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# Improving water-use efficiency by decreasing stomatal conductance and transpiration rate to maintain higher ear photosynthetic rate in drought-resistant wheat

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ABSTRACT

In wheat, the ear is one of the main photosynthetic contributors to grain filling under drought stress conditions. In order to determine the relationship between stomatal characteristics and plant drought resistance, photosynthetic and stomatal characteristics and water use efficiency (WUE) were studied in two wheat cultivars: the drought-resistant cultivar ‘Changhan 58’ and the drought-sensitive cultivar ‘Xinong 9871’. Plants of both cultivars were grown in pot conditions under well-watered (WW) and water-stressed (WS) conditions. In both water regimes, ‘Changhan 58’ showed a significantly higher ear photosynthetic rate with a lower rate of variation and a significantly higher percentage variation of transpiration compared to control plants at the heading stage under WS conditions than did ‘Xinong 9871’ plants. Moreover, ‘Changhan 58’ showed lower stomatal density (SD) and higher stomatal area per unit organ area (A) under both water conditions. Water stress decreased SD, A, and stomatal width (SW), and increased stomatal length in flag leaves (upper and lower surfaces) and ear organs (awn, glume, lemma, and palea), with the changes more pronounced in ear organs than in flag leaves. Instantaneous WUE increased slightly, while integral WUE improved significantly in both cultivars. Integral WUE was higher in ‘Changhan 58’, and increased by a greater amount, than in ‘Xinong 9871’. These results suggest that drought resistance in ‘Changhan 58’ is regulated by stomatal characteristics through a decrease in transpiration rate in order to improve integral WUE and photosynthetic performance, and through sustaining a higher ear photosynthetic rate, therefore enhancing overall drought-resistance.



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## 1. Introduction

Wheat (*Triticum aestivum* L.) is one of the most important food crops in northern China and worldwide. In all areas where it is grown, drought is a major limiting factor influencing yield [1]. Farmers face numerous challenges involving irrigation, such as limited sources of water, pumping costs, and inadequate engineering capacity [2]. The need to improve crop yield and water management has encouraged investigation of possible mechanisms for enhancing water use efficiency (WUE). Zhang et al. [3] reported that plant WUE is regulated by genetic and environmental factors and by cultivation methods. Accordingly, investigation of drought resistance and water conservation needs to include an analysis of the physiological properties of different wheat genotypes.

Stomata are important portals for gas and water exchange in plants and have a strong influence on characteristics associated with photosynthesis and transpiration. As stomata control temperature and WUE, they are vital to the existence of the plant. Stomata vary in size and density among different species and among cultivated varieties within species. Moreover, stomatal characteristics are greatly influenced by environmental conditions. Woodward et al. [4,5] showed that a rise in atmospheric $CO_2$ concentration and temperature results in a decrease in stomatal density (SD). Under conditions of short-term water stress, plants increase their WUE by reducing stomatal aperture and thereby transpiration rate; however, under conditions of prolonged water deficit, plants frequently also produce leaves with reduced maximum stomatal conductance ($g_{w(max)}$) resulting from altered SD and/or size [6–8].

Flag leaf photosynthesis is generally considered the main source of assimilates for grain filling [9], although the contribution of ear photosynthates to $C_3$ cereal productivity has also been a subject of debate for several years [10]. As a consequence of this debate, considerable research on leaf stomatal structure and characteristics in wheat has been carried out. It is now accepted that ear photosynthesis is a major contributor to final grain yield [11–13], especially during drought conditions, when it may be the main photosynthetic contributor to grain filling [14–16].

Various factors that contribute to superior photosynthetic performance of non-leaf green organs under stress conditions have been studied, including osmotic adjustment, anatomical structure, and aging conditions [12,14–19]; however, their relationship to stomatal structure and properties is still not entirely established. Although some studies have analyzed the distribution of stomata in the wheat ear, there have been no systematic studies to date of the relationships between photosynthetic characteristics in the flag leaf and ear and stomatal structure and WUE under different conditions of water availability. In the present study, the correlation between stomatal characteristics and WUE in two wheat cultivars with different drought resistance characteristics was analyzed in order to provide information of potential use for increasing wheat yield and WUE by exploiting the stress-tolerance ability of non-leaf photosynthetic organs.

## 2. Materials and methods

### 2.1. Plant materials and experimental settings

Two wheat varieties with different drought resistance abilities, 'Changhan 58' and 'Xinong 9871', which are resistant and sensitive to water stress, respectively, were used in the present study [20,21].

A pot experiment was conducted over two years, in 2013–2014 and 2014–2015. Soil was collected from Shaanxi province, northwestern China (local red Loessial soil), with a net water content of 3.2%. Plastic pots (top diameter 24 cm, bottom diameter 17 cm, and height 24 cm) were each filled with 7 kg of soil. The soil in each pot was fertilized with the equivalent of 0.347 g (urea) $kg^{-1}$ (soil) and 0.2 g ($K_2HPO_3$) $kg^{-1}$ (soil) prior to sowing. Twenty seeds, previously cultivated for two days in an incubator at 25 °C, were sown in each pot on October 20, 2013 or October 20, 2014; after germination, seedlings were thinned to 10 plants per pot. Plants in the normal water supply treatment were grown in soil with a moisture content of 80% ± 5% (well-watered, WW) of field capacity and those in the water deficit treatment were grown in soil with 40% ± 5% (water stress, WS) water content. Water control was initiated at the late elongation stage by a weighing method, using irrigation as the water control standard every day. Pots were weighed twice every day, in the morning and at dusk, in order to determine the rate of transpirational water loss, and soil water content was maintained by compensating for this water loss by adding tap water to maintain the initial weight. In making these measurements, increased plant weight with growth was taken into account.

### 2.2. Gas exchange parameters

Gas exchange parameters were measured in the morning (9:00–11:00 a.m.), using five replicates for each treatment, at the heading stage (HS), and at early (five days after anthesis; DAA), middle (15 DAA), and late (25 DAA) grain-filling stages. Leaf gas exchange was measured using an open infrared gas analyser (IRGA; LI-COR 6400 system, LI-COR Inch, Lincoln, NE, USA), with a mixed sequence across treatments to reduce timing bias. The spike gas exchange parameters were measured under natural light conditions using the LI-COR 6400 system with a specially constructed cylindrical measuring chamber [22]. The IRGA chamber was irradiated with a photosynthetic photon flux density (PPFD) of 1000 $\mu mol\ m^{-2}\ s^{-1}$, after which ear gas exchange parameters were measured under a PPFD of approximately 1000 $\mu mol\ m^{-2}\ s^{-1}$ (equivalent to natural light). Plants were also irradiated with PPFD at 1000 $\mu mol\ m^{-2}\ s^{-1}$ for at least 30 min prior to photosynthesis measurements. The spike surface area was calculated as described previously for fringe area measurement [23]. Instantaneous WUE was measured according to the ratio between the rates of photosynthesis and transpiration (instantaneous WUE = $P_N / E$).

### 2.3. Stomatal morphology and characteristics

#### 2.3.1. Sample collection

Flag leaf, awn, glume, lemma, and palea samples were obtained from the pot experiment at 15 DAA, between 9:00 and 11:00 h in the study period in 2014–2015.