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Diurnal oscillation in the intercellular CO_2 concentration of spring wheat under the semiarid conditions

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Abstract

Yields of wheat in semiarid and arid zones are limited by drought, and water condition is very important at each stage of development. Studies carried out at Loess Plateau in the northwestern part of China indicated that yield of spring wheat (*Triticum aestivum* L.) cv. Dingxi 81-392 was reduced by 41 % when subjected to water stress. The effects of two water regimes on net photosynthetic rate (P_N), stomatal conductance (g_s), and intercellular CO_2 concentration (C_i) were investigated at the jointing, booting, anthesis, and grain filling stages. Low soil moisture in comparison to adequate one had invariably reduced P_N during the diurnal variations at the four growth stages. P_N and g_s in both soil moisture regimes was maximally reduced at midday. C_i and the stomatal limitation fluctuated remarkably during photosynthesis midday depression processes, especially at the grain filling stage. Hence atmospheric drought at midday was one of the direct causes inducing stomata closure and the g_s depression, but it was beneficial for maintaining stable intrinsic water use efficiency. Fluctuation in C_i implicated that non-stomatal limitation also plays an important role during the period of photosynthesis midday depression. Consequently stomatal and/or non-stomatal limitation are the possible cause of the midday photosynthesis decline.

Additional key words: net photosynthetic rate; soil and atmospheric drought; stomatal conductance; *Triticum aestivum*.

Introduction

Hilly and gully area of the Loess Plateau in the northwestern part of China is a typical semiarid area where dry land farming has been practiced for more than 4000 years. Wheat with very low yield is the major grain crop occupying 43.9 % of the total cultivated area of the Plateau. The average yield in this area is 1.5 t ha^{-1} compared to 6.0 t ha^{-1} in traditional areas (Huang 1993). A decrease in photosynthesis caused by the drought environment of the Plateau, despite abundance of solar radiation (Chen and Mu 1993), is a possible cause of the realised low yields. Most of the previous studies on effects of photosynthesis stress on the crop yield were done in the laboratory under controlled conditions (Azcón-Bieto 1983, Maroco *et al.* 1997, Allen *et al.* 1998). However, the findings of these studies are not sufficient for fully understanding the regulatory mechanisms of plant photosynthesis under natural field conditions. Several researchers (Kalt-Torres *et al.* 1987, Shan and Chen 1993, Xu and Wu 1996, Escalona *et al.* 1999) also emphasised the necessity of the case studies. The experiment described in this paper was undertaken to assess the effects of drought on the diurnal photosynthetic parameters at major growth stages of spring wheat in the semiarid environment.

Materials and methods

An experiment was conducted at Guyuan Ecological Research Station, which is located in a typical semiarid area of the Loess Plateau. Spring wheat (*Tirticum aestivum* L.) cv. Dingxi 81-392 was sown in plastic pots placed in the field and covered by polyvinyl sheet only when it was raining. Water was supplied from plastic pipes inserted vertically into the soil. Forty-two days after sowing, soil moisture was kept constant at 17 % or

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adjusted to 11 % to represent control and water stress treatments, respectively. Soil moisture was checked diurnally and lost water was replenished by bringing the pots back to their original mass set for the planned moisture contents.

Expanded top leaves or flag leaves were selected at the jointing, booting, anthesis, and grain filling stages for investigations. Leaf net photosynthetic rates (P_N) were measured with a gas-exchange-measuring system according to Long and Hallgren (1985). Infrared gas analyzer (*LCA2 Shimadsu*, Nagoya, Japan) and dew point meter (*HMI33 Vaisala OY*, Finland) was used for measuring P_N and transpiration rate. The microclimate factors including air temperature, relative humidity (RH), and photosynthetically active radiation (PAR) were recorded at the same time with a series of irradiance sensors and thermo-sensors (*Licor Li-193B*, Lincoln, NE, USA). Vapour pressure deficit (VPD) in the atmosphere was converted from the relative humidity and saturated water vapour at air temperature. Stomatal conductance (g_s) and intercellular CO_2 concentration (C_i) as well as stomatal limitation (L_s) were calculated according to the equations of Caemmerer and Farquhar (1981) and Jones (1998).

Experimental values were analysed for significance by Turkey's HSD. The curves were obtained from diurnal time on clear days at the jointing, booting, anthesis, and grain filling stages. Polynomial regressive equations were used to represent the diurnal cases of the changes in PAR, VPD, P_N, g_s, and C_i by data fitting.

Results

During the initial stage of the experiment, seedling establishment was excellent. Seedling growth was rapid. Average plant height, 42 d after sowing, was 8.0±0.4 cm. Soil moisture stress, imposed 42 d after sowing, did not affect the onset of plant growth stages or physiological maturity. Jointing, booting, anthesis, and grain filling in both control and stress treatments were first observed 50, 60, 78, and 85 d after sowing, respectively. Physiological maturity, as indicated that heads lost of green colour, and grain ripening, was reached at about 108 d irrespective of soil moisture status. Under soil water stress, plant height, shoot and root biomass of wheat were reduced by 23.9, 38.6, and 34.2 %, respectively. Soil water stress caused water consumption, grain yield, and biomass of wheat reduced by 50.70, 41.15, and 38.63 %, respectively. However, water use efficiency based on grain yield (WUEg) increased by 19.4 % (Table 1).

Table 1. Effect of soil water stress on the growth, yield, and water use of spring wheat. ET, evapotranspiration amount during whole growing season; WUEg, grain yield/ET.

Soil water content [%]	Plant height [cm]	Top biomass [g pot^{-1}]	Root mass [g pot^{-1}]	Seed mass [mg seed^{-1}]	Seed number per head	Grain yield [g pot^{-1}]	ET [kg pot^{-1}]	WUEg [g kg^{-1}(H_2O)]
17	77.69±0.94	54.96±0.97	15.54±0.52	44.31±0.43	27.64± 0.39	25.55± 0.64	19.11±0.16	1.34±0.04
11	59.11±0.73	33.77±0.63	10.22±0.45	38.58±0.30	18.56± 0.49	15.04± 0.34	9.42±0.14	1.60±0.04

P_N indicated a two-peak diurnal curve for both control and soil water stress treatments (Fig. 1). Diurnal variation of leaf P_N, irrespective of soil water status, increased drastically at 11:00 h, then declined to a very low value at midday, and gradually recovered in the afternoon. Plants stressed by low soil moisture invariably had a lower P_N than the control. The maximum differences between treatments were recorded at midday. Recovery of P_N from the midday decline was slower for the stressed plants than the control at the grain filling stage.

Diurnal variation of g_s, irrespective of soil moisture status, showed a similar trend to that of leaf P_N. The recovery of g_s after midday depression was, invariably, slower in stressed than non-stressed plants. The one-peak curve of diurnal change in vapour pressure deficit showed that the most severe water stress in the atmosphere also occurred at midday. At booting stage leaf water potential, irrespective of soil moisture status, was higher than that at grain filling stage and at the same time leaf temperature was about 10 °C lower than that at grain filling. Leaves of stressed plants invariably had lower water content (86.3 and 76.8 %) than those of the control (90.1 and 83.1 %, Table 2). These results indicated that leaf photosynthetic capacity was closely related to leaf age, water status, and air temperature. Diurnal variations of P_N, however, were almost parallel with that of g_s.

Diurnal g_s fluctuations reflected the stomata aperture, which is controlled by osmotic adjustment in the surrounding cells (Jones 1995, Grill and Ziegler 1998). A closely linear correlation between P_N and g_s was obtained ($r^2 = 0.924^{**}$; Fig. 2). Under either atmospheric drought or soil water stress conditions stomata operate probably in such a way as to minimise water loss relative to the amount of CO_2 uptake. The stable ratio of P_N to g_s

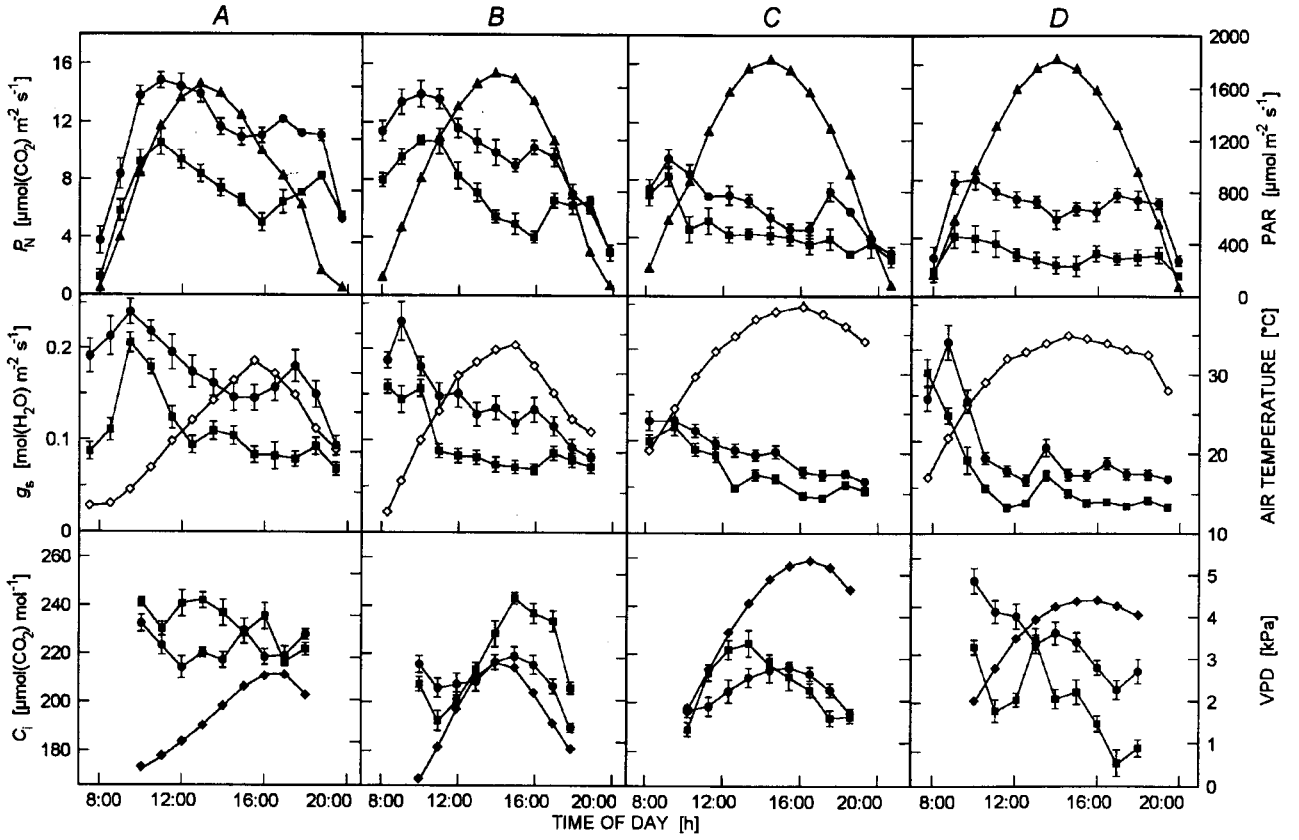

Fig. 1. Diurnal variations of net photosynthetic rate (P_N), stomatal conductance (g_s), intercellular CO_2 concentration (C_i), photosynthetically active radiation (PAR), air temperature, and vapour pressure deficit (VPD) at the jointing (*A*), booting (*B*), anthesis (*C*), and grain filling (*D*) stages of spring wheat on the Loess Plateau. ●: control, ■: water stress treatment, ▲: PAR, ◇: air temperature, ♦: VPD. *Vertical bars* represent standard error.

Table 2. Leaf water status and temperature at midday of four growth stages.

Growth stages	Water content [%]		Water potential [Mpa]		Leaf temperature [°C]	
	control	stressed	control	stressed	control	stressed
jointing	93.34±0.55	91.05±0.64	-0.09±0.02	-0.13±0.02	20.8±0.2	21.2±0.3
booting	90.07±0.67	86.28±0.38	-0.16±0.02	-0.27±0.03	25.7±0.3	27.1±0.2
anthesis	86.70±0.69	81.52±0.47	-0.25±0.03	-0.53±0.05	30.7±0.4	33.0±0.5
grain filling	83.06±0.52	76.75±0.43	-0.43±0.04	-1.06±0.07	35.6±0.3	38.9±0.7

indicated that under the semiarid conditions spring wheat trended to maintain optimum intrinsic WUE so as to assist in conserving water (Ludlow 1980, Cowan 1982, Davies and Pereira 1992, Schulze 1994).

Diurnal variations in C_i and L_s showed significant fluctuations, and these oscillation phenomena occurred in all the four stages both under stress and non-stress conditions, however, the oscillation range and frequency were variable at the fourth growth stage. At the jointing stage the stomatal limitation of the stressed plants was higher than that of the control during photosynthesis midday depression process. In contrast, at the grain filling stage, the stomatal limitation values of the stressed plants were relatively lower than that of non-stressed plants. Hence both stomatal and non-stomatal limitation may induce photosynthesis midday depression alternatively and/or multiplied. Non-stomatal limitation was closely linked with leaf senescence, high air temperature, and with high vapour pressure deficit in the semiarid area of Loess Plateau.

Discussion

It is easy to study the effect of environmental factors such as water, irradiance, carbon dioxide, and temperature on crop photosynthesis separately under controlled conditions (Kirschbaum and Farquhar 1984, Nobel 1991, Comstock and Ehleringer 1993, Barradas *et al.* 1994).

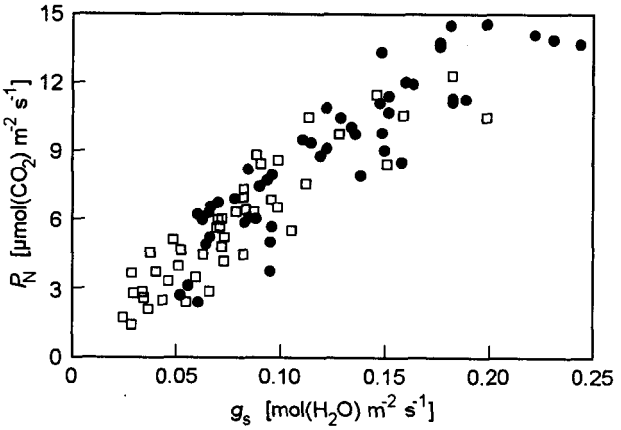

Fig. 2. Relationship between P_N and g_s at four growth stages of spring wheat. •: control, □: water stress treatments.

Under natural conditions, however, factors contributing to photosynthesis variation are more complex (Kobayashi *et al.* 1999). Usually several of the factors involved vary simultaneously and these anticipate intricacy (Jones 1992). According to Ferris *et al.* (1998), P_N of the soybean leaf was fully recovered under water deficit in elevated CO_2, while it remained reduced under water deficit in ambient CO_2. Leaf P_N of millet and rice increased at 22 °C and decreased at 42 °C, whereas in wheat it was the highest at 22 °C and decreased at lower temperature (Kassim and Paulsen 1999). In spite of carbon dioxide and temperature effects, there are at least three other factors that have a direct connection with the effect of water stress on photosynthesis. We found that photosynthesis was variable under different soil moisture contents. Under the gradual soil drying, wheat exhibited higher P_N than under the fast soil drying conditions. Under the former osmotic adjustment process it increased to a certain extent while under the latter process it remained constant. Osmotic adjustment allows for maintenance of photosynthesis and growth by stomatal adjustment and photosynthetic adjustment (Turner *et al.* 1986, Deng *et al.* 1990, Shangguan *et al.* 1999). In addition, photosynthetic limitation was affected variably by the different strengths of soil water stress. We found that under the mild and/or moderate soil water stress, photosynthetic depression was caused by stomatal closure or by stomatal limitation but not by biochemical reactions. However, under severe soil water stress, non-stomatal factors including some limiting enzymes were probably responsible for the decline in photosynthetic capacity (Du *et al.* 1996, 1998). Photosynthetic depression was greatly linked to the water stress position and this agrees with the findings of Schulze (1986). Midday declines in photosynthesis were mainly induced by severe vapour pressure deficit, and stomatal limitation was suggested as a major cause (Xu and Shen 1997). Under the natural semiarid conditions, however, this decline usually resulted from soil water stress that induced leaf water potential decrease at midday. Similar results were reported by Sheriff (1982) and by Shi *et al.* (1997). Both soil water stress and atmospheric drought simultaneously induced the midday depression in P_N (Fig. 1). This is consistent with that both stomatal and non-stomatal limitations were responsible for photosynthetic decline in spring wheat under semiarid environment (Figs. 2 and 3).

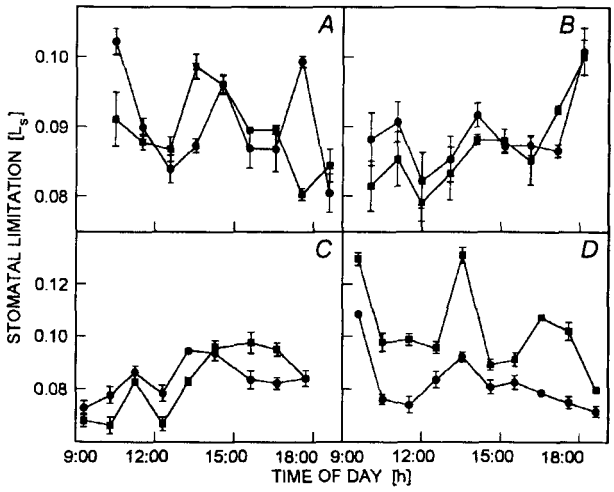

Fig. 3. Diurnal oscillations of stomatal limitation (L_s) at the jointing (*A*), booting (*B*), anthesis (*C*), and grain filling (*D*) stages of spring wheat in the semiarid environment. •: control, ■: water stress treatments. *Vertical bars* represent standard error.

It is possible that the relation of g_s and soil moisture stress was created or caused by synthesis of abscisic acid (ABA) by roots in response to soil drying. ABA is then transported through the xylem to leaves, causes the regulation of several ion channels in guard cells, and triggers stomatal closure (Berkowitz and Whalen 1985, Davies and Zhang 1991, Hartung and Slovik 1991, Slovik and Hartung 1992). Some researchers linked this with the role of farnesylations that has been connected with ABA signal conduction (Grill 1998, Pei *et al.* 1998). However, photosynthetic carbon assimilation catalyzed by ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBPCO), an enzyme located in the chloroplast stroma, can not be ruled out. The RuBPCO holoenzyme is assembled in a

catalytically inactive form and is activated by RuBPCO activase (RCA) (Miziorko and Lorimer 1983, Portis 1992, Mott *et al.* 1997). Expression of RCA is organ-specific, developmentally regulated by the leaf age, and it is light inducible. Study on the transcription of the RCA gene showed that relative mRNA abundance is in form of oscillation, and thus there are multiple clock-response elements (CREs) that act additively or multiple-actively to confer high-amplitude oscillation (Liu *et al.* 1996). Diurnal oscillation in intercellular CO_2 concentration (Fig. 3) under the semiarid conditions is closely connected with the activation of RuBPCO, which is affected by the oscillated transcription of the RCA gene. Activation status of RuBPCO plays one of the important roles in the diurnal oscillation of stomatal limitation.

Diurnal photosynthetic changes in some spring wheat cultivars were closely related to local climatic and soil moisture (Grantz 1990, Ray and Sinclair 1997). Even for the sufficient soil moisture conditions, the notable midday decline in g_s that was parallel to P_N depression resulted from severe water vapour deficit at midday (Figs. 1 and 3). Farquhar *et al.* (1980) and Dai *et al.* (1992) reported similar effects. The deviation of g_s between the control and soil moisture stress treatments was closely related to the leaf water status that was obviously affected by the prevailing soil moisture stress. This is consistent with results of Farquhar and Sharkey (1982). The consistency in the diurnal variation of g_s with the notable reduction of P_N (Figs. 1 and 2) suggests that under either atmospheric drought or soil water stress conditions stomata operate in the approach to minimise water loss relative to the amount of CO_2 uptake. Under the semiarid conditions spring wheat tended to maintain optimum intrinsic WUE so as to assist in conserving water. Daily oscillation of C_i (Figs. 1 and 3) reflects the limitation of semiarid environment to the leaf P_N of spring wheat. It indicates that stomatal and non-stomatal limitations play an important role to restrict the carbon assimilation of wheat. This suggests that the molecular mechanism of g_s variation and C_i oscillation is closely linked to ABA-reduced stomatal response and activation status of RuBPCO affected by circadian oscillation of RCA.

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