, we conducted a field warming experiment using winter wheat and spanning its life-history to test the following hypotheses related to thermal acclimation to seasonality and warming effect:

(1) Photosynthesis of winter wheat acclimates to both the seasonal temperature changes and warming effects within its established life history temperature range (HY1).
(2) Winter wheat may exhibit different acclimation capabilities (high in late fall, winter and spring, but low in early summer) and varying acclimation mechanisms and processes in response to warming during different seasons (HY2).
(3) The differences of photosynthetic acclimation to warming in different seasons will explain the observed response of increased biomass accumulation and decreased productivity under warming (HY3).
(4) Seasonal-temperature-induced acclimation and experimental-warming-induced acclimation may share similar underlying processes and mechanisms (HY4).

2. Materials and methods

2.1. Site description and experimental design

Our experiment was conducted at the Yucheng Comprehensive Experiment Station of Chinese Academy of Sciences (36°51′N, 116°34′E; an elevation of 20 m), from November 2011 to May 2012. The mean annual precipitation at the experimental site is 567 mm, of which 70% occurs between June and September, and the annual mean temperature is 13.4 °C. The soil in the study site is classified as a Calcaric fluvisol with a surface composition of 12% sand, 66% silt and 22% clay (Hou et al., 2012). Winter wheat (*Triticum aestivum* L.) and summer corn (*Zea mays* L.) are double cropped in the study site. Winter wheat was irrigated using groundwater following the local agriculture standard

(around 300 m^3 per hectare in total with precipitation) with each plot of the study site receiving the same amount of water.

Eight 2 × 4 m blocks, separated by 1–5 m within a big open field, were used for our study: each block was divided into two 2 × 2 m plots with one randomly assigned the control treatment, and the other the warming treatment. Approximately 1000 winter wheat were planted in each plot following the local agriculture standard. In order to analyze warming effects together with natural temperature changes experienced by plants (diurnal and seasonal variation), infrared radiators were used for the warming treatment in the field experimental site. Infrared radiators, 165 × 1.5 cm (Kalglo Electronics Inc, Bethlehem, Pennsylvania), were suspended 3 m above the ground between two steel plates (5 cm-wide, 3 m-high), at the edge of the warming plots to increase the ambient temperature without generating visible light (Hou et al., 2012). "Dummy" heaters of the same shape and size were suspended in the same fashion in corresponding control plots to account for the impacts of the heater itself on microclimate, such as light, wind, and precipitation. Heaters were checked regularly and plots in which heaters experienced technical problems were removed from data collection. Consequently, the data presented represents the 5 continuously-heated blocks. In order to control for spatial variation in heating within the plot, we sampled plants in the middle of each plot directly underneath the radiator for both the control and warming experiments to minimize the spatial variation of the warming effect. For different seasons, we didn't measure exactly the same plants, because of destructive sampling. Instead, we chose identical individuals within 10 cm of one another and of the same height, leaf size and leaf color. Photosynthetic active radiation (PAR) and relative humidity (RH) were measured once per minute in the plots with automatic data-logging systems, and averaged for each hour. Canopy temperatures of warming and control plots were measured by a thermal imager; correction for heat radiation and sky radiation reflected off the crop canopy were made as outlined by Hou et al. (2012). For November and January, ground surface temperatures approximated canopy temperatures due to low vegetation coverage and height.

Measurements of the winter wheat (sowed 7 October 2011) were made in five control and warming plots during the four major seasonal periods. Each period we visited these blocks to take samples and perform measurements, and recorded the block numbers for all the measurements. These periods correspond to (1) seedling establishment stage in late fall (November), (2) winter dormancy and tillering stage (January), (3) seedling elongation stage in spring (April), and (4) flowering and milk development stage in early summer (May). These periods also represent the temperature variation experienced throughout the whole life history of winter wheat; January is the lowest, while mid-May is the highest temperature for photosynthetic activity. During measurements, the soils were not frozen at daytime, and the winter wheat performed photosynthesis. Winter irrigation allowed the plants to avoid water stress due to physiological drought. For each season, we chose the leaves that developed in the focal period and fully expanded right before the measurements to reduce the leaf age effect. The leaves we measured were the third leaf for November, the fourth leaf for January, the sixth leaf for April and the last leaf (the flag leaf) for May.
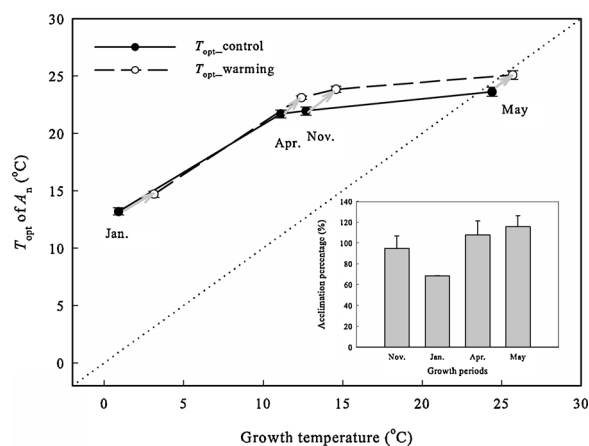
2.2. Gas exchange measurements

The gas exchange measurements were conducted 19–24 November 2011, 10–14 January 2012, 1–5 April 2012 and 12–18 May 2012 (n ≥ 4, except for control plot in January, n = 2). The low number of replicates in January resulted from low photosynthetic rates which impacted detectability. Leaf gas exchanges were measured using a standard 2 × 3 cm^2 leaf chamber with a red/blue LED light source of LI-6400 (Li-Cor Inc., Lincoln, NE, USA). In order to obtain temperature response curves of net photosynthesis (A_n_T curve), the original temperature control system was modified to enhance the temperature

Table 1
Mean values of climate factors and warming effects when the measurements were conducted for the four experimental periods.

	Mean midday temperature (°C)	Warming effects in canopy temperature (°C)	Maximum temperature (°C)	Mean daily PAR(mol/m^2)	RH(%)
November	12.7(0.7)	1.9(0.3)	20.8	13.28(1.04)	64.9(3.4)
January	0.9(0.3)	2.2(0.1)	7.7	9.86(0.54)	58.7(3.3)
April	11.1(1.0)	1.3(0.1)	24.4	24.09(1.51)	42.8(3.7)
May	24.4(0.6)	1.3(0.2)	30.7	33.69(1.93)	60.1(3.0)

Mean midday temperature: mean temperature from 9:00–15:00 in control plots; Warming effects in canopy temperature: the increase of canopy temperature in warming plots compared to their corresponding control plots in the same block in different periods; Maximum temperature: the maximal temperature occurring during the month; Mean daily PAR: mean of the total daily photosynthetic active radiation. All data were shown as mean (SE).

Fig. 1. The growth temperature at four seasonal periods and corresponding optimal temperature (T_{opt}) for net assimilation rate (A_n) for control (solid black line) and warming experimental (dashed line) fields. The dotted line shows the 1:1 line. Grey arrows connect the control data point with its corresponding warming data point. The inset graph shows the acclimation percentage which is the percentage change of T_{opt} compared with the warming intensity for each seasonal period (the difference of T_{opt} between warming and control plots/ experimental warming effect × 100%), error bars represent standard error.
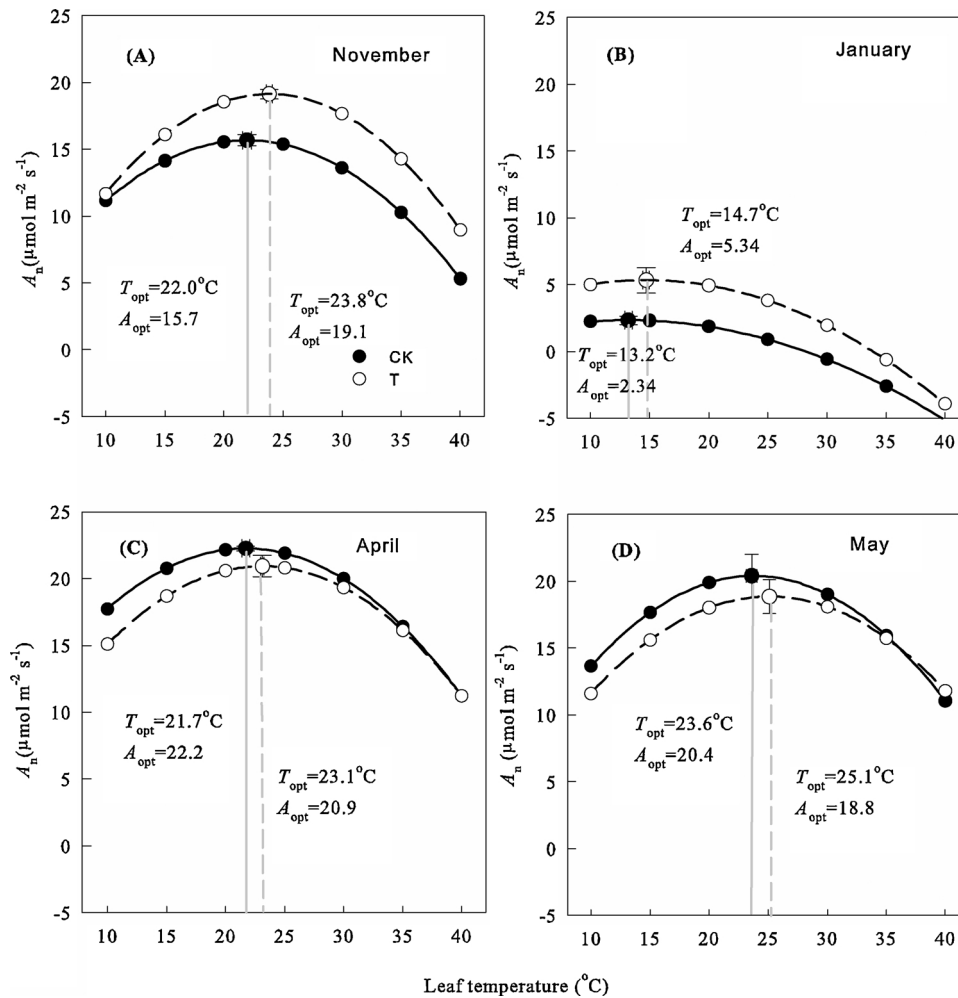
control range from ± 6 °C to 0–40 °C as detailed in Zhou et al. (2015).

A_n_T curves were obtained by measuring leaf photosynthesis from 10 °C to 40 °C at 5 °C increments. Leaves were equilibrated for 15 to 30 min for assimilation reaching steady states under a CO_2 concentration of 400 ppm and a light intensity of 1500 μmol m^{-2} s^{-1} for each temperature. Vapor pressure deficit (VPD) and stomatal conductance (g_s) were recorded simultaneously. Intercellular CO_2 response curves of photosynthesis (A_C_i curves) were measured by controlling the ambient CO_2 concentration gradients at 200, 100, 75, 50, 100, 200, 400, 600, 800, 1000, 1200, 1400 ppm under 1500 μmol m^{-2} s^{-1} for each of the seven temperatures (5 °C increment from 10 °C to 40 °C). Following the A_n_T curve and A_C_i curves, we measured the respiration response curves to temperature (R_{dark}_T curves) at CO_2 of 400 ppm by turning off the LED light source and covering the chamber with a piece of black cloth for 30 min.

We measured A_n_T, R_{dark}_T and A_C_i curves for the temperature gradients discussed above for each replicate. In total, we obtained 34 A_n_T curves, 34 R_{dark}_T curves and 226 A_C_i curves.

2.3. Temperature response curves of photosynthesis

A_n_T curves were fitted with a simple parabola (Säll and Pettersson, 1994; Battaglia et al., 1996; Luo, 2007),

Fig. 2. Temperature response of area-based net assimilation (A_n) of winter wheat in warming and control experiments at four seasonal periods. Mean curves were obtained by simulating with mean values of parameters of all the leaves in Eq. (11), $A(T) = A_{opt} - b(T - T_{opt})^2$. Error bars indicate standard error for mean values of T_{opt} and A_{opt}. The CO_2 concentration was 400 ppm, and the light intensity was 1500 μmol m^{-2} s^{-1}. CK represents the control experiment, and T represents the warming experiment. Vertical lines indicate the mean of T_{opt} for control experiments (solid grey lines) and warming experiments (dashed grey lines).

$$A(T) = A_{opt} - b(T - T_{opt})^2 \qquad (1)$$

in which $A(T)$ is the net assimilation rate at each temperature, A_{opt} represents the net assimilation rate at optimal temperature, b is the spread of the parabola, where the lower the b, the broader the spread (Gunderson et al., 2010), and T_{opt} represents the optimal temperature.

Because the warming effects may differ among the four seasons and among different studies, in order to make our acclimation capability comparable among periods and with other studies, we calculated the acclimation percentage index, which equals the difference of T_{opt} between warming and control plot over experimental warming effect × 100%.

2.4. Underlying processes and mechanisms of photosynthesis and their temperature responses

The framework of the Farquhar photosynthesis model (FvCB model) (Farquhar et al., 1980) provides a useful way to analyze these acclimation processes and mechanisms (Zhou et al., 2015). The photosynthesis is determined by two biochemical sub-processes of biochemistry: (1) the RuBP carboxylation process (also called Rubisco carboxylation), which is the process that CO_2 is fixed with RuBP to produce 3PGA by the enzyme Rubisco, and (2) the RuBP regeneration process, through which sugar is created from 3PGA and RuBP is regenerated using ATP and NADPH from photon/electron transport
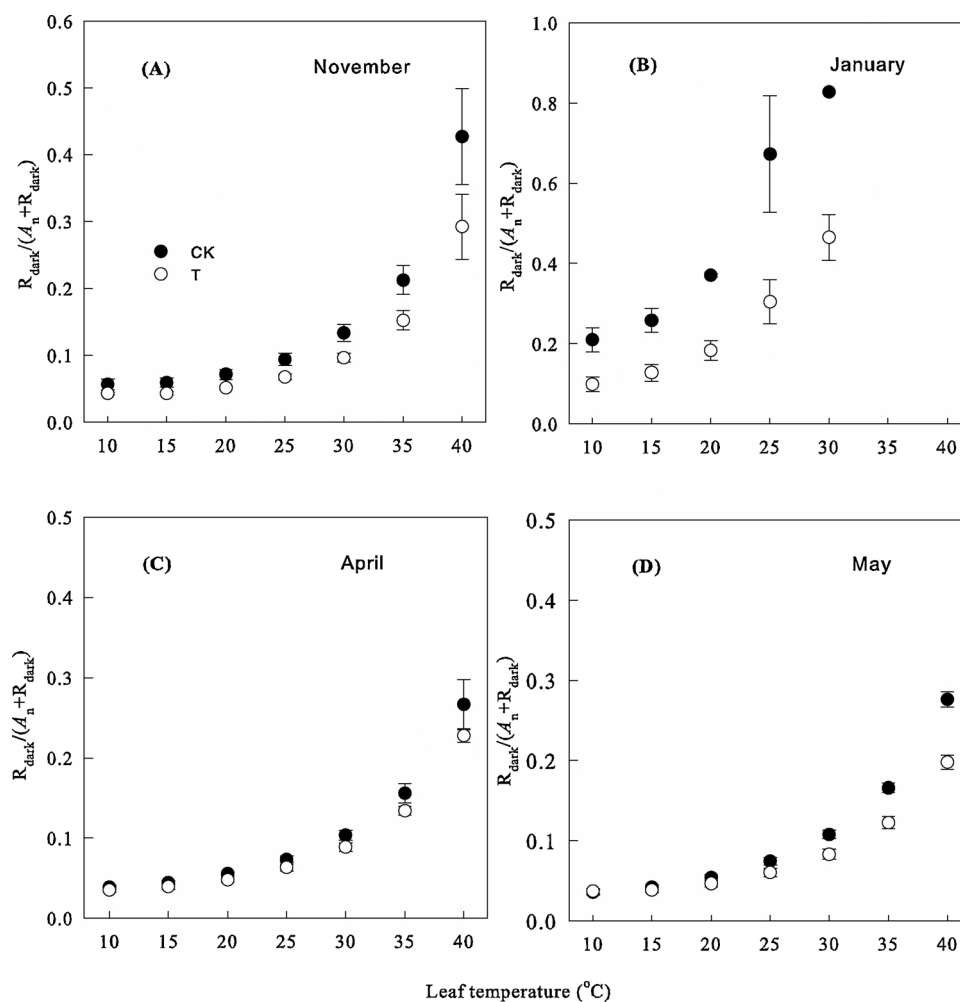
chain. The RuBP carboxylation process and the RuBP regeneration process can be inferred by the temperature response of the maximum velocity of Rubisco carboxylation (V_{cmax}) and the maximum rate of electron transport (J_{max}) respectively. Furthermore, the allocation of nitrogen between RuBP carboxylation and RuBP regeneration processes may affect A_n_T, which can be tested by J_{max}/V_{cmax} (Kirschbaum and Farquhar, 1984; Hikosaka, 1997; Onoda et al., 2005). Finally, the balance between photosynthesis and dark respiration (R_{dark}) is indicated by R_{dark}/A_n (Way and Sage, 2008).

V_{cmax} and J_{max} at each temperature were obtained by fitting each A_C_i curve using the Farquhar photosynthesis model (Sharkey et al., 2007) (examples of A_C_i curve fitting in Appendix A in Supplementary material). The temperature responses of V_{cmax} and R_{dark} were fitted by an Arrhenius exponential equation in Sigmaplot v.11.0 (Systat software, Chicago, IL, USA):

$$(R_{dark}, V_{cmax}) = ref(25)e^{\left(\frac{\Delta H_a(T_k - 298)}{RT_k}\right)} \qquad (2)$$

where $ref(25)$ is the value of V_{cmax} or R_{dark} at 25 °C, ΔH_a is the enthalpy of activation, which describe the exponential increase of enzyme activity with increasing temperature (Crous et al., 2013), T_k is the absolute leaf temperature in Kelvin and R is the universal molar gas constant, 0.008314 kJ K^{-1} mol^{-1}. A bell-shaped model was used to fit the temperature response of J_{max} (Harley et al., 1992):

Fig. 3. Mean ratios of leaf respiration to the total of respiration and net assimilation ($R_{dark}/(A_n + R_{dark})$) of winter wheat at four seasonal periods at the ambient atmospheric CO_2 level of 380 ppm and light intensity of 1500 μmol m^{-2} s^{-1} for A_n at each temperature gradient (Mean ± SE). CK represents control, and T represents warming experiment.

$$J_{max} = \frac{e^{(c-\Delta H_a/RT_k)}}{1 + e^{[(\Delta ST_k - \Delta H_d)/RT_k]}} \qquad (3)$$

where ΔH_a is the enthalpy of activity, similar in Eq. (2), ΔH_d is a term of deactivation, ΔS is a term of entropy and c is a scaling constant. ΔH_d and ΔS together depict the decrease of the electron transport activity when the temperature is above optimal (Crous et al., 2013). The parameter ΔH_d was assumed to be 200 kJ mol^{-1} for J_{max}, in order to avoid over-parameterization (Kattge and Knorr, 2007). Eq. (4) depicts the calculation of optimal temperatures of J_{max} from the above temperature response parameters:

$$T_{opt} = \frac{\Delta H_d}{\Delta S - R \quad \ln[\Delta H_a/(\Delta H_d - \Delta H_a)]} \qquad (4)$$

The photosynthetic and temperature sensitivity parameters calculated as above, were used in the FvCB models to calculate the RuBP carboxylation limited assimilation (A_c) and RuBP regeneration limited assimilation rate (A_j) (Zhou et al., 2015). The net photosynthetic assimilation rate (A_n) is the minimum of A_c and A_j. By this calculation, we can determine which process limits the photosynthesis under specific conditions.

2.5. Statistical analyses

Three-way mixed ANOVA, with warming and season as fixed factors and block as a random factor, were conducted with R 3.4.1, using package "lme4" (Bates et al., 2015), to examine the differences of stomatal conductance, kinetic parameters for photosynthetic parameters (c_J_{max}, ΔH_a, R_{dark}(25) V_{cmax}(25) for V_{cmax}, J_{max} and R_{dark}), photosynthesis (A_{opt} and T_{opt} for A_n, A_c and A_j), $R_{dark}/(A_n + R_{dark})$ and J_{max}/V_{cmax} between control and warming experiments and among different seasons (Tables S1–S4). The interaction terms of warming and season in the statistical analysis will show whether the acclimation to warming is season-dependent. Pairwise tests with Posthoc correction of turkey method were conducted to find whether there were significant differences between warming and control experiments in each season, and whether there were significant differences among seasons. All figures were created using Sigmaplot v.11.0.

3. Results

3.1. Warming effect and seasonal climate variation

The seasonal climatic variation in the control plots, and the increase in canopy temperature in the warming plots compared to control plots (warming effects) are shown in Table 1. November and April had similar average temperatures, which were approximately 11 °C higher than that of January, and 12 °C lower than that of May. The warming effects differed slightly among the four seasons; highest in January and lowest in April and May, with an average warming effect of 1.7 °C. In addition to temperature, other climatic factors differed among the four periods. April showed a lower RH than the other three seasons which

Table 2
Temperature dependence parameters of photosynthesis and respiration parameters of winter wheat in warming and control experiments at four seasonal periods.

parameter	November		January	
	Control	Warming	Control	Warming
ΔH_{av} (kJ mol^{-1})	61.2(1.9)^{ab}	69.1(0.4)*^{B}	36.3(2.4)^{c}	32.3(1.5)^{C}
V_{cmax}(25)	85.3(1.7)^{b}	99.5(2.6)^{A}	26.3(1.5)^{c}	39.2(3.6)^{B}
ΔH_{aj} (kJ mol^{-1})	29.8(2.6)^{ab}	37.4(1.3)^{A}	21.5(0.2)^{b}	21.3(1.8)^{B}
c_J_{max}	17.2(1.0)^{ab}	20.2(0.5)^{A}	12.9(0.1)^{b}	13.2(0.8)^{B}
T_{opt} of J_{max} (°C)	32.4(0.4)^{a}	33.5(0.2)^{A}	22.5(0.6)^{b}	21.7(1.5)^{B}
ΔH_{ar} (kJ mol^{-1})	42.2(1.3)^{a}	45.9(1.4)^{A}	42.8(7.8)^{a}	49.0(4.0)^{A}
R_{dark}(25)	2.64(0.3)^{a}	2.29(0.1)^{A}	2.44(0.4)^{a}	2.32(0.1)^{A}
parameter	April		May	
	Control	Warming	Control	Warming
ΔH_{av} (kJ mol^{-1})	56.5(1.4)^{b}	66.6(0.4)*^{B}	62.5(1.4)^{a}	75.0(1.7)*^{A}
V_{cmax}(25)	117(2.6)^{a}	104(5.4)^{A}	93.7(3.7)^{b}	93.8(5.9)^{A}
ΔH_{aj} (kJ mol^{-1})	26.4(1.5)^{ab}	32.6(1.0)^{A}	32.8(2.8)^{a}	37.7(1.1)^{A}
c_J_{max}	15.8(0.8)^{ab}	18.4(0.3)^{A}	18.3(1.2)^{a}	20.2(0.4)^{A}
T_{opt} of J_{max} (°C)	31.9(0.3)^{a}	32.8(0.1)^{A}	32.8(0.4)^{a}	34.3(1.1)^{A}
ΔH_{ar} (kJ mol^{-1})	42.3(1.5)^{a}	44.2(1.9)^{A}	52.3(2.3)^{a}	46.5(2.1)^{A}
R_{dark}(25)	2.89(0.2)^{a}	2.25(0.2)^{A}	2.53(0.2)^{a}	1.96(0.1)^{A}

ΔH_{av}, energy of activation of maximal carboxylation rate (V_{cmax}); V_{cmax}(25), V_{cmax} at 25 °C; ΔH_{aj}, energy of activation of maximum rate of electron transport (J_{max}); c_J_{max}, a scaling constant of J_{max}; T_{opt}, optimum temperature; ΔH_{ar}, energy of activation of mitochondrial respiration rate in the dark (R_d); R_d(25), R_d at 25 °C. Data represented as mean (SE). ANOVA test shown in Table S4 and multiple comparisons performed using Turkey method: abc indicates significant differences among four seasonal periods in control plots ($p < 0.05$); ABC indicates significant differences among four seasonal periods in warming plots ($p < 0.05$); * indicates significant differences between control and warming in the same seasonal period ($p < 0.05$). Notations of abc and ABC follows the numerical value from large to small. Control represents control experiment, and Warming represents warming experiment.

had similar RH. PAR varied for each season, listed in decreasing order: May, April, November and January.

3.2. Effects of seasonality and warming on temperature response of photosynthesis

The A_n_T curve changed significantly among different seasonal periods ($p < 0.001$ for both T_{opt} and A_{opt}, Figs. 1 , S1, Tables S1, S2). T_{opt} of A_n_T were similar in November and April, when the growth temperatures were similar, while T_{opt} in January was significantly lower and T_{opt} in May was significantly higher. The 11 °C difference in growth temperature between November/April and January resulted in an 8.7 °C higher T_{opt} in A_n_T in November/April; however, the 12 °C difference in growth temperature between May and November/April only resulted in a 1.9 °C higher T_{opt} in A_n_T in May (Fig. 1, Tables 1, S2).

Warming significantly increased the T_{opt} of A_n_T (Figs. 1, S1, Tables S1, S2). The increase of T_{opt} of A_n_T was 1.8 °C ($p = 0.0008$), 1.5 °C ($p = 0.016$), 1.4 °C ($p = 0.0042$), and 1.5 °C ($p = 0.0009$) respectively for November, January, April and May. The acclimation percentage also differed among the four seasons (Fig. 1): the acclimation percentages were lower in January (68.1%) compared to November (94.7%, $p = 0.343$), April (107.7%, $p = 0.016$) and May (115.4%, $p = 0.007$). For the changes in A_{opt}, warming increased A_{opt} in November and January and decreased, but not significantly, A_{opt} in April and May, (Table S2, Fig. 2).

In order to see whether the effects of experimental warming on T_{opt} match its response to seasonal temperature change, we drew a line to connect the control data point with its corresponding warming data point (grey arrows in Fig. 1). If the slope of the connection follows the black control acclimation line, it suggests that the two effects match each other. We compared acclimation to seasonality and experimental warming. In January, the acclimation response to experimental warming follows the seasonal acclimation line (January grey arrow follows the solid black line in Fig. 1); however, in November, April and May, the acclimation process to experimental warming diverges from the seasonal acclimation line (grey arrows and solid black line diverge in Fig. 1). Because we are interested in how well the plant could acclimate to its temperature range/change (i.e. how winter wheat responds physiologically to different growth temperatures in its life history), here we ordered the seasonal periods according to their growth temperature, as opposed to chronologically.

3.3. Effects of seasonality and warming on the underlying processes and mechanisms: balance between photosynthesis and respiration, biochemical reactions and stomatal conductance

We used the $R_{dark}/(A_n + R_{dark})$ ratio to represent the balance between photosynthesis and dark respiration, which yielded values between 0 and 1. The ratio represents the proportion of photosynthesis assimilation used for respiration: 0 indicates no respiration, and 1 indicates all the photosynthetic assimilation is used for respiration. $R_{dark}/(A_n + R_{dark})$ did not show significant differences among November, April and May; however, the $R_{dark}/(A_n + R_{dark})$ ratios were significantly higher in January (all $p < 0.025$), when the temperature was under 30 °C (Fig. 3). $R_{dark}/(A_n + R_{dark})$ did not significantly change between warming and control in November, April and May. In January, under warming, $R_{dark}/(A_n + R_{dark})$ significantly decreased. The effect of warming on $R_{dark}/(A_n + R_{dark})$ is dependent on seasonality (significant interaction term in Table S3).

The temperature sensitivity of RuBP carboxylation was significantly different among seasons and between control and warming (Tables 2 , S3; Figs. S1, S2). The highest activation energy of V_{cmax} (ΔH_{av}) was observed in May and the lowest in January, while the difference in ΔH_{av} between November and April was not significant. In addition, for V_{cmax} at 25 °C (V_{cmax}(25)), the minimum seasonal value, occurring in January, was significantly lower than those of November, April and May, where no significant difference was found. Warming significantly increased ΔH_{av} by 7.9 kJ mol^{-1}, 10.1 kJ mol^{-1}, and 12.5 kJ mol^{-1}, in November, April and May, respectively, but did not affect V_{cmax}(25).

The temperature sensitivity of RuBP regeneration was significantly different among seasons; however, RuBP regeneration did not differ between warming and control (although Table S4 indicates potential significant change, the pairwise test did not detect significant differences shown in Table 2). We found that the maximum activation energy of J_{max} (ΔH_{aj}) in May and the minimum in January. T_{opt} of J_{max}, in January was significantly lower than those of November, April and May, where no significant difference was observed among these three months.

Seasonality and warming showed no effect on the J_{max}/V_{cmax} ratio during the whole experimental period (Fig. 4), as no significant change of the regression line occurred among the four seasonal periods or between control and warming.

The limitation steps of photosynthetic assimilation showed differences among the four seasons (Fig. 5). In November, April and May, assimilation was limited by A_c, while in January assimilation was mostly limited by A_c at lower leaf temperatures, while at higher temperatures (above 35 °C) this was limited by A_j. Limitation steps of assimilation were the same in both warming and control experiments (Figs. 5, S3).

Stomatal conductance (g_s) differed significantly among the four seasons; experimental warming did not significantly change the temperature sensitivity of stomatal conductance in the four seasons (Table S5). T_{opt} of g_s were similar between November and April, while the T_{opt} of g_s was lowest in January and highest in May (Fig. 6). Values of g_{sopt} were similar among November, April and May, while the g_{sopt} of January was significantly lower than those of the other seasons. In addition, the T_{opt} of stomatal conductance in warming experiments and control experiments did not show significant differences in the four
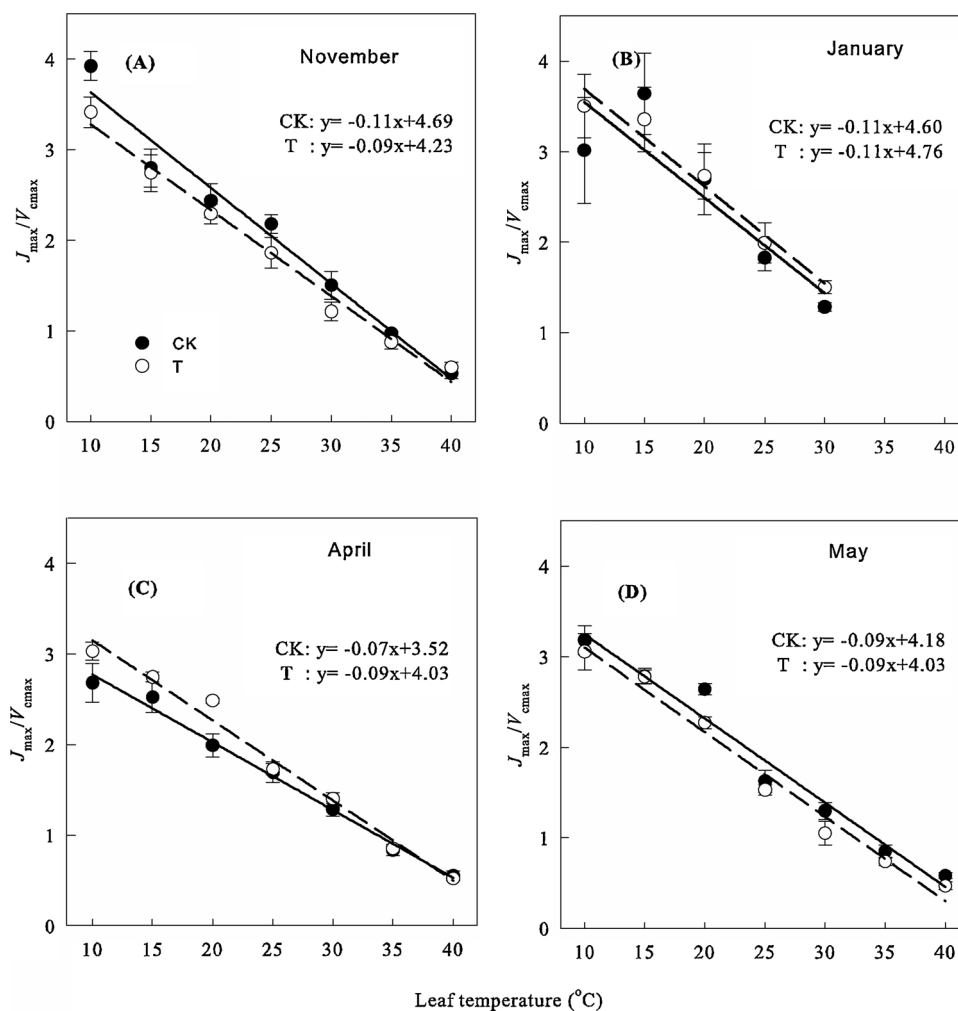
Fig. 4. Temperature responses of the ratio between Rubisco carboxylation and the maximum rate of electron transport (J_{max}/V_{cmax}) of winter wheat in warming and control experiments at four seasonal periods. Curves were fitted with mean values. Error bars indicate standard error of J_{max}/V_{cmax} at each temperature. CK represents control experiment, and T represents warming experiment.

seasons. However, warming marginally decreased the g_{sopt} in May ($p = 0.055$), while it did not significantly affect those of November, January and April.
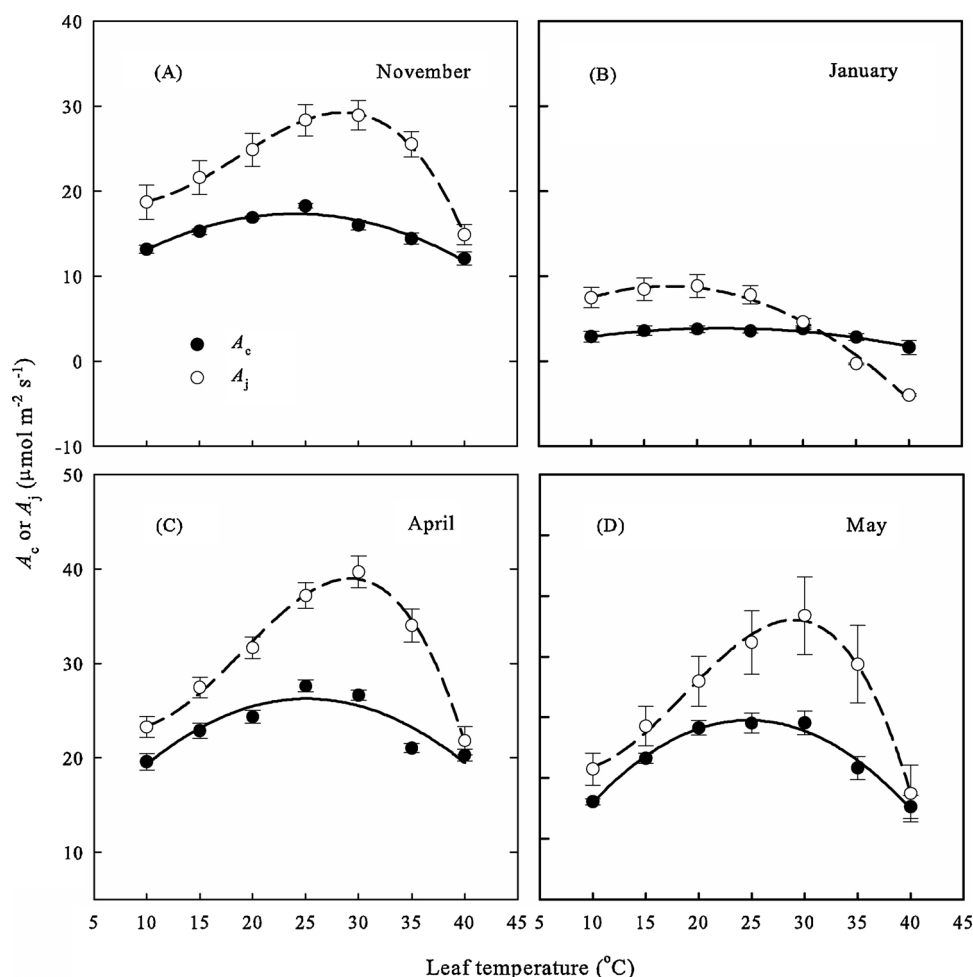
4. Discussion

4.1. Photosynthesis showed nonlinear acclimation to seasonal temperature change

The acclimation of winter wheat to the seasonal temperature change occurred, yielding nonlinear relationships (HY1, Fig. 1). Comparing the T_{opt} with the growth temperatures, data collected in May showed consistency between growth temperature and T_{opt}; T_{opt} of January, November and April exceeded the corresponding growth temperatures, which resulted in nonlinear acclimation. The phenomenon, T_{opt} exceeding the growth temperature, did not cause a dramatic decrease of A_n; still, A_n at growth temperature remained at 90% of the A_{opt}, shown by the flat shape of A_n-T curve (small b values for Eq. (1)) (Fig. 2). Previous studies also noted inconsistency between T_{opt} and growth temperature in winter wheat (Yamasaki et al., 2002) and in the evergreen tree, *Eucalyptus globulus* (Crous et al., 2013). However, Gunderson et al. (2010) demonstrated that T_{opt} shifted linearly along with seasonal temperature changes in five deciduous trees.

4.2. Photosynthetic acclimation to experimental warming depends on seasons

During the four seasonal periods, photosynthesis of winter wheat showed significant acclimation to warming (HY1, Fig. 2), but acclimation capability to experimental warming differed among the four periods (HY2, Fig. 1). The percent changes of T_{opt} to warming illustrates that winter wheat has high acclimation capabilities in November, April and May, but less in January, which is not as expected. Yamasaki et al. (2002) found that winter wheat could fully acclimate to 15, 25 and 30 °C in growth chambers by adjusting T_{opt}. Gunderson et al. (2010) did not find a significant difference for the change of T_{opt} toward 2–4 °C warming between different seasonal periods in five deciduous trees, while Crous et al. (2013) did find difference toward 3 °C warming among seasonal periods in *Eucalyptus globulus* trees. These results indicate that winter wheat may be able to thermally adjust photosynthesis to compensate for global warming in most seasonal periods; however, at lower temperatures (January), winter wheat displays less ability to adjust. Future studies should increase warming beyond 2 °C to determine whether this conclusion remains true at warmer temperatures.

Like T_{opt}, we found that the acclimation of A_{opt} toward warming may also depend on seasonal periods (Fig. 2; HY2). Warming tended to increase A_{opt} in November and January, but tended to decrease A_{opt} in April and May. This seasonal divergence may result from a trade-off

Fig. 5. Temperature response of RuBP carboxylation limited assimilation (A_c) and RuBP regeneration limited assimilation rate (A_j) of winter wheat in control plots at four seasonal periods. Error bars indicate standard error of A_c and A_j at each temperature. Net photosynthetic assimilation rate (A_n) is the minimum of A_c and A_j.

between temperature tolerance and assimilation rate. In November and January, when leaves devote energy to tolerate a cold environment, warming may help to save that energy and, instead, use it to increase the assimilation rate. In April and May, when leaves prepare to tolerate hotter environment, warming added more heat; plants were required to invest more energy in the heat tolerating system, reducing the assimilation rate. The different effects of A_{opt} to warming among seasons explained why warming decreased the winter wheat yield and increased biomass at our experimental site (Table 3 and Zhao et al., 2016; HY3). November and January are the growth periods for winter wheat to accumulate biomass; the higher A_{opt} under warming resulted in higher biomass. April and May represent the seedling elongation stage and the flowering/milk development stage, which are critical for seed production; productivity decreased due to the decrease of A_{opt} under warming (Fig. 2C, D), along with shortening growth phenology (Asseng et al., 2015). These results illustrated that even though the winter wheat was able to fully respond to warming by using energy to maintain the heat-tolerance system, achieving such responses would be at the cost of decreased productivity.
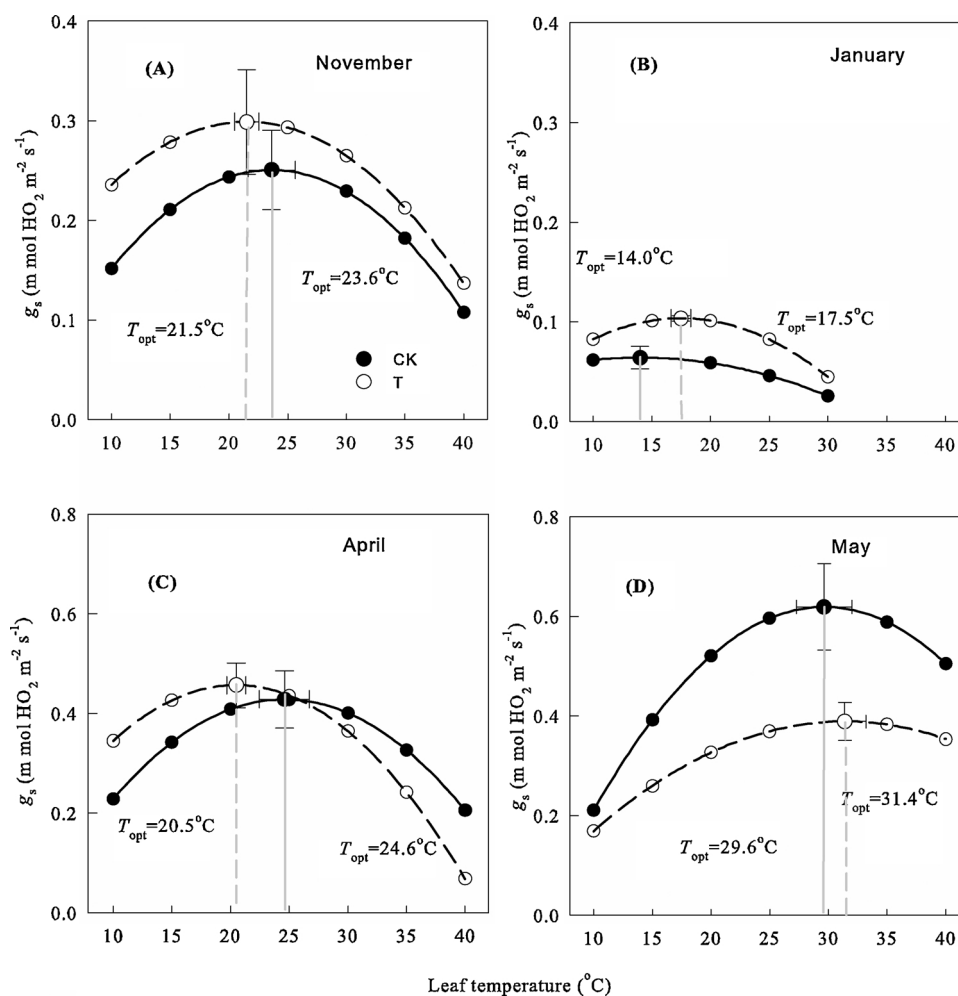
4.3. Mechanisms of photosynthesis acclimation toward warming were different among the four seasons

In addition to the difference in acclimation of T_{opt}, mechanisms leading to acclimation diverged among the four seasonal periods (HY2, interaction terms in Table S4, Table 2). November and April employed similar mechanisms. RuBP carboxylation contributed heavily to the acclimation of photosynthesis, while the balance between respiration and photosynthesis, the balance of V_{cmax} and J_{max}, and stomatal conductance made little contribution. In January, RuBP carboxylation and RuBP regeneration processes did not change under warming, but respiration offset a larger portion of photosynthesis. This indicates that adjustment of the balance between respiration and photosynthesis was the major contributor to the acclimation. Although acclimation capabilities were similar between May and April/November, the mechanisms differed: in May, the lower stomatal conductance in the warming plots suggests that stomatal controls contribute to the acclimation effects (Hikosaka et al., 2006). The differences in the underlying processes and mechanisms responding to experimental warming among different seasonal periods also suggest that the acclimation could be season-dependent.

The current study emphasizes the importance of not only measuring the temperature response and sensitivity of photosynthesis, but also of analyzing the underlying processes and mechanisms. Previous studies emphasized the necessity of including acclimation dynamics in models of biogeochemical cycles, geographical distribution and biodiversity in order to accurately predict the consequences of global warming (Medlyn et al., 2002; Kattge and Knorr, 2007; Hanson et al., 2005; Smith and Dukes, 2013). Adjusting the sensitivity parameters (input parameters for the models) by the growing period and warming according to Table 2 provides the way to model acclimation dynamics in productivity and biogeochemical cycles.

Fig. 6. Temperature response of stomatal conductance (g_s) of winter wheat in warming and control experiments at four seasonal periods. Mean curves were obtained by simulating with mean values of parameters of all the leaves in Eq. (11), $g_s = g_{opt} - b(T - T_{opt})^2$. Error bars indicate standard error of mean values of T_{opt} and A_{opt}. The CO_2 concentration was 400 ppm, and light intensity was 1500 $\mu mol\ m^{-2}\ s^{-1}$. CK represents control experiment, and T represents warming experiment.

Table 3
Productivity and biomass data in control and warming plots of the year 2011.

	Control	Warming	p value
Productivity (Mg ha^{-1})	6.70(0.08)	6.29(0.20)	0.089
Biomass (Mg ha^{-1})	12.16(0.29)	14.46(0.31)	< 0.005

p-value from results of paired t-test in corresponding control and warming plots. The trends of the data agree with Hou et al. (2012), the values are a little different because we only used productivity and biomass data from the plots we conducted measurements. The data is shown as mean (SE).

4.4. Further connections between seasonal-temperature-induced acclimation and experimental-warming-induced acclimation

After a careful comparison of acclimation to seasonal temperature variation and acclimation to experimental warming, we have uncovered both consistencies and divergences existed (HY4, Fig. 1). The acclimation of T_{opt} to experimental warming matched the plant's response toward seasonal variation in January (Fig. 1). However, in November, April and May, the acclimation of T_{opt} under experimental warming did not match. Gunderson et al. (2010) found that the change of T_{opt} was equivalent for both experimental warming and seasonal temperature variation. In addition, the two scenarios shared consistencies in mechanisms (HY4, Table 2). Temperature response of RuBP carboxylation differed from April to May, which was the same

mechanism that contributed to the acclimation response to warming in April and May. Another example could be that the balance between photosynthesis and respiration made the major contribution to acclimation in January, and this was also the mechanism responsible for warming response in January. Our results suggest that it is possible to use both the seasonal temperature variation and experimental warming to investigate the potential acclimation capability, and mechanisms, of photosynthesis in adapting to future global warming (Bradshaw and Holzapfel, 2006; Skelly et al., 2007; Diffenbaugh and Field, 2013).

5. Conclusions

We found photosynthesis of winter wheat is able to fully acclimate to warming effects in November/April/May and to partially acclimate in January, and shows nonlinear acclimation to seasonal temperature changes. More importantly, the mechanisms vary among seasons; displaying the necessity of investigation into acclimation of photosynthesis and sub physiological processes to warming in the whole life-history of species. Assimilation rate increased in November and January under warming, but decreased in April and May, explaining the reduction of yield and the increase in biomass under warming conditions from a physiological perspective. In addition, seasonal-temperature-induced acclimation and experimental-warming-induced acclimation share similar underlying processes and mechanisms. Both experiments can provide information to better understand thermal acclimation of photosynthesis to future global warming. Lastly, we have provided season-

dependent acclimation data and parameters for the warming effect, which can be used in future biogeochemical modeling.

Author contributions

HZ and MX conceived the ideas, designed methodology, analyzed the data and led the writing of the manuscript; HZ, YZ and YC collected the data; RH and ZO set up the warming experiment and measured climate factors, productivity and biomass. HZ and MX coordinated the study. All the authors contributed to the critical review of the manuscript and approved its final version.

Conflict of interest

None declared.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.envexpbot.2018.04.001.

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