

# Physiological regulation of high transpiration efficiency in winter wheat under drought conditions

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## ABSTRACT

Pot experiments were conducted to study the variation and physiological regulation of transpiration efficiency (TE) of four winter wheat (*Triticum aestivum* L.) varieties that are widely grown in different ecological regions in North China. Plants were grown under two soil moisture regimes, normal and drought stress. The results showed that under drought stress condition, both TE at plant level and TE at leaf level (TEI) increased significantly. The transpiration rate (Tr) was reduced more strongly than leaf net CO<sub>2</sub> assimilation rate (Pn). The decline of Tr was mainly affected by stomatal conductance and the decline of Pn was affected by non-stomatal factors, which was confirmed by the decline in net photosynthetic oxygen evolution rate. The leaf soluble sugar content and proline content were significantly increased under drought stress. The stomatal density was increased and the stomatal length was reduced. These results led us to make the following conclusions: (1) Under drought stress, the increase in TEI appears to be regulated in two ways: via the stomata by regulating Tr, and independent of the stomata through regulation of Pn; regulation via the stomata was more sensitive; (2) Osmotic adjustment was closely correlated to the non-stomatal regulation, and stomatal aperture was closely correlated to the stomatal way.

**Keywords:** winter wheat; drought; transpiration efficiency; stomata; osmotic adjustment; stomatal aperture

Drought is a worldwide issue that impacts seriously on the security of food production. Global climate change makes this even worse (Elisabeth et al. 2009). Winter wheat is almost the most important crop in the world. However, its main growth period is in the winter to spring season when rainfall is inadequate in most parts of the world. To improve wheat biomass and harvest index it is critical for the crop to make better use of the limited availability of water.

Improving the transpiration efficiency (TE) is the inevitable choice. Many studies suggested that TE was affected by the crop genotype and soil mois-

ture content (Salvatore et al. 2007, Sankar et al. 2008), and physiological research was significantly contributed to the selection of high TE crops. However, a lack in understanding of the physiological and molecular regulation of TE presents a real constraint for further improvement of TE and selection of new crop varieties (Richards 2006). Recently, most studies on winter wheat focused on the effect of irrigation regime and soil moisture content on yield, TE, the relationship between photosynthetic traits and environmental factors, agronomic traits (Xue et al. 2006, Kahlow et al. 2007). The results show that crop yield was de-

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Supported by the Key Projects from CAS, Projects No. KSCX2-YW-N-004 and KSCX2-YW-N-042-01, by the Key Project in the National Science & Technology Pillar Program of China, Project No. 2009BADA3B-03-08, by the National Project of 863 of China, Project No. 2006AA100221 and by the National Natural Science Foundation, Project No. 30870411.

creased or changed under water stress; the water use efficiency was increased. However, the physiological mechanism for this was not clear.

Giorio et al. (1999) reported that stomatal regulation was the major physiological factor in the optimization of water use under drought conditions. Yang et al. (2007) studied the stomatal width of *Leymus chinensis* in different longitudes (with different soil moisture content) in the North of China and came to a similar conclusion. However, DaMatta et al. (2003) concluded that osmotic adjustment under drought conditions was the main factor contributing to maintain higher transpiration efficiency. However, there was no uniform view on the physiological basis on which TE was improved so far.

The objective of this study was to further investigate the regulatory mechanism controlling changes in TE and its physiological components, with the aim to provide a theoretical underpinning for improved water-saving in winter wheat cultivation and for the early selection of high-TE winter wheat varieties.

## MATERIAL AND METHODS

**Experimental design.** Four winter wheat varieties (*Triticum aestivum* L., Shi4185, Kenong199, Jinmai47 and Luohan2) widely grown in different ecological regions in North China, were used in the study. Seeds, surface-sterilized with 0.1%  $\text{HgCl}_2$ , were sowed in 'Zero-evaporation' pots ( $11.5 \times 9 \times 12 \text{ cm}^3$ ), which were made according to a new method, 'a precise method and equipments to measure plant TE' (State patent), containing 1.7 kg loam with 13.2 mg/kg nitrogen, 47.6 mg/kg phosphorus and 35.8 mg/kg potassium. After sowing, the pots were sealed with plastic cloth. The little holes which just allowed wheat coleoptiles through were poked in the plastic cloth above the wheat coleoptiles. Then the wheat coleoptiles were picked out the holes with needle. Two levels of soil moisture were given (CK: 75% maximum capillary water capacity; and drought stress (DS): 45% maximum capillary water capacity) with 6 replications, and the seedling density was 20 for each pot.

**Physiological measurements and sampling.** Twenty eight days after sowing, all the indexes were measured, and the samples were taken.

The water consumption ( $Cw_i$ ) was measured by weighing the pots every 2 days. The total water consumption ( $Cw$ ) for the growth period was calculated as follows:  $Cw = \sum Cw_i$ . Because the evaporation

could be neglected, the transpiration efficiency at the plant level (TE<sub>p</sub>) could be calculated with the ratio of plant biomass (BM)/ $Cw$ .

Net  $\text{CO}_2$  assimilation rate ( $P_n$ ), transpiration rate (Tr), stomatal conductance ( $g_s$ ) and intercellular  $\text{CO}_2$  concentration ( $C_i$ ) of seedling leaves were measured with a Li-6400 (LI-COR, Lincoln, NE, USA) under  $25 \pm 0.3$ ,  $1500 \mu\text{mol}/\text{m}^2/\text{s}$  intensity of radiation and  $380 \pm 2.83 \mu\text{mol}/\text{mol}$   $\text{CO}_2$  concentration between 9:30 am and 11:00 am. Net photosynthetic oxygen evolution rate ( $P_n(\text{O}_2)$ ) was measured at  $25 \pm 0.3$ , with Yaxin-1151 biological oxygen determinator (Yaxinliyi Technology Co., Ltd. Beijing; Zheng 2006). Total chlorophyll content (Chl(a + b)) was measured by the grinding extraction methods in 95% ethanol, using UV-vis spectrophotometer (UV2450, Tokyo, Japan). Soluble sugar and proline content were determined by ninhydrin colorimetric and the authrone colorimetric method, respectively, using UV-vis spectrophotometer (Zheng 2006). A WP4 Dewpoint Potential Meter (Decagon Devices, Inc., Pullman, WA DC., USA) was used to determine leaf water potential ( $\Psi_w$ ). The second fully-developed leaves were selected and the abaxial epidermis and mesophyll were scraped off to observe the adaxial epidermal stoma to calculate stomatal density under a Zeiss Axioplan 2 imaging MOT microscope ( $40 \times$  magnification). And the stomatal length was measured under 200 multiple vision with Axio Vision 4.0 software.

**Data analysis.** The data were analyzed by two-way analysis of variance, followed by LSD test at  $P = 0.05$  level to compare the means, and the correlation was analyzed by Pearson Product-moment Correlation Coefficient method using SPSS 13.0 for Windows.

## RESULTS AND DISCUSSION

### The change of transpiration efficiency at plant and leaf level

Under drought stress, the dry biomass of the four varieties significantly decreased by 15.1% (Shi4185), 26.6% (Kenong199), 10.2% (Jinmai47) and 5.8% (Luohan2) (Figure 1). And the water consumption for plant growth was decreased by more than 42.0%, 48.6%, 53.6% and 53.3%, respectively (Figure 2). However, the transpiration efficiency at plant level was significantly increased by 46.4%, 42.8%, 93.4% and 101.7% (Figure 3). Shi4185 and Kenong199 had significantly higher TE<sub>p</sub> than Jinmai47 and Luohan2 in CK, but lower TE<sub>p</sub> in the drought treatment.

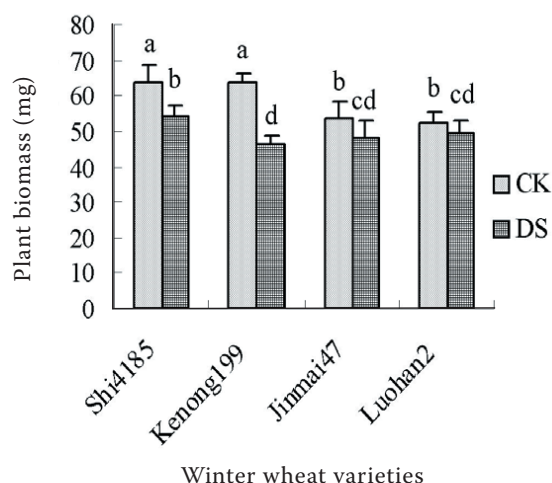


Figure 1. The plant biomass of the 4 varieties in different soil moisture. Determined after sowing 28 days. Different letters above the bars indicated significant difference at  $P \leq 0.05$ . The little bars represent S.E., and DS means drought stress. The same as below

Transpiration efficiency at leaf level was measured with the ratio of  $P_n/Tr$ . The results show that TEL of the 4 varieties significantly increased by 5.1%, 7.9%, 19.0% and 19.9% under drought stress. Shi4185 and Kenong199 had higher TEL than Jinmai47 and Luohan2 in controls, however, the opposite trend was observed for the drought treatment (Figure 4).

Transpiration efficiency at both plant and leaf level was improved. A close linear relationship ( $R^2 = 0.9208$ ) was found between TE<sub>p</sub> and TEL (Figure 5). However, comparing the changes of TE<sub>p</sub> and TEL, it could be seen that the increase of TE<sub>p</sub> was much higher than that of TEL.

It has been demonstrated that there is a TE difference amongst different wheat genotypes (Dong et al. 2008, Blum 2009). In this study, the 4 varieties grown under the same soil moisture conditions had different TE. The TEL and TE<sub>p</sub> determined using a zero-evaporation pot sample significantly increased when soil water content decreased. This is consistent

with other researchers' results at leaf and grain yield level (Xue et al. 2006, Kahlown et al. 2007). The linear regression relationship between TE<sub>p</sub> and TEL suggests that TEL was the basis of TE<sub>p</sub>. However, the measurement of TEL was affected by diurnal variation of  $P_n$  and  $Tr$  and the position on the leaf, so that TE<sub>p</sub> should be better for showing the characteristics of plant water consumption.

### The physiological way to regulate TEL improvement

In the drought treatment, the  $P_n$  was reduced by 44.4%, 51.4%, 32.1% and 41.3% for the varieties, while the  $C_i$  was increased (Table 1), which indicated that the decline of  $P_n$  was possibly mainly affected by non-stomatal factors ( $CO_2$  assimilation ability of mesophyll cells is weaker).

The rate of  $P_n/g_s$  (Inner transpiration efficiency, Figure 6) can reflect the status of photosynthesis

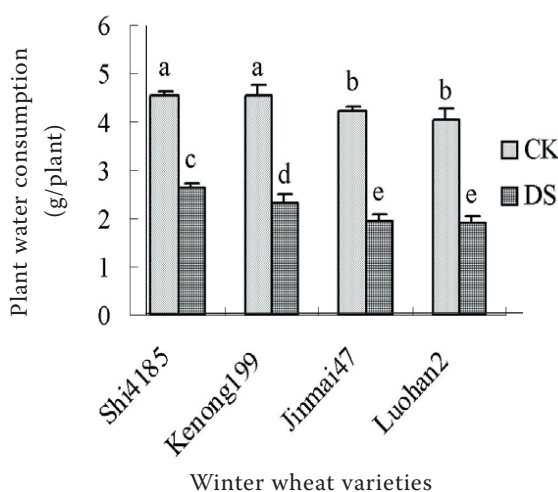


Figure 2. The plant water consumption of the 4 varieties in different soil moisture

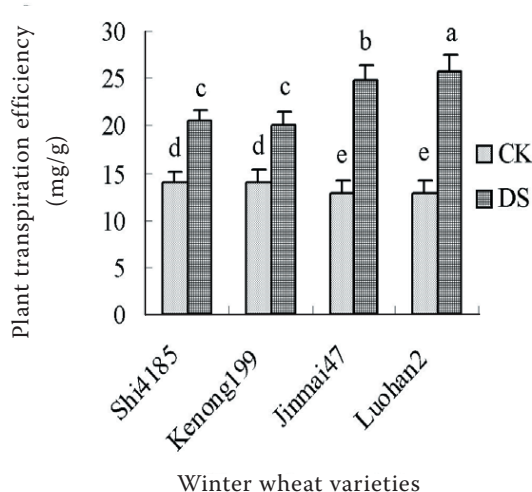


Figure 3. The transpiration efficiency at plant level of the 4 varieties in different soil moisture

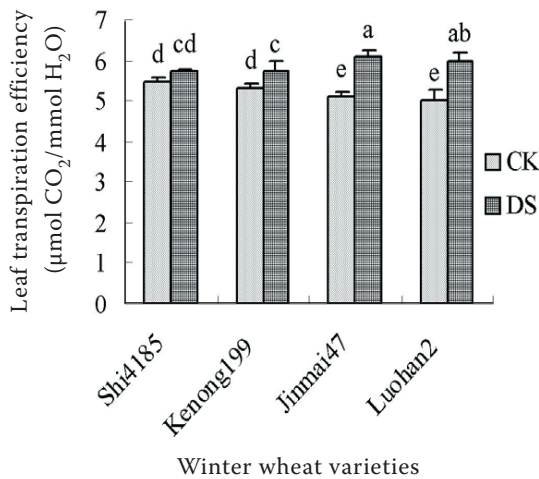


Figure 4. The leaf transpiration efficiency of the 4 varieties in different soil moisture

(Osmond et al. 1980). The inner transpiration efficiencies of Shi4185 and Kenong199 decreased when soil water content was low, and the inner transpiration of Kenong199 decreased significantly, while the rate of Jinmai47 and Luohan2 were increased. This suggests that a strong non-stomatal limitation of photosynthesis occurred in the case of Shi4185, especially to Kenong199, while Jinmai47 and Luohan2 were relatively less affected by non-stomatal limitation.

In order to further testify the existence of non-stomatal limitation, we determined the net photosynthetic oxygen evolution rate of leaf. In determining Pn(O<sub>2</sub>) conditions, photorespiration and CO<sub>2</sub> flow limitation to chloroplasts through stoma (stomatal limitation) are almost eliminated and it is possible to analyze photosynthesis without

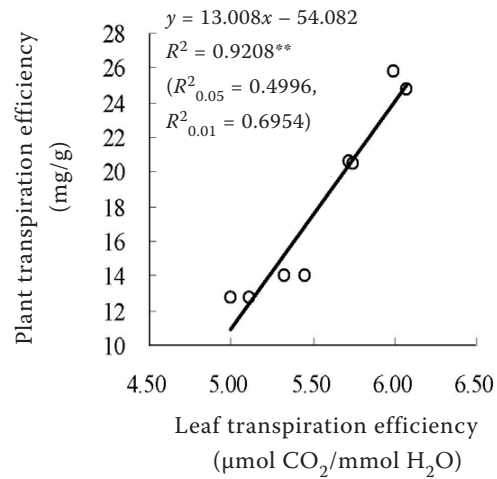


Figure 5. The relationship between leaf transpiration efficiency and plant transpiration efficiency

these limitations (Riberio et al. 2003). The result showed that Pn(O<sub>2</sub>) was reduced by 46.4%, 51.8%, 32.3% and 42.4% for the four varieties, respectively (Table 1), and a significant relationship ( $R = 0.999$ ) was found between Pn and Pn(O<sub>2</sub>) (Figure 7).

$g_s$  was decreased by 42.9%, 43.6%, 34.2% and 53.2% for the four varieties, respectively, and a close linear relationship was found between Tr and  $g_s$  ( $R^2 = 0.9547$ , Figure 8), which suggests that transpiration was regulated by the stomata. This result is similar to that observed by Osmond et al. (1980).

The reasons for the Pn decrease are not beyond the scope of stomata closing and the photosynthetic capability of mesophyll declining. The decrease of Pn was attributed to non-stomatal limitation when  $g_s$  decreased and  $C_i$  increased simultaneously

Table 1. The photosynthetic traits of the 4 varieties in different soil moisture

		Pn ( $\mu\text{molCO}_2/\text{m}^2/\text{s}$ )	Tr ( $\text{mmol}/\text{m}^2/\text{s}$ )	$g_s$ ( $\text{mol}/\text{m}^2/\text{s}$ )	$C_i$ ( $\mu\text{mol}/\text{mol}$ )	Pn(O <sub>2</sub> ) ( $\mu\text{molO}_2/\text{m}^2/\text{s}$ )
Shi4185	CK	25.7 ± 2.1 <sup>a</sup>	4.73 ± 0.13 <sup>a</sup>	0.71 ± 0.023 <sup>a</sup>	148.5 ± 6.1 <sup>d</sup>	24.8 ± 0.88
	DS	14.3 ± 1.1 <sup>c</sup>	2.5 ± 0.2 <sup>c</sup>	0.41 ± 0.021 <sup>c</sup>	233.2 ± 7.0 <sup>b</sup>	13.3 ± 0.30
Kenong199	CK	25.5 ± 1.8 <sup>a</sup>	4.8 ± 0.1 <sup>a</sup>	0.73 ± 0.028 <sup>a</sup>	154.8 ± 9.0 <sup>d</sup>	24.7 ± 0.88
	DS	12.4 ± 1.8 <sup>c</sup>	2.15 ± 0.02 <sup>d</sup>	0.41 ± 0.080 <sup>c</sup>	261.5 ± 7.7 <sup>a</sup>	11.9 ± 0.62
Jinmai47	CK	22.4 ± 1.5 <sup>b</sup>	4.39 ± 0.72 <sup>b</sup>	0.60 ± 0.006 <sup>b</sup>	185.1 ± 6.2 <sup>c</sup>	21.7 ± 0.52
	DS	15.2 ± 1.0 <sup>c</sup>	2.5 ± 0.05 <sup>c</sup>	0.40 ± 0.015 <sup>c</sup>	194.5 ± 8.7 <sup>c</sup>	14.7 ± 0.54
Luohan2	CK	22.3 ± 2.1 <sup>b</sup>	4.47 ± 0.05 <sup>b</sup>	0.69 ± 0.001 <sup>a</sup>	157.3 ± 8.2 <sup>d</sup>	21.7 ± 0.59
	DS	13.1 ± 1.4 <sup>c</sup>	2.18 ± 0.03 <sup>d</sup>	0.32 ± 0.026 <sup>d</sup>	187.5 ± 7.1 <sup>c</sup>	12.5 ± 0.86

The means followed by different letters are significantly different at  $P \leq 0.05$ ,  $\pm$  S.E. The parameters were determined at  $25 \pm 0.3^\circ\text{C}$ . Pn, Tr,  $g_s$ ,  $C_i$ , and Pn(O<sub>2</sub>) in the table mean net photosynthetic rate. Transpiration rate, stomatal conductance and net photosynthetic oxygen evolution rate, respectively.



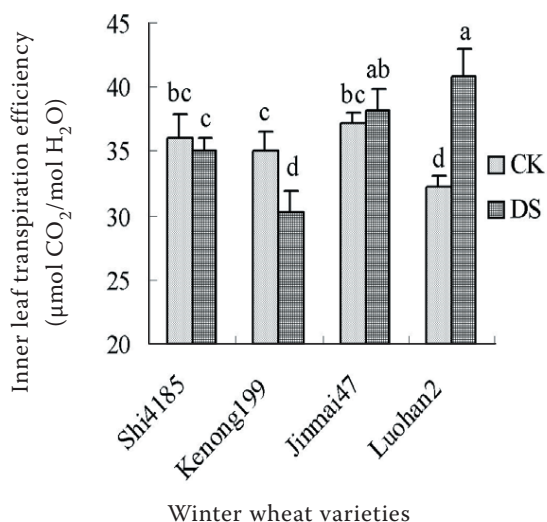


Figure 6. The inner leaf transpiration efficiency of the 4 varieties in different soil moisture

(Farquhar and Sharkey 1982). We thus concluded that Pn of the four varieties was limited by non-stomatal factors in drought stress. This was consistent with the results of DaMatta et al. (2007) and Rouhi et al. (2007) for coconut and almond plants, respectively. The significant correlation between Pn and Pn(O<sub>2</sub>) further confirmed this result. As stomatal conductivity of H<sub>2</sub>O was 1.56 times as large as that of CO<sub>2</sub> (Grant et al. 2005), the relationship between Tr and g<sub>s</sub> was closer than that between Pn and g<sub>s</sub>. And the linear relationship between g<sub>s</sub> and Tr indicates that Tr was mainly controlled by stomatal factors.

The results above show that there was a larger decrease scope of Tr than Pn under drought, which

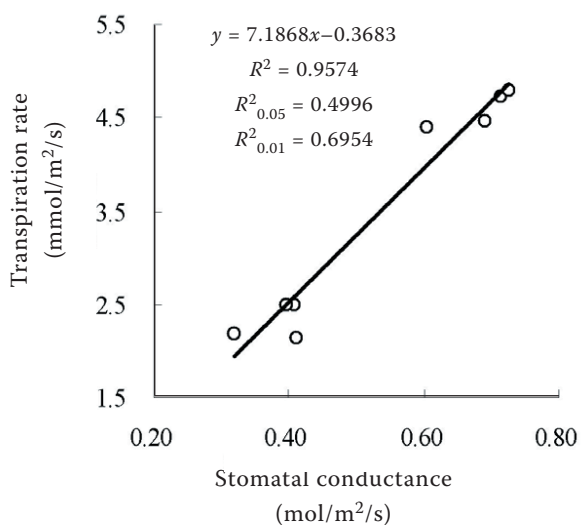


Figure 8. The relationship between transpiration rate and stomatal conductance (determined at 25 ± 0.3°C)

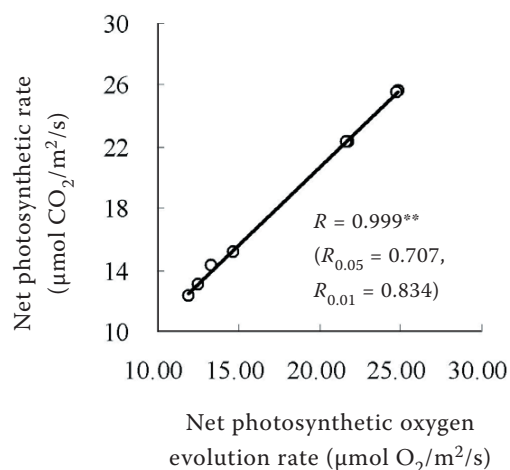


Figure 7. The correlation analysis between net photosynthetic CO<sub>2</sub> assimilation and net photosynthetic O<sub>2</sub> evolution rate (determined at 25 ± 0.3°C)

was the main reason why TEI increased. This result was similar to Warren's (2008) conclusion; they pointed out that the increase of TEI was mainly caused by the larger decrease scope of Tr, not by the decrease of Pn.

Our results indicate that TE improvement of the 4 varieties under drought was regulated via the stomata (regulating Tr) and via mechanisms that do not involve the stomata (regulating Pn). The stomatal mechanism is more sensitive than the non-stomatal mechanism because of the larger decline of Tr than Pn.

### Physiological activities associated with the regulation way of TE

**Activities with non-stomatal way.** Soluble sugars and proline are osmolytes induced by adverse conditions. Within a certain range of severity of water stress, many plants can maintain cell function and relative water content by osmotic regulation (Sara et al. 2009). Under drought condition, soluble sugars and proline content of all 4 varieties, Shi4185, Kenong199, Jinmai47 and Luohan2, significantly increased by 52.3%, 60.0%, 103.3%, 92.9%, and by 174.7%, 175.0%, 249.2%, 242.9%, respectively. Proline content was more sensitive (induced to a higher level) to soil water deficit (Figures 9–10).

The main factors limiting Pn under drought stress are the decrease of intracellular free water content, and the destroyed environment of photosynthesis. Ψ<sub>w</sub> was significantly lower after drought treatment in our study (Figure 11).

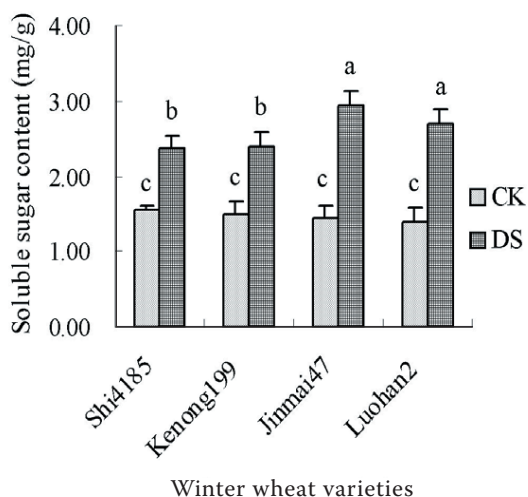


Figure 9. The soluble sugar content of the 4 varieties in different soil moisture

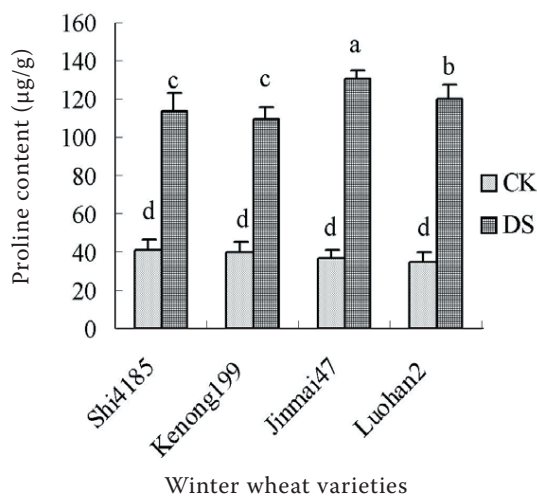


Figure 10. The proline content of the 4 varieties in different soil moisture

The total chlorophyll contents of all 4 varieties significantly decreased under drought condition (Figure 12). Shi4185 and Kenong199 exhibited the characteristics of higher Chl(a + b) in CK, while lower in drought treatment.

TEI is determined by Pn and Tr, so any factor which influences Pn and Tr would have a certain effect on TE. Leaf water potential is the best index which reflects the water status of plant. Low leaf water potential results in TE increase- and adaptation response to water deficit. According to the relation formula of osmotic potential (Lambers et al. 2005):  $\Psi_w = \Psi_s + \Psi_p$ , it can be achieved that leaf keeps low osmotic potential and high water potential, simultaneously, as soil moisture de-

creased. The increase of osmolytes can improve leaf relative water content, scavenge active oxygen and protect the integrity of membrane. DaMatta et al. (2003) believed that the osmotic adjustment (OA) under drought conditions was the main factor to maintain high transpiration efficiency. In this study, the varieties with higher soluble sugar and proline content had higher  $\Psi_w$ , Chl(a + b), Pn and TEI under drought stress (Figures 4 and 10). Hence, we concluded that OA kept leaf water condition well, membrane and photosynthetic system stability was one of the ways by which winter wheat maintained higher Pn. Chl(a + b) was the physiological foundation of photosynthesis. So this suggested the decrease of Chl(a + b) was possibly one of the

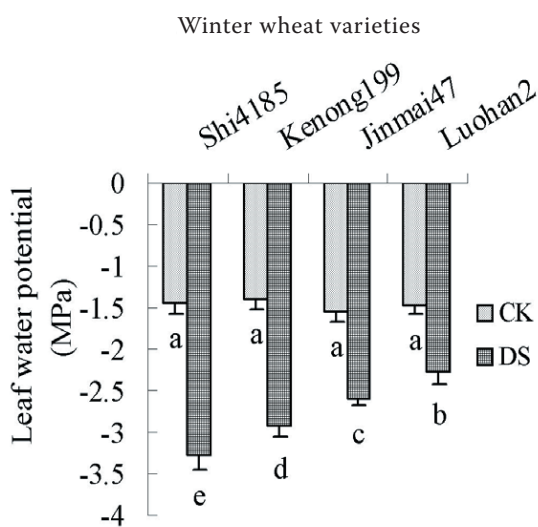


Figure 11. The leaf water potential of the 4 varieties in different soil moisture (determined at 25 ± 0.3°C, 11:00–12:00)

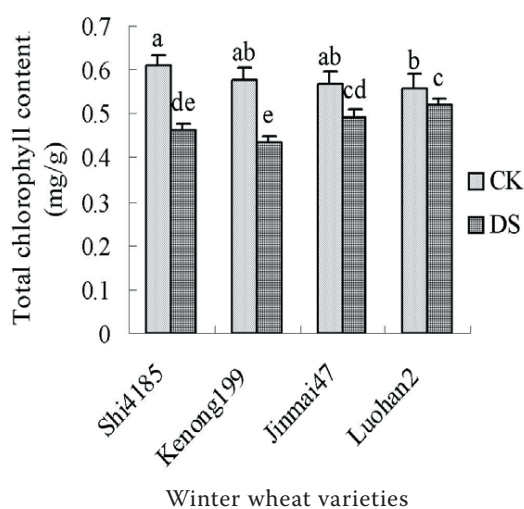


Figure 12. The total chlorophyll content of the 4 varieties in different soil moisture

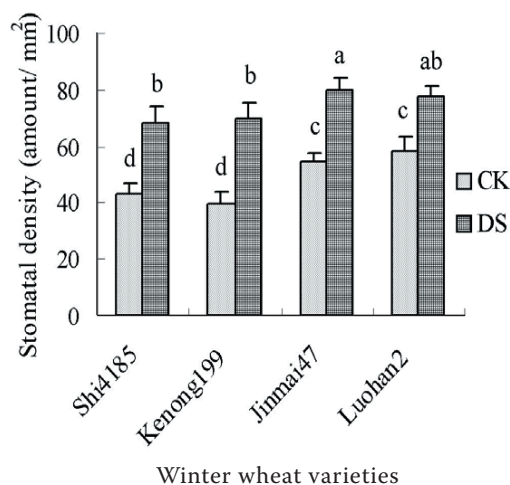


Figure 13. The response of stomatal density of the 4 varieties to soil moisture

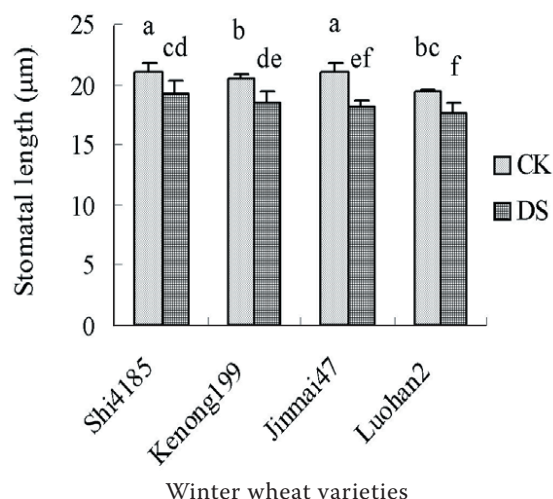


Figure 14. The response of stomatal length of the 4 varieties to soil moisture

reasons why non-stomatal limitation of photosynthesis occurred under drought condition.

**Stomatal activities with stomatal way.** The increase in stomatal density and the decline of stomatal length are considered as an indication of plant adaptability to drought stress (Maes et al. 2009). The adaxial stomatal density of the four varieties increased by 58.7% (Shi4185), 75.4% (Kenong199), 45.4% (Jinmai47) and 33.2% (Luohan2) under drought, respectively (Figure 13); in the contrary, stomatal length of the four varieties significantly decreased in drought treatment, namely by 9.0%, 9.4%, 13.2% and 9.0%, respectively (Figure 14).

According to the model of stomatal conductance reported by Jarvis (1976),  $g_s = g_{max} \times G(x)$ ;  $g_{max}$  means max stomatal conductance, which is determined by stomatal morphology traits and environment factors,  $G(x)$  means relative degree of stomatal opening. In our study, the seedlings in different treatments were grown in the same environment. Yet, the  $g_s$  was reduced by 42.9%, 43.6%, 34.2% and 68.1%, respectively, which indicated that the  $g_s$  decline was mainly controlled by the decline of stomatal aperture.

The scope of stomatal density increased much more than the variation of stomatal length in drought. However, the  $g_s$  significantly decreased, and its decline was mainly caused by the closing of stomata. This is consistent with the view of White et al. (2000). Now, a clear threat presents: soil moisture affected stomatal density, stomatal length, especially stomatal aperture, which kept  $g_s$  low;  $g_s$  determined  $T_r$ , and then, lower  $T_r$  improved TEL.

## REFERENCES

- Blum A. (2009): Effective use of water (EUW) and not water-use efficiency (WUE) is the target of crop yield improvement under drought stress. *Field Crops Research*, 112: 119–123.
- Dong B.D., Liu M.Y., Shao H.B., Li Q.Q., Shi L., Du F., Zhang Z.B. (2008): Investigation on the relationship between leaf water use efficiency and physio-biochemical traits of winter wheat under rainfed condition. *Colloid Surface B*, 62: 280–287.
- Elisabeth S., Evan D.G.F., Mette T., Piers M.F., Andrew J.D., (2009): Typologies of crop-drought vulnerability: an empirical analysis of the socio-economic factors that influence the sensitivity and resilience to drought of three major food crops in China (1961–2001). *Environmental Science and Policy*, 12: 438–452.
- DaMatta F.M., Chaves A.R.M., Pinheiro H.A., Ducati C., Loureiro M.E. (2003): Drought tolerance of two field-grown clones of *Coffea canephora*. *Plant Science*, 164: 111–117.
- Rouhi V., Samson R., Lemeur R., Van Damme P. (2007): Photosynthetic gas exchange characteristics in three different almond species during drought stress and subsequent recovery. *Environmental and Experimental Botany*, 59: 117–129.
- Farquhar G.D., Sharkey T.D. (1982): Stomatal conductance and photosynthesis. *Annual Review of Plant Physiology*, 33: 317–345.
- Giorio P., Sorrentino G., d'Andria R. (1999): Stomatal behaviour leaf water status and photosynthetic response in field-grown olive trees under water deficit. *Environmental and Experimental Botany*, 42: 95–104.
- Grant R.F., Arain A., Arora V., Barr A., Black T.A., Chen J., Wang S., Yuan F., Zhang Y. (2005): Intercomparison of techniques to model high temperature effects on CO<sub>2</sub> and energy exchange in temperate and boreal coniferous forests. *Ecological Modelling*, 188: 217–252.

- Jarvis P.G. (1976): The interpretation of the variations in leaf water potential and stomatal conductance found in canopies in the field. *Philosophical Transactions of the Royal Society of London. B: Biological Sciences*, 273: 593–610.
- Maes W.H., Achten W.M.J., Reubens B., Raes D., Samson R., Muys B. (2009): Plant-water relationships and growth strategies of *Jatropha curcas* L. seedlings under different levels of drought stress. *Journal of Arid Environment*, 73: 877–884.
- Kahlowan M.A., Raoof A., Zubair M., Kemper W.D. (2007): Water use efficiency and economic feasibility of growing rice and wheat with sprinkler irrigation in the Indus Basin of Pakistan. *Agricultural Water Management*, 87: 292–298.
- Lambers H., Chapin III F.S., Pons T.L. (2005): *Plant Physiological Ecology*. Springer-Verlag, New York, 114.
- Osmond C.B., Bjoerkman O., Anderson D.J. (1980): *Physiological Process in Plant Ecology toward a Synthesis with Atriplex*. Ecological Studies 36. Berlin, Heidelberg, New York, Springer-Verlag, 347–354.
- Riberio R.V., Machado E.C., Oliveira R.F. (2003): Early photosynthetic responses of sweet orange plants infected with *Xylella fastidiosa*. *Physiological and Molecular Plant Pathology*, 62: 167–173.
- Richards R.A. (2006): Physiological traits used in the breeding of new cultivars for water-scarce environments. *Agricultural Water Management*, 80: 197–211.
- Rouhi V., Samson R., Lemeur R., Damme P.V. (2007): Photosynthetic gas exchange characteristics in three different almond species during drought stress and subsequent recovery. *Environmental and Experimental Botany*, 59: 117–129.
- Salvatore L.C., Cristina P., Emanuele S., Venera C., Salvatore F. (2007): Effects of soil water content and nitrogen supply on the productivity of *Miscanthus × giganteus* Greef et Deu. *Mediterranean Environment. Industrial Crop Production*, 25: 75–88.
- Sankar B., Abdul J.C., Manivannan P., Kishorekumar A., Somasundaram R., Panneerselvam R. (2008): Relative efficacy of water use in five varieties of *Abelmoschus esculentus* (L.) Moench. Under water-limited conditions. *Colloid Surface B*, 62: 125–129.
- White S.D., Ganf G.G. (2000): Influence of stomatal conductance on the efficiency of internal pressurisation in *Typha domingensis*. *Aquatic Botany*, 67: 1–11.
- Warren K.C. (2008): Evaluation of wild *Solanum* species for drought resistance: 1. *Solanum gandarillasii* Cardenas. *Environmental and Experimental Botany*, 62: 221–230.
- Xue Q.W., Zhu Z.X., Musick J.T., Stewart B.A., Dusek D.A. (2006): Physiological mechanisms contributing to the increased water-use efficiency in winter wheat under deficit irrigation. *Journal of Plant Physiology*, 163: 154–164.
- Yang L.M., Han M., Zhou G.S., Li J.D. (2007): The changes in water-use efficiency and stoma density of *Leymus chinensis* along Northeast China Transect. *Acta Ecologica Sinica*, 27: 16–23.
- Zheng B.S., Yan Y.L., Wu J.S., Wang J.G. (2009): *Modern Plant Physiology and Biochemistry Research*. China Meteorological Press, Beijing.

Received on November 5, 2009

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