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VARIATIONS IN ADAPTATION STRATEGIES OF WHEAT CULTIVAR REPLACEMENTS UNDER SHORT-TERM OSMOTIC STRESS

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Abstract

Wheat (*Tritium aestival* L.) production has increased substantially with wheat cultivar replacements, but little is known about how different-year released wheat cultivars maintain whole-plant water balance especially under drought stress. We investigated a series of indices of plant water balance under two water conditions to identify the mechanisms underlying this process in seedlings of four wheat cultivars released in Shaanxi Province, China, from the 1960s to the present decade. The newer cultivars maintained good water status under well-watered conditions by a high uptake of water by roots. The various cultivars released at different times, however, maintained whole-plant water balance differently under osmotic stress. The newer cultivars decreased water loss by decreasing foliar stomatal conductance and severely down-regulating *TaPIP1-2*, a gene encoding an aquaporin. The expression of root aquaporin genes was higher in the older cultivars than in the newer cultivars. Root hydraulic conductance was significantly and positively correlated with the relative expression of another aquaporin homologue, *TaPIP2-1*. The older cultivars maintained high levels of transpiration by a relatively high root hydraulic conductance or a large root surface area. The newer cultivars, with lower root hydraulic conductance, maintained water balance by synchronously decreasing foliar water loss. Wheat breeders should seek more effective solutions for improving the capacity of roots to take up water and for reducing foliar water loss to be able to cope with the expected lower availability of water resources for agriculture in the future.

Key words: Wheat; Plasma intrinsic proteins; Hydraulic conductance; Transpiration.

Introduction

Drought is an important stress factor determining plant growth and productivity worldwide and can decrease biomass and yield in many crops including wheat (Kang *et al*., 2002; Liu *et al*., 2006; Cano *et al*., 2013). Severe and widespread droughts are expected in the next 30–90 years from decreased precipitation and/or increased evaporation (Dai, 2013). Most of the major wheat-producing regions in northern China were increasingly impacted by drought from 1983 to 2008 (Shi & Tao, 2014). Plant growth depends on an optimum balance between water uptake by the roots and water loss from the shoots. Water uptake by roots, which provides the original water source for whole-plant water balance, plays a vital role in maintaining plant water balance under drought conditions (Steudle & Peterson, 1998; Wang *et al*., 2013). Under drought, root-sourced signals induce a series of physiological and molecular changes in crops for adaptation to water-deficit conditions, including changes in hydraulic and stomatal conductances, transpiration rate, antioxidant enzyme activities, and expression of drought-associated genes (Blackman & Davies, 1985; Xiong *et al*., 2006; Ahuja *et al*., 2010).

The response to abiotic stress has been extensively studied in wheat, a widely cultivated and consumed crop throughout the world and especially in Northwestern China (Kudoyarova *et al*., 2011; Wang *et al*., 2013; Biswas *et al*., 2013; Bencze *et al*., 2014; Bloom *et al*., 2014). Wheat production has increased substantially with wheat cultivar replacements (Guarda *et al*., 2004). In past 70 years, at least six wheat cultivar replacements have been recorded in Shaanxi Province in Northwestern China (Zhuang, 2003). Field research conducted in Shaanxi Province has indicated that the modern cultivars are more sensitive to drought stress (Sun *et al*., 2014). However, the mechanism of this process remains unclear. Previous studies about different-decade wheat cultivars were superabundant in photosynthetic rates, stomatal conductances, and antioxidant enzyme activities (Adjei & Kirkham, 1980; Richards, 2000; Brancourt *et al*., 2003; Xiong *et al*., 2006; Wang *et al*., 2008), but little is known about the ability of their roots to take up water. Most studies have also been conducted under favourable conditions of soil conditions. Therefore, the mechanisms of maintaining whole-plant water balance under drought stress between old and new remain unclear.

Ogbaga *et al*. (2014) found Sorghum (*Sorghum bicolor* L.) varieties used strongly contrasting strategies to maintain transpiration and photosynthesis in response to drought. Here, we test whether this phenomenon exists in different-year wheat cultivars adapting to drought stress. We investigated the mechanisms for maintaining whole-plant water balance in four wheat cultivars released in different decades in Shaanxi Province. We collected physiological and molecular data to assess the sensitivities of the cultivars growing under conditions of osmotic stress simulated by the application of polyethylene glycol (PEG-6000).

Materials and Methods

Plant material and treatments: We selected four wheat cultivars released in Shaanxi Province in Northwestern China in the 1960s, 1980s, 2000s, and 2010s (Table 1). FC and XY are here referred to as older cultivars, and CW and CH are referred to as newer cultivars. All four cultivars are also typical representatives of high-yield varieties in the process of wheat cultivars replacement in Shaanxi Province.

Table 1. Chinese wheat cultivars cultivated in different years. They were planted in Shaanxi province in 1960s, 1980s, 2000s and 2010s, respectively.

Cultivar	Growing years	Logogram
Fengchan 3	1960s	FC
Xiaoyan 6	1980s	XY
Changwu 134	2000s	CW
Changhan 58	2010s	CH

Seeds of the four cultivars were disinfected with 2% sodium hypochlorite and then germinated in the dark at 25°C. The seedlings were raised hydroponically in pots in a growth chamber under a 12/12 h photoperiod (25/18°C; RH=50–60%; 400 µmol photons $m^{-2}s^{-1}$) in half-strength modified Hoagland's nutrient solution (pH=6.0), which was well aerated using aquarium diffusers. The plants of all cultivars were divided into two groups at the fifth-leaf stage fifteen days after germination: one was well-watered and served as controls and the other was treated with 10% (m/v) PEG-6000 (-0.20 MPa, determined by a dew point microvolt meter (Model 5520, Wescor, Logan, UT, USA) to induce osmotic stress. Measurements were taken 24 h after treatment. The experiments were performed in triplicate.

Measurements of foliar gas exchange and water potential: Stomatal conductance (g_s) and transpiration rate (E) were measured between 10:00 and 11:00 at the centre of the newest fully expanded leaf under ambient conditions with a Li-6400 portable photosynthesis system (Li-COR Biosciences, Lincoln, NE, USA). Gas exchange was measured from eight randomly selected plants. Leaf water potential (Ψ_{leaf}) of the newer fully expanded leaf was measured between 10:00 and 11:00 by a Model 3500 pressure chamber (Soilmoisture Corp., Santa Barbara, USA).

Assays of foliar water loss and relative water content: Foliar water loss was measured by the method described by Jammes *et al*. (2009). Briefly, the fresh weights of 10 leaves from 2-week-old plants were determined seven times within 100 minutes. The rate of water loss was represented by the weight of the leaves at the various time points divided by the original weight. Relative water content of the latest fully expanded leaves was calculated by (Kocheva *et al*., 2014):

$$\text{Relative water content (\%)} = \frac{(\text{FW-DW})}{(\text{TW-DW})} \text{ x } 100$$

where FW is the fresh weight, DW is the dry weight obtained after drying the leaves at 80 °C in a forced-air oven to a constant weight, and TW is the turgid weight obtained after soaking the leaves in distilled water for 24 h. Briefly, the leaf was insighted into a 50ml centrifuge tube with distilled water. Then the tube was lidded and placed in the 4°C refrigerator with black cloth covered.

Measurements of hydraulic conductance: Whole-plant hydraulic conductance (K_{plant}) was calculated as Eplant/(Ψ_{soil}-Ψ_{leaf}) (Tsuda & Tyree, 2000; Martre *et al*., 2002), where Ψ_{soil} represents the water potential of the nutrient solution. Eplant was measured from plants in a controlled environmental room and was estimated from the weight of the water lost from the plants. Each pot contained one plant was weighed by a digital balance after an acclimation period of >1□h and again after ca. 1□h. Eplant was calculated from ΔW/ (AΔt), where Δt is the time in seconds between the two weighings, ΔW is the weight change (kg) between the two weighings, and A is the leaf area, which was determined at the end of the experiments. Ψ_{leaf} was measured as above. All leaves were sampled to determine the root surface area using a scanner and analysed by WinRHIZO PRO 2009 software (Regent Inc., Quebec, Canada).

Root hydraulic conductance, Lp, was based on the root surface area and was measured with a pressure chamber (Liu *et al*., 2014). The individual seminal root was cut from the base of each plant and was then placed in the pressure chamber. The pressure in the chamber was raised to 0.3 MPa at increments of 0.1 MPa. Exuded sap was collected with glass capillary tubes. The volumes of sap exuded from the root system at the various gas pressures were plotted against time. The slope of this relationship referred to the unit root surface area. This yielded the volume flow, Jvr, in m s^{-1}. Lp was calculated from the slope of the plot of Jvr against driving force, which consisted of Pgas and the osmotic gradient. Lp was thereby determined from the slope of the plot of Jvr against Pgas only:

$$\text{Jvr} = \text{Lp} \times \text{Pgas}$$

After the amount of exuded sap was measured, the root was sampled to determine the root surface area using a scanner and analysed by Win RHIZO PRO 2009 software (Regent Inc., Quebec, Canada). The whole-plant root surface area was also measured.

Quantitative real-time PCR: Total RNA was extracted from the samples using an RNAprep pure Plant Kit (TIANGEN, Beijing, China). The RNA extract was digested with DNase I and examined using a dissociation curve to ensure that DNA was eliminated. cDNA was synthesised in vitro using a Takara RT-PCR Kit (Takara, Dalian, China) according to the manufacturer's instructions. Quantitative real-time PCR was performed on a LightCycler 480 using Takara SYBR Premix EX Taq (Perfect Real Time). The relative expression of two genes encoding putative intrinsic plasma-membrane aquaporins, *TaPIP1-2* and *TaPIP2-1*, were investigated (Zhou *et al*., 2012; Wang *et al*., 2013). The primers used are listed in Table 2. The PCR reaction was conducted as described previously (Wang *et al*., 2013). The data were analysed using the $2^{-\Delta\Delta Ct}$ method and normalised against the data from the well-watered FC cultivar as a relative unit.

Table 2. Primer sequences and general information used in this study.

Primer name	Primer sequence(5'to 3')	Reference
TaPIP1-2 F	ATGGGCTACAGCGGTGCCACCTCC	(Wang *et al.*, 2013)
TaPIP1-2 R	ACGAGCGCGAAGATCATGCCG	
TaPIP2-1 F	GGCCGGACTGAAGTGTAGAT	(Zhou *et al.*, 2012)
TaPIP2-1 R	ACAGGACAAAGGTGTGGGAT	
TaActin F	TGCTATCCTTCGTTTGGACCTT	
TaActin R	AGCGGTTGTTGTGAGGGAGT	

Statistical analyses: The statistical analyses were performed with SPSS version 13.0. One-way anova analysis was used to ascertain the effect of Rht allele in non-stressed and stressed conditions. The figures and regressions were produced using SigmaPlot version 12.01 (Systat Software; http://www.sigmaplot.com).

Results

E, g_s, and Ψ_{leaf}: Under well-watered conditions, FC had a g_s of 0.2674 mol H_2O m^{-2} s^{-1} and CH had a g_s of 0.4096 mol H_2O m^{-2} s^{-1}, an increase of 34.75%. Except for CW, g_s tended to increase from the 1960s to the 2010s (Fig. 1A). Ψ_{leaf} also increased, from -0.6500 MPa (FC) to -0.3950 MPa (CH) (Fig. 1C). Under osmotic stress, g_s and E did not differ significantly between FC and XY but were significantly higher than in CW and CH ($p<0.05$). FC had the highest Ψ_{leaf} among the four cultivars (Fig. 1A-C).

Foliar water loss and relative water content: We measured foliar water loss to determine if the significantly lower E in CW and CH was due to a fast stomatal response. CH closed its stomata firstly, followed by CW, FC, and XY, thereby likely contributing to lower water losses from the leaves (Fig. 2A). The results were similar to the foliar E under osmotic stress. The relative water contents did not differ significantly ($p>0.05$) among the four cultivars after 24 h of osmotic stress relative to the well-watered control treatment (Fig. 2B).

Hydraulic conductance: K_{plant} was significantly lower in FC than that in the other three cultivars ($p<0.05$; Fig. 3). K_{plant} did not differ significantly among XY, CW, and CH but was highest in CH (8.1080 mmol H_2O m^{-2} s^{-1} MPa^{-1}). K_{plant} was lower in all four cultivars under osmotic stress due to the low E (Fig. 4). Lp increased from FC to CW (Fig. 5) but did not differ significantly among the four cultivars under osmotic stress. Lp, however, was lower in the two most recent cultivars under osmotic stress. Lp was significantly positively correlated with K_{plant} (Fig. 6).

Root surface area: Root surface areas ranged from 103.10 to 124.86 cm^2 per plant (Fig. 5B). FC had the largest root surface area, and XY had the smallest. This index, however, did not differ significantly ($p>0.05$) among the cultivars.

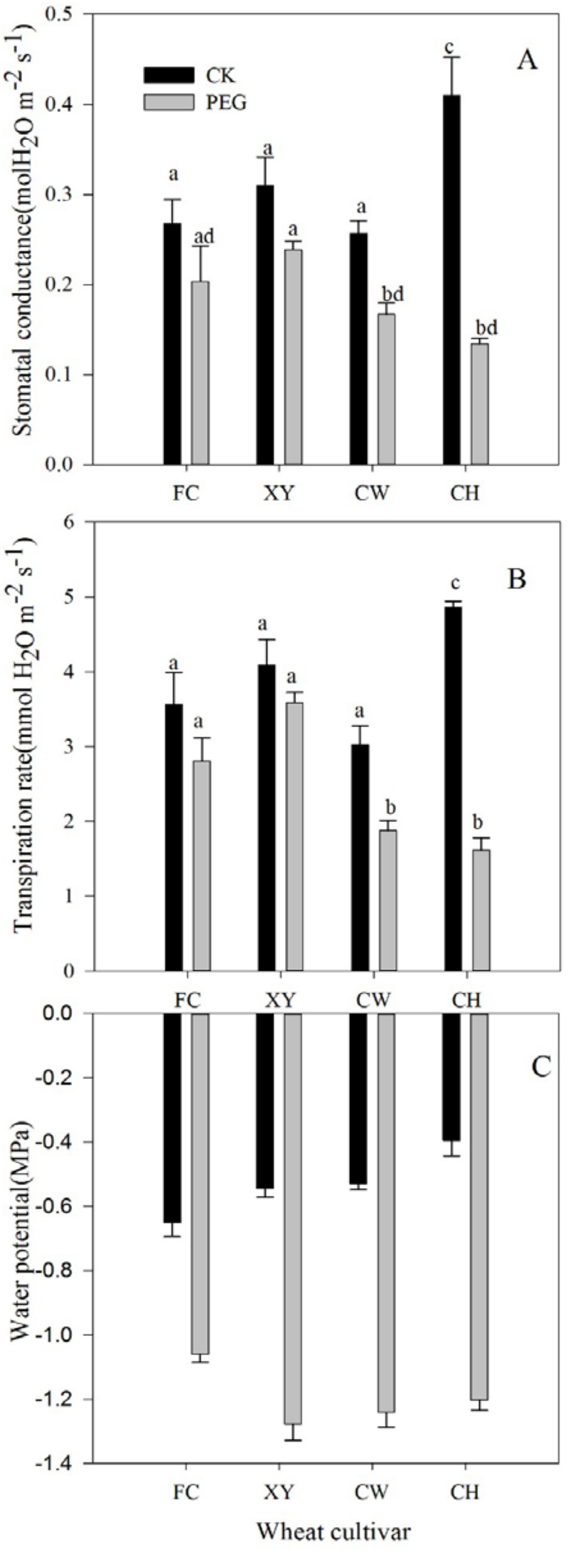

Fig. 1. Effects of osmotic stress on stomatal conductance (A), transpiration rate (B) and water potential (C) in hydroponic culture. New fully expanded leaves were used for measurement in a portable photosynthesis system (Li-6400) after 24 h osmotic treatment. Water potential was measured by a pressure chamber. Values are means ± SE of six replicates. Different letters indicate a significant difference ($p<0.05$).

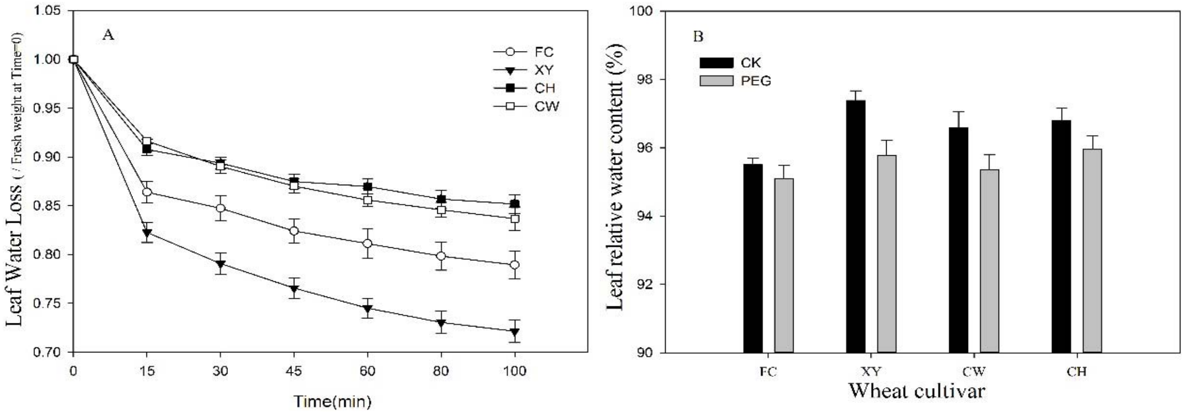

Fig. 2. Leaf water loss (A) and relative water content (B). Leaf water loss of wheat cultivars cultivated in different years. The measurement was conducted in the room with 40% humidity. Detached leaves was weighed using sensitive balance every 15 or 20 min. leaf relative water content was investigated used the latest fully expanded leaves. Values are means ± SE of six replicates.

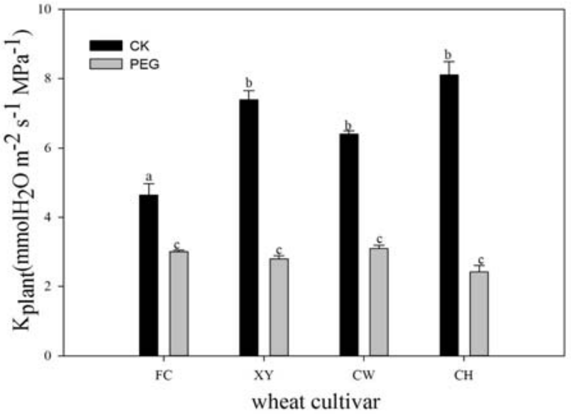

Fig. 3. Effects of osmotic stress simulated by PEG-6000 on whole-plant hydraulic conductance (Kplant). The Kplant was calculated by the transpiration rate determined gravimetrically divided by the difference between root medium and leaf water potential. The transpiration rate was determined gravimetrically. The leaf water potential was measured using a pressure chamber. Average and SE (error bars) of four independent plant analyses was showed. Different letters indicate a significant difference (p<0.05).

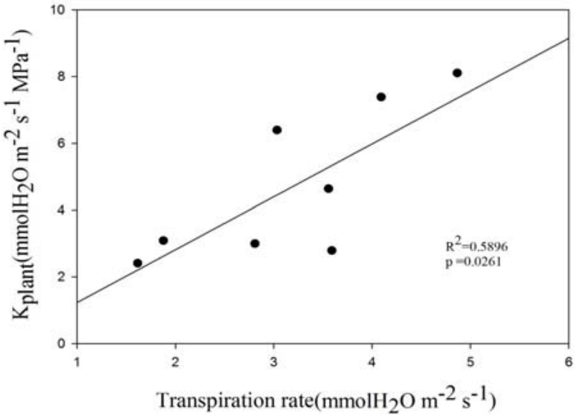

Fig. 4. Correlations between the whole-plant hydraulic conductance and the leaf transpiration rate. The correlation analyses were performed using SigmaPlot version 12.0, and the relation coefficient (R^2) and significant level (P) are shown.

Expression of aquaporin genes: Aquaporins play a crucial role in the regulation of hydraulic conductivity. The relative expression of the aquaporin homologues *TaPIP1-2* and *TaPIP2-1* in the roots and leaves was measured using real-time PCR (Fig. 7) to obtain evidence of their function in the various cultivars. The expression of *TaPIP1-2* varied little among the cultivars under well-watered conditions. The expression of *TaPIP2-1* was positively correlated with Lp. Expression was highest in CW, 5.6-fold higher than in FC. The results were opposite under osmotic stress. The expression of both *TaPIP1-2* and *TaPIP2-1* was higher in FC and XY than in CW and CH. The relative expression of *TaPIP2-1* remained positively correlated with Lp (Fig. 8A). The relative expression of both aquaporin genes was positively correlated with foliar E (Fig. 8B). *TaPIP1-2* expression was lower in leaves relative to the well-watered control plants, while the expression of *TaPIP2-1* was higher, except in CW. The expression of *TaPIP1-2* in leaves was 8% to 33% lower in FC and CH.

Discussion

Plant growth in natural environments depends on an optimum balance between water uptake from soil by roots and water losses from the shoots. Plant roots normally absorb water from the soil, and plant leaves loose water by transpiration to the atmosphere from the stomata (Jackson *et al*., 2000). The newer cultivars maintained good water status under well-watered conditions by a high uptake of water by roots (Figs. 1C and 5).

Plants must maintain the movement of water from the soil to the leaves, and rapid stomatal responses to environmental change are a major feature of this maintenance (Raven, 2002). When the amount of available soil water is moderately or severely limiting, the first option for plants is to close their stomata (Chaves *et al*., 2002; Chaves *et al*., 2009). Our findings supported this strategy. The newer wheat cultivars had rapid stomatal responses (Figs. 1A and 2), but the relative water content did not decrease significantly under osmotic stress in any of the four cultivars (Fig. 2B). We thought that when plant undergone the abiotic stress, they would produce a series of changes (phytohormone and antioxidant system). These solutes can change the leaf water potential, while couldnot change the relative water content. Root-sourced chemical signals (e.g. abscisic acid) may be important in regulating this stomatal responses (Jia *et al*., 1996, Liang *et al*., 1997; Xiong *et al*., 2006; Chaves & Davies, 2010). Chemical signals are sensed earlier in the newer cultivars. The earlier the response of plants to osmotic stress, the better their osmotic adjustment and the better their stress tolerance. Researches also showed foliar aquaporins was invloved in root-sourced signals mediated stomatal control and transpiration at earlier the response of plants to osmotic stress (Martinez *et al*., 2003; Kaldenhoff *et al*., 2008; Lopez *et al*., 2008; Heinen *et al*., 2009). The expression of *TaPIP1-2*, which regulates the hydraulic conductivity of leaves and their cells (Qian *et al*., 2014), decreased more in the newer cultivars. Lower transpiration can thus also be attributed to the down-regulation the foliar aquaporin gene, *TaPIP1-2*. Under osmotic stress, g_s was lower in CW and CH, and the strong down-regulation of foliar *TaPIP1-2* led to decreased water loss.

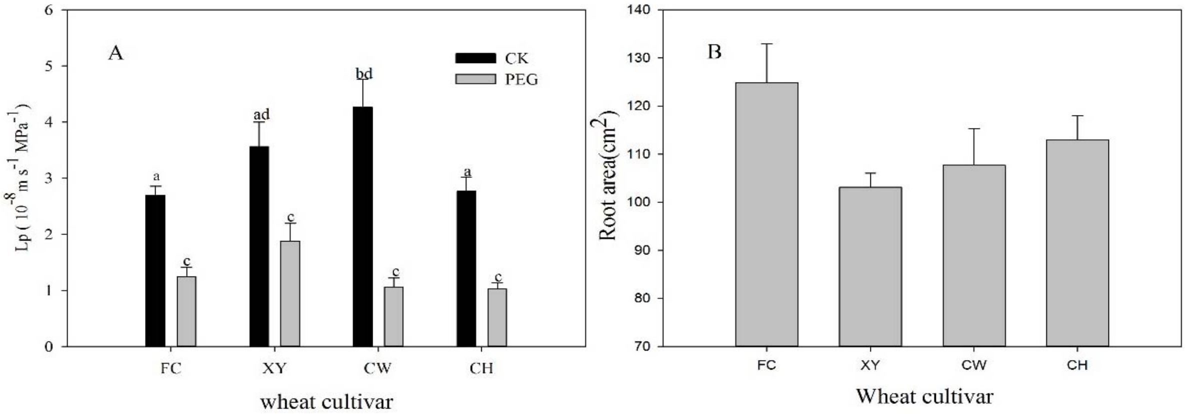

Fig. 5. Effect of osmotic stress on the individual seminal root hydraulic conductance (Lp) in hydroponic culture (A). The individual seminal root of seedlings under control or PEG treatment was cut off near the root base and inserted into the pressure chamber. For a given applied gas pressure, the volume exuded from the root system was plotted against time. The single root surface was also detected to calculate the Lp. Root area of these four cultivars was shown in Fig. B. Values are means ± SE of five replicates. Different letters indicate a significant difference (p<0.05).

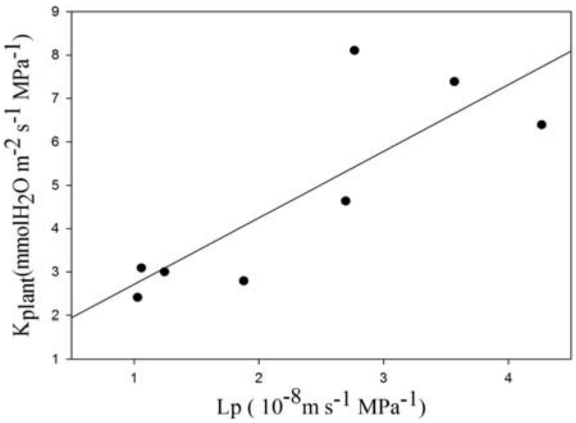

Fig. 6. Correlations between the whole-plant hydraulic conductance and root hydraulic conductance. The correlation analyses were performed using SigmaPlot version 12.0, and the relation coefficient (R^2) and significant level (P) are shown.

K_{plant} consists of the hydraulic conductances of the leaves, stems, and roots and represents the water-channelling capacity of the entire plant (Martre *et al*., 2002). Wheat breeding has increased K_{plant} under well-watered conditions, but not under water deficits (Fig. 3), through higher E and Lp (Figs. 4 and 6). Lp under osmotic stress, though, was higher in XY than in CH and CW, and K_{plant} in XY did not differ from those in CW and CH, indicating that XY had a high stem-water resistance (Javot *et al*., 2003).

Seminal roots supply most of the water needed by 15-day-old wheat or barley seedlings (Knipfer & Fricke, 2011; Fricke *et al*., 2014). We measured the seminal-root Lp and single-plant root surface area to determine how the older cultivars maintained a high E under osmotic stress. Lp represents the capacity of roots to take up water, which is a function of root surface, root anatomy, and root permeability controlled by proteins such as aquaporins (Liu *et al*., 2014). Lp was lower under osmotic stress in the newer cultivars than the older cultivars.

The expression of genes encoding aquaporins, which play important roles in the transport of water through cellular membranes (Preston *et al*., 1992; Martre *et al*., 2002), was tested. The relative expression of these genes was significantly lower in the newer cultivars under osmotic stress. Many studies have confirmed that aquaporins control the cell-to-cell pathway of water uptake (Steudle & Peterson, 1998; Kjellbom *et al*., 1999; Javot *et al*., 2003), and the two aquaporin genes we tested are pivotal in wheat drought resistance (Zhou *et al*., 2012; Wang *et al*., 2013). The relative expression of the aquaporin genes was positively correlated with Lp (R^2=0.5120), indicating that the aquaporins may have contributed to the lower Lp in the newer cultivars. Our results also confirmed that aquaporins are involved in Lp, as reported by previous studies (Wang *et al*., 2013; Liu *et al*., 2014; Qian *et al*., 2014). The regulation of the expression of root aquaporin genes by the foliar transpirational demand has been widely reported (Aroca *et al*., 2006; Sakurai *et al*., 2011; Laur & Hacke, 2013; Vandeleur *et al*., 2014). In our study, the relative expression of the root aquaporin genes under osmotic stress was positively correlated with foliar E, indicating that foliar E was involved in regulating the uptake of water by the roots. FC had a low Lp but a large root surface area (Fig. 5), which enabled this cultivar to maintain its whole-plant water balance.

This study suggests that the various wheat cultivars maintain whole-plant water balance under osmotic stress in different ways. The older cultivars maintain high levels of transpiration with a relatively high Lp or a large root surface area, but the newer cultivars maintain water status by quickly closing their stomata and thereby reducing transpiration becuase they can sense the root-sourced signals earlier. A lower transpirational demand affects the expression of root aquaporin genes to regulate root water uptake (Aroca *et al*., 2006; Sakurai *et al*., 2011; Laur & Hacke, 2013). All four wheat cultivars can thus maintain whole-plant water balance under short-term osmotic stress, but the newer cultivars consume less water to sustain this status. This also explains why newer cultivars can thus also survive longer under drought stress (suspended water supply) (Wang *et al*., 2008). Wheat breeders need to find more effective solutions to improve the capacity of root water uptake and reduce foliar water loss to cope with a growing population and the expected reduction in water resources.

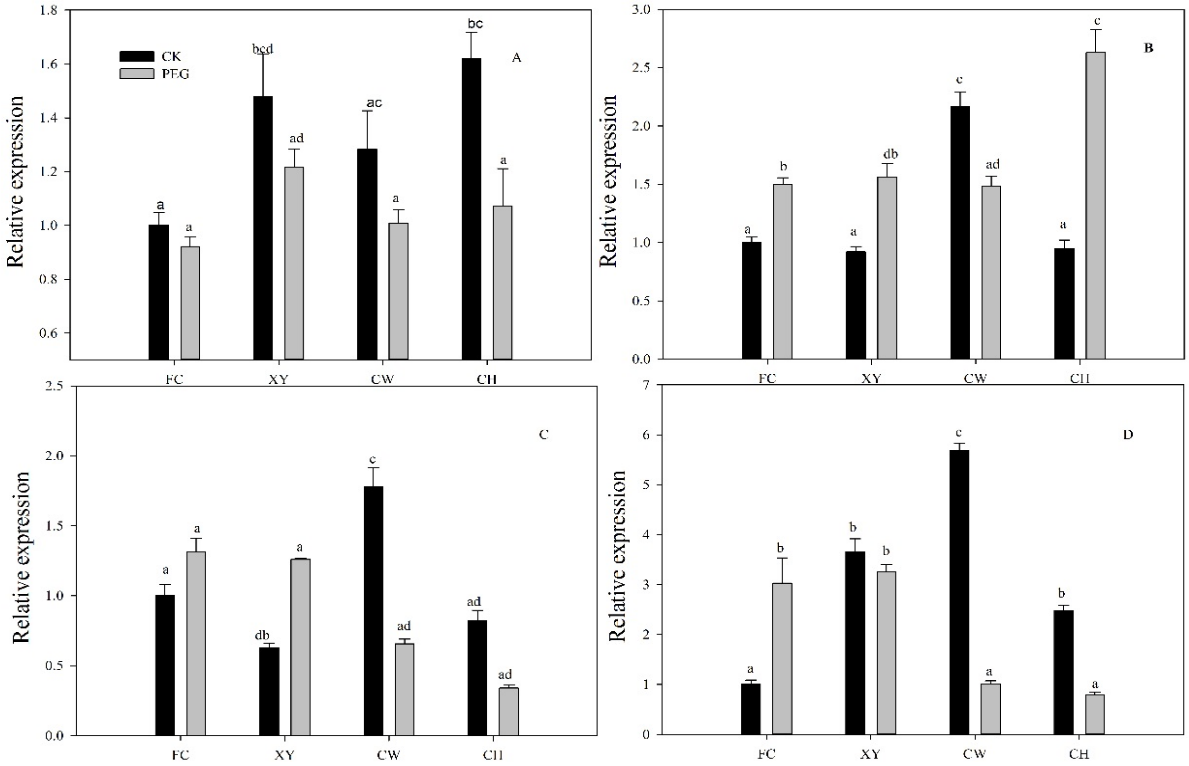

Fig. 7. Effects of osmotic stress simulated by PEG-6000 on the expression levels of leaf and root aquaporin genes *TaPIP1-2*(A:leaf; C:root) and *TaPIP2-1*(B:leaf; D:root). Samples were collected after 24 h osmotic treatment. The relative expression was determined by qRT-PCR. Values are means ± SE of three replicates. Different letters indicate a significant difference (p<0.05).

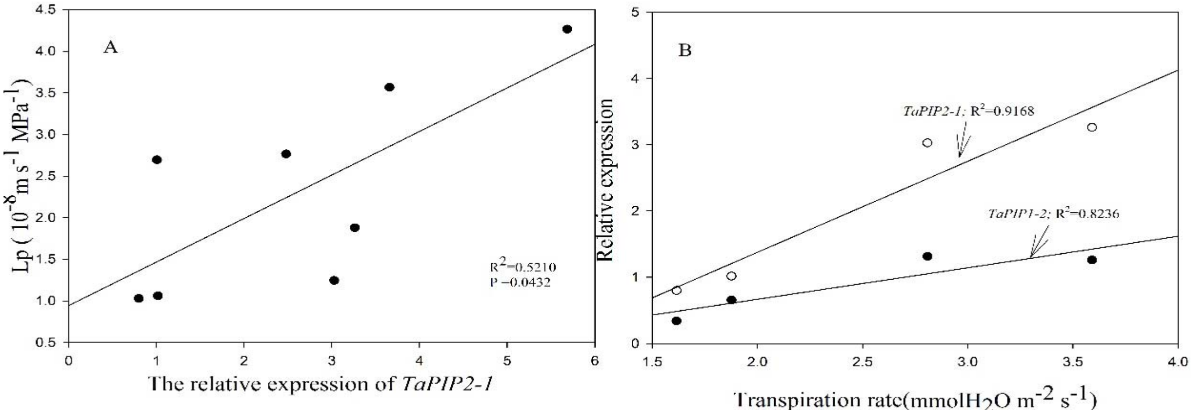

Fig. 8. Root hydraulic conductance (Lp) is positively correlated with the relative expression of *TaPIP2-1* in the roots (A). The correlations between root aquaporins and leaf transpiration rate under osmotic stress (B). The correlation analyses were performed using SigmaPlot version 12.0, and the relation coefficient (R^2) and significant level (P) are shown.

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