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Response of leaf dark respiration of winter wheat to changes in CO_2 concentration and temperature

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Accurate evaluation of dark respiration of plants is important for estimation of the plant carbon budget. The response of leaf dark respiration of winter wheat to changes in CO_2 concentration and temperature was studied, using an open top chamber during 2011–2012, to understand how leaf dark respiration of winter wheat will respond to climate change. The results indicated that leaf dark respiration decreased linearly with increased CO_2 concentration. Dark respiration decreased by about 11% under 560 μmol mol^{-1} CO_2 compared with that under 390 μmol mol^{-1} CO_2. Leaf dark respiration showed an exponential relationship with temperature, and the temperature constant (Q_{10}) was close to 2. Moreover, the responses of leaf dark respiration to CO_2 concentration and temperature were independent. A leaf dark respiration model based on CO_2 concentration and temperature responses was developed. This model provides a method for estimation of the leaf dark respiration rate of winter wheat under future climate change and guidance for establishment of crop carbon countermeasures.

elevated CO_2 concentration, temperature, leaf dark respiration, winter wheat

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Plant dark respiration is the aerobic respiration of a plant in the absence of light. It is a redox process by which the plant absorbs oxygen and releases carbon dioxide, and is affected by the external environment, including temperature, moisture, oxygen and carbon dioxide. Therefore, dark respiration is an important part of the plant carbon budget [1]. To evaluate plant carbon sequestration accurately, it is important to understand the response of plant dark respiration to environmental change. Crops and agricultural ecosystems are sensitive to climate change, which is a matter of great concern to researchers worldwide. However, previous studies have focused mainly on the impact of changes in atmospheric CO_2 concentration (hereafter expressed as [CO_2]), moisture, and temperature on crop photosynthesis [2–6] and agricultural ecosystem soil respiration [7–10]. Studies on the response of crop respiration to changes in [CO_2], moisture and temperature are still inadequate [11,12]. This restricts accurate assessment of crop respiration and affects accurate simulation of product yield. Although studies of the impacts of [CO_2] enrichment on respiration of soybean and rice have been carried out through experiments employing free-air carbon dioxide concentration enrichment (FACE) and open top chambers (OTC), the study results show great divergence [12–15] and quantitative evaluation of the relationships of dark respiration has not been established yet.

To enhance understanding of crop respiration responses to global change and provide parameters for accurate simulation of crop carbon sequestration, in this study we examined the response of leaf dark respiration of winter wheat to changes in CO_2 concentration and temperature, by means of an experiment in which winter wheat plants were subjected to elevated CO_2 concentrations in an OTC, in combination with large fluctuations in temperature overnight, and investigated the relationship between leaf dark respiration of winter wheat and changes in [CO_2] and temperature.

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1 Materials and methods

1.1 Experimental design

The experiment was carried out at the Gucheng Ecology and Agrometeorology Experiment Station, Chinese Academy of Meteorological Sciences (Dingxing County, Hebei province; 39°08′N, 115°40′E) during 2011–2012. The station is located in the piedmont plain irrigated agricultural area in North China and experiences a mean annual temperature of 11.7°C and mean annual precipitation of 551.5 mm. The area is one of the main high-yield production regions of winter wheat in China. The soil is a typical cinnamon soil, with organic matter content of 12.1 g kg^{-1} and total nitrogen content of 0.56 g kg^{-1}. The experiment was carried out in three OTCs. Each chamber was contained in an octagonal plastic–steel–glass structure 2.5 m high with an internal area of 10 m^2. Uniform ventilation in the chamber was achieved through a PVC piping system from a 2000 m^3 h^{-1} centrifugal fan.

The experiment included the control (atmospheric concentration, AC) and two elevated [CO_2] (EC) treatments. For one of the elevated [CO_2] chambers, elevated CO_2 treatment was applied from the green wheat stage to maturity (CO_2 concentration 560 μmol mol^{-1}; EC560); for the other elevated [CO_2] chamber, the [CO_2] was adjusted from 560 to 700 μmol mol^{-1} (EC700) three days before measurement of respiration and continued to the end of the experimental period. The elevated [CO_2] treatment in 2011 was applied from 26 February until 9 June. Normally, the elevated [CO_2] treatment was applied during the day, but it was applied during both the day and night three days before measurement of respiration. The elevated [CO_2] treatment was applied in both the day and night from 5 March to 10 June, 2012.

The CO_2 gas source was high-purity cylinder gas. The [CO_2] in the gas chamber was real-time monitored with an infrared gas analyzer (QGS-08C, BAIF-Maihak, Beijing, China) and the gas transmission capacity was real-time adjusted with a rotameter. During the experimental period in 2011, the [CO_2] in the control chamber (AC) and treatment chambers I (EC560) and II (EC700) was 391 ± 11, 567 ± 28, and 694 ± 34 μmol mol^{-1}, respectively. In 2012, the [CO_2] in the control chamber (AC) and treatment chambers I (EC560) and II (EC700) was 393 ± 15, 564 ± 32, and 706 ± 31 μmol mol^{-1}, respectively.

Direct seeding of winter wheat was adopted. Seeds of JIMAI-22, a semi-winter cultivar, were sown on 10 October. For all chambers, standard management procedures were adopted and adequate water was supplied. Base fertilizer (60 g m^{-2}) was applied at the time of sowing, and at the turning-green stage urea and diammonium phosphate (each 25 g m^{-2}) were applied. During the respiration observation period, the developmental stage of the control group and treatment chambers was essentially identical, and the night temperature was 10–24°C.

1.2 Observation procedure

Dark respiration of the flag leaf of winter wheat plants was observed *in situ* with a Li-6400 photosynthesis system (LI-COR, Lincoln, NE, USA) at night under clear sky and calm conditions from the booting to the milk stages. The leaf chamber input concentration (observed concentration) was controlled with a CO_2 cylinder, which avoids the influence of [CO_2] fluctuation in the gas chamber on the observations, and measurement of the response of respiration rate to short-term changes in [CO_2]. Observations were carried out at night from 21:00 to 04:00. The observation CO_2 concentration was set to the treatment concentration for all gas chambers (390, 560, or 700 μmol mol^{-1}) to observe the long-term effects of [CO_2], for each treatment, three flag leaves were observed at each time-point; in the three chambers, elevated [CO_2] (100–1000 μmol mol^{-1}) was applied to the selected leaves to observe the direct influence of short-term change of [CO_2], the response time for each CO_2 concentration was 5–7 min. The dark respiration rate was expressed as μmol CO_2 m^{-2} s^{-1}.

1.3 Data processing

Data processing and mapping were performed with Excel, and the significance of differences among the treatments was analyzed with SPSS statistical software version 14.0.0 (SPSS, Inc., Chicago, USA).

2 Results

2.1 Response of leaf dark respiration of winter wheat to changes in temperature

The plant respiration rate (R_d) has an exponential relationship with temperature [16]:

$$R_d = K \cdot Q_{10}^{\frac{T-25}{10}}, \quad (1)$$

where K is the respiratory strength at 25°C (also termed the coefficient of dark respiration), T is the temperature (°C), and Q_{10} is the dark respiration temperature coefficient, for which the value is 1.6–3.0 for different plant species [16]. The Q_{10} value of crops is usually about 2.0 [16–18]. When the [CO_2] and other factors are unchanged, the values of K and Q_{10} can be calculated according to the respiration rate under different temperatures.

The relationship between R_d and T is shown in Figure 1, based on data recorded at four time-points in the control chamber (AC) during the night of 12 April 2011 for winter wheat plants at the booting stage. In Figure 1, R_d values were $\log_{10}$-transformed and T is the canopy air temperature observed with the Li-6400.

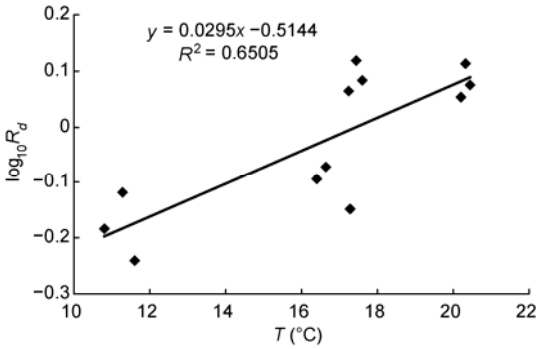

Figure 1 Relationship between leaf dark respiration rate of winter wheat and temperature.

Based on the line of best fit, the values of K and Q_{10} were 1.577 and 1.977, respectively, which provided further validation that the temperature coefficient Q_{10} of the crop is close to 2 [16]. Thus, the relationship between the leaf dark respiration rate of winter wheat at the booting stage and canopy air temperature can be expressed as

$$R_{\mathrm{d}} = 1.577 \times 2^{\frac{T-25}{10}}. \quad (2)$$

This finding indicated that dark respiration of winter wheat leaves is enhanced at an elevated temperature, and that with each rise in temperature of 10°C, the respiratory rate is enhanced by about one-fold.

2.2 Response of leaf dark respiration of winter wheat to changes in [CO_2]

(i) Short-term changes in [CO_2]. Figure 2 shows the response of leaf dark respiration of winter wheat to short-term change in [CO_2] under three [CO_2] conditions at the flowering and milk stages, that is, the direct response of leaf dark respiration to change in [CO_2]. The trend of changes in leaf dark respiration rate with elevated [CO_2] was essentially identical among the treatments, that is, the dark respiration rate decreased with short-term elevation of [CO_2]. When the atmospheric condition in the chamber changed from a low [CO_2] environment to a high [CO_2] environment, dark respiration was inhibited; in contrast, when the atmospheric condition changed from a high [CO_2] environment to a low [CO_2] environment, the dark respiration rate was enhanced. No significant differences among the treatment groups were observed.

(ii) Long-term elevated [CO_2]. The leaf dark respiration rate under three [CO_2] long-term treatments (390, 560, and 700 μmol mol^{-1}) was observed at the booting stage in 2011 and the early filling stage in 2012. In the AC and EC560 air chambers, the observation CO_2 concentration was the same as the [CO_2] in the winter wheat growth environment. In the EC700 air chamber, the winter wheat plants were acclimatized for three days. Elevated [CO_2] in the winter wheat growth environment resulted in a decrease in the leaf dark respiration rate (Figure 3), which was corrected for temperature with eq. (2). Under [CO_2] of 560 μmol mol^{-1}, the dark respiration rate was 11% less on average than that of the control [CO_2]. In contrast, under 700 μmol mol^{-1} [CO_2], the dark respiration rate was decreased by 25% on average compared with that of plants grown under atmospheric [CO_2]. The two-year test results showed that, when grown under a high [CO_2] environment for a long period or after a long period of acclimation under high [CO_2], the leaf dark respiration rate of winter wheat decreased. Thus, the effect of long-term elevated [CO_2] was inhibition of leaf dark respiration.

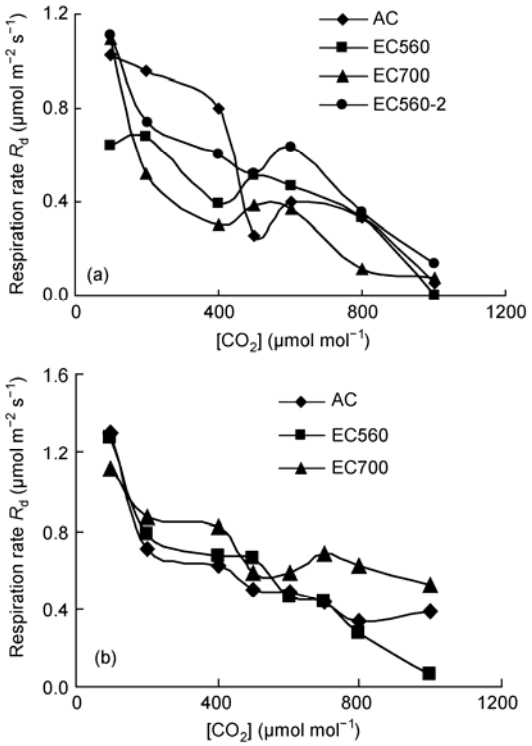

Figure 2 Response of leaf dark respiration rate of winter wheat to short-term changes in [CO_2]. (a) Flowering stage; (b) milk stage; AC: control (atmospheric CO_2 concentration); EC560: treatment I (560 μmol mol^{-1} CO_2 concentration); EC560-2: repeated observation of treatment I; EC700: treatment II (700 μmol mol^{-1} CO_2 concentration).

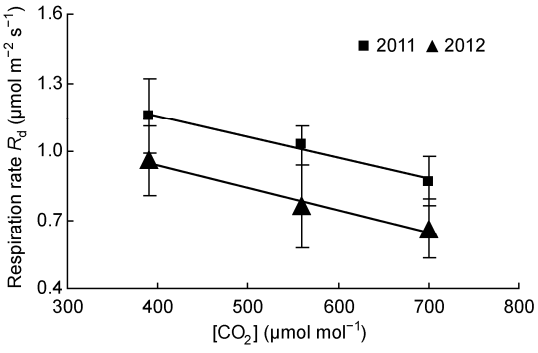

Figure 3 Leaf dark respiration rate of winter wheat under prolonged exposure to different [CO_2] concentrations.

(iii) Relationship between leaf dark respiration rate of winter wheat and [CO_2]. The long-term and short-term responses in leaf dark respiration rate of winter wheat to elevated [CO_2] showed similar characteristics (Figures 2 and 3). Within the 100–1000 μmol mol^{-1} [CO_2] range, the dark respiration rate declined with the increase in [CO_2]. Thus elevated [CO_2] inhibited the leaf dark respiration of winter wheat. As shown in Figure 3, the dark respiration rate was linearly correlated with [CO_2]. In Figure 2, a linear relationship between the two variables showed a better fit than for other functions, but over a wider range of [CO_2] the relationship between the two variables may be described by a power function. To simplify the calculation, within the range of 100–1000 μmol mol^{-1} [CO_2], the relationship between leaf dark respiration rate and [CO_2] may be expressed by a linear function. As shown in Figures 2 and 3, the response of leaf dark respiration rate of winter wheat to change in [CO_2] may be expressed as

Booting stage: R_d=1.520–0.00091C_{co_2} (R^2 = 0.986, n = 3),
Flowering stage: R_d =0.917–0.00088C_{co_2} (R^2 = 0.950, n=7),
Early filling stage: R_d =1.330–0.00098C_{co_2} (R^2=0.982, n=3),
Milk stage: R_d = 1.093–0.00086C_{co_2} (R^2 = 0.837, n = 8),

where R_d is the leaf dark respiration rate (μmol CO_2 m^{-2} s^{-1}), and C_{co_2} is [CO_2] (μmol mol^{-1}). Student's t test indicated that the four fitting functions were significant (P <0.01). This finding showed that, at different developmental stages and under different temperatures, with increase in [CO_2] the decline in leaf dark respiration rate was essentially consistent; that is, when [CO_2] increased by 100 μmol mol^{-1}, the leaf dark respiration rate decreased by about 0.09 μmol CO_2 m^{-2} s^{-1}. This result indicated that [CO_2] influences the leaf dark respiration rate of winter wheat independent of developmental stage and temperature. Previous studies showed that the influence of elevated [CO_2] on the leaf dark respiration of alfalfa is independent of temperature [19]. Similarly, temperature and [CO_2] independently affect leaf dark respiration of a variety of tree species [20].

To summarize the above fitting relationships, within the range 100–1000 μmol mol^{-1} [CO_2], the relationship between leaf dark respiration rate of winter wheat and [CO_2] can be expressed as

$$R_d = R_p - r \cdot C_{CO_2}, \quad (3)$$

where r is the [CO_2] influence coefficient, which can be 0.0009 μmol CO_2 m^{-2} s^{-1}, and R_p is the dark respiration intensity of a leaf not affected by [CO_2] but affected by temperature and other environmental factors.

2.3 Relationship of leaf dark respiration of winter wheat with [CO_2] and temperature

Based on eqs. (2) and (3), the relationship of leaf dark respiration rate with [CO_2] and temperature can be expressed by the following formula:

$$R_d = K_p 2^{\frac{T-25}{10}} - r \cdot C_{co_2}, \quad (4)$$

where K_p is the leaf dark respiration intensity at 25°C. In the formula, r takes the approximation 0.0009 μmol CO_2 m^{-2} s^{-1}, and thus K_p can be calculated based on the observation data. The results showed that, at the same developmental stage, the K_p value was relatively stable with a small standard deviation (Table 1), but at different developmental stages significant differences were observed. Thus the value of K_p changed significantly at different developmental stages and declined from the booting stage to the milk stage of winter wheat development.

Based on the observation data at different stages of winter wheat development and the K_p value at the same developmental stage, the relationship between the leaf dark respiration rate simulation value and the observed value is shown in Figure 4. Independent data validation showed that the response in leaf dark respiration rate of winter wheat to temperature and [CO_2] was well simulated by eq. (4).

3 Discussion

At present, few studies have investigated the responses of leaf dark respiration rate of winter wheat to elevated [CO_2]. An experiment on spring wheat showed that short-term change in [CO_2] had no effect on dark respiration rate, but maintenance respiration rate decreased by 13% when plants were grown under double [CO_2] for a long period [21]. The present study showed that the leaf dark respiration rate of

Table 1 Change in K_p with stage of winter wheat development[a)]

	Booting stage	Flowering stage	Early filling stage	Milk stage
K_p mean	2.445a	1.878b	1.578c	1.354c
SD	0.272	0.285	0.160	0.194

a) Different lower-case letters represent a significant difference at the significance level of 0.05.

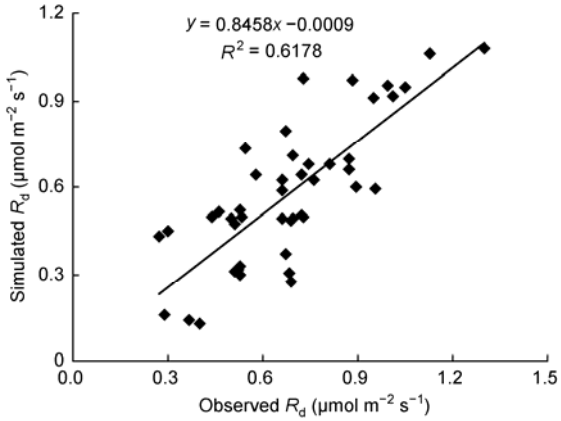

Figure 4 Relationship between simulated and observed R_d of winter wheat.

winter wheat grown under 560 μmol mol^{-1} [CO_2] was decreased by 11% compared with that of plants grown under 390 μmol mol^{-1} [CO_2], which was similar to observation data reported for spring wheat [21]. However, the leaf dark respiration rate of winter wheat is also very sensitive to short-term change in [CO_2]. Although some experiments indicated that the respiration rate at the crop leaf level is unaffected by [CO_2] or increased with elevated [CO_2], a number of experiments showed that the proportional increase in the total respiration of the crop canopy was less than the proportion of biomass growth caused by elevated [CO_2] [11]. These findings suggest that the respiration rate of the crop leaves or plants is actually decreased under high [CO_2], and observation data at the leaf level may be subject to interference from other factors.

Free-air CO_2 enrichment of soybeans showed that the response characteristics of leaf respiration rate to elevated [CO_2] differ when the respiration rate is expressed in different units [13]. If respiration intensity per unit leaf area is used, increase in [CO_2] has no influence on respiration rate. If respiration intensity per unit dry weight of leaf is used, the respiration rate significantly decreases with elevated [CO_2] because elevated [CO_2] makes the dry weight per unit leaf area increase by 23%. The present study showed that, under the high [CO_2] condition, the specific leaf weight of winter wheat increased slightly (about 5%; Figure 5). If respiration rate is expressed as dry weight, then the inhibitory effect of elevated [CO_2] on leaf respiration rate is more significant.

The present study showed that, when [CO_2] and temperature are constant, the leaf dark respiration rate (K_p) of winter wheat gradually declined from the booting stage to the milk stage, which was similar to observations reported for paddy rice [22,23]. Previous studies also show that the nitrogen content in the above ground parts of winter wheat under the natural growth condition declines with developmental stage after the jointing stage [24], whereas in a variety of crops maintenance respiration shows a significant positive correlation with nitrogen content [25]. Experiments show that the wheat plant dark respiration coefficient after correction to 25°C has a positive linear relationship with leaf nitrogen (N) content: $R_d = 4.74N - 1.45$ [17]. Thus it can be inferred that the K_p value might show a positive linear correlation with leaf N (i.e. $K_p = a + bN$, where a and b are constants). In the present study, K_p is the respiration eigenvalue after separating the influence of [CO_2], but the influence of environmental [CO_2] on leaf N content is still not known. Previous studies show that, under suitable conditions of moisture and N supply, high [CO_2] treatment has little effect on wheat leaf N content [26], whereas the effect of CO_2 enrichment treatment on the leaf N content of rice and soybean varies [2,14,27,28]. Establishment of the formula $K_p = a + bN$ requires further validation with additional experiments.

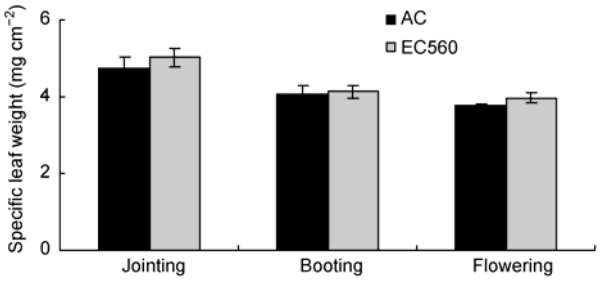

Figure 5 Influence of elevated [CO_2] on the specific leaf weight of winter wheat. AC: control (atmospheric [CO_2]); EC560: treatment I (560 μmol mol^{-1} [CO_2]).

Measurement of crop dark respiration is difficult. The dark respiration rate is small, its measurement is affected by many factors, and the data show great variability. When the respiration rate is monitored under two [CO_2] concentrations with a difference of 200 μmol mol^{-1}, the measurement values do not show stable trends. This phenomenon is validated by the observation data reported in the current study and in related studies [18]. Usually, the [CO_2] of FACE is enriched by 200 μmol mol^{-1} above the control or is doubled, which may lead to the inconsistency of experimental results. The experiment carried out by Tjoelker et al. [29] on 12 species of grassland plants also proved this. When comparing two [CO_2] levels (360 and 700 μmol mol^{-1}), the change in respiration rate of detached leaves of the grassland species was within the range of −6.4% to 2.4%, but with five [CO_2] levels in the range from 360 to 1300 μmol mol^{-1}, the respiration rate showed a significant linear decline with the increase in [CO_2]. This result suggests that it is easy to determine the response of the respiration rate with change in [CO_2] when observed over a wide range of CO_2 concentrations. The results of the present experiment also support this conclusion.

A consensus has been reached on the relationship between the crop dark respiration rate and ambient temperature [16–18]. However, with regard to whether the crop dark respiration temperature coefficient Q_{10} differs among cultivars of crops and whether the Q_{10} value is consistent or changes in different temperature ranges, there is no agreement yet. In the present study, the Q_{10} value recorded for winter wheat from four measurements over the course of one night under the ambient temperature range (10–21°C) needs further verification.

4 Conclusions

The present CO_2 enrichment experiment in OTCs showed that elevated [CO_2] inhibited leaf dark respiration of winter wheat, and the leaf dark respiration rate showed a linear decline with elevated [CO_2]. The responses of leaf dark respiration rate to short-term and long-term elevated [CO_2] were identical. The effects of temperature and [CO_2] on leaf dark respiration of winter wheat were independent. The

temperature coefficient Q_{10} of winter wheat leaf dark respiration is close to 2.

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