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REVIEW

# Improving Water Use Efficiency of Wheat Crop Varieties in the North China Plain: Review and Analysis

MEI Xu-rong[1], ZHONG Xiu-li[1], Vadez Vincent[2] and LIU Xiao-ying[1]

[1] *Institute of Environment and Sustainable Development in Agriculture, Chinese Academy of Agricultural Sciences/State Engineering Laboratory of Efficient Water Use and Disaster Mitigation for Crops/Key Laboratory for Dryland Agriculture, Ministry of Agriculture, Beijing 100081, P.R.China*

[2] *International Crop Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru 502324, India*

## Abstract

The North China Plain (NCP), one of the most important agricultural regions in China, is facing a major water-resource crisis evoked by excessive exploitation of groundwater. To reduce water use while maintaining high crop production level, improving variety water use efficiency (WUE) is an urgent need, especially because other water-saving measures such as water delivery, irrigation, and agricultural practices have already achieved most possible progresses. Evaluation of variety WUE can be performed accurately at the individual plant level ($WUE_p$). Reviewing the studies on physiological factors affecting $WUE_p$ performed up to date, stomatal conductance was considered to be an important trait associating closely with $WUE_p$. The trait showed a large degree of varietal variability under well-watered conditions. Crop varieties differ highly in sensitivity of stomata to soil and air drying, with some varieties strongly reducing their stomatal conductance in contrast with those lightly regulating their stomata. As a result, difference among varieties in $WUE_p$ was enlarged under water deficit conditions in contrast with those under well-watered conditions. The relationship between stomatal conductance and yield depends on water availability of whole growing period in local areas. Usually, large stomatal conductance results in a high yield under good irrigation system, whereas a low stomatal conductance can lead to yield benefit under limited stored soil moisture conditions. In the NCP, winter wheat is the largest consumer of irrigation water, improvement strategies for high WUE aiming at wheat crops are in urgent need. We suggest, for the well-irrigated areas with excessive exploitation of groundwater, the wheat breeding program need to combine medium stomatal conductance (0.35 mmol $H_2O$ $m^{-2}$ $s^{-1}$ or so), high carboxylation efficiency, and high harvest index. Areas with partial/full access to irrigation, or infrequent drought, should target wheat varieties with high stomatal conductance under no water stress and low sensitivity of stomata to soil water deficit. Drought-prone rain-fed areas characterized by frequent and long terminal drought should target wheat varieties with low stomatal conductance under no water stress and high stomata sensitivity to soil drying to make water available during grain filling.

Key words: water use efficiency, yield, stomatal conductance, water deficit

## INTRODUCTION

The North China Plain (NCP) is one of the most important agricultural regions in China, with winter wheat (*Triticum aestivum* L.) and summer maize (*Zea mays* L.) being the most common double-cropping system. The NCP now supplies more than 73% of China's wheat and 33% of its maize (National Bureau of Statistics of China 2006). More than 70% of annual precipitation

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Correspondence MEI Xu-rong, Tel/Fax: +86-10-82109333, E-mail: meixr@ieda.org.cn


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falls from July to September, during the maize growing season, whereas precipitation during the wheat growing season meets only about 25-40% of its water requirements. Due to the excessive exploitation of groundwater for irrigation from both shallow and deep aquifers, the groundwater table has declined rapidly from about 10 m below the soil surface in the 1970s to about 32 m in 2001. Recently, it has been falling steadily at a rate of about 1 m per year (Zhang *et al.* 2003).

With a deepening water-resource crisis, the challenge to meet the future food needs of a rising human population in the NCP is to improve water use efficiency (WUE), by reducing water use while maintaining the current high level of crop production. In recent decades, many studies on water-saving technology, such as water delivery and irrigation (Liu *et al.* 2003), and agricultural practices (Sun and Wang 2001; Zhang *et al.* 2001), have been carried out and the management of water resources has improved WUE (crop output per water input) significantly. In this context, genetically improving WUE appears to be the only solution for further enhancing agricultural WUE (Shan *et al.* 2006). Deng *et al.* (2006) reviewed the progresses in water-saving technologies for the Northern China, and highlighted the need to breed new varieties for high WUE. Compared with agronomic water-saving methods, breeding new crop varieties with a high yield and WUE has the merits of being less investment intensive, greater uptake, and sustainable efficiency to the grower, and therefore has a great promise for the future (Shan *et al.* 2006; Zhang *et al.* 2011).

As a consequence of many efforts in breeding, yield has significantly increased in modern varieties, and this is mainly or at least partly attributed to the increased harvest index (HI) (Siddique *et al.* 1990; Shearman *et al.* 2005; Zhang *et al.* 2010). Since HI was used as the main selection index for selecting high yielding varieties under favorable conditions, this approach has, to a certain extent, indirectly improved yield under water-limiting conditions, as pointed out by Cattivelli *et al.* (2008). WUE is positively related to yield and drought resistance in many water-limited cases (Zhang *et al.* 2011). In wheat varieties bred in past 20 years in the NCP, wheat field WUE had also been increased significantly as yields increased in newer varieties (Zhang *et al.* 2005). The amount of water use, however, still remains high. Further progress in WUE improvement thus needs to be achieved to reduce water use when maintaining the current production level.

## EVALUATION AND GENETIC IMPROVEMENT OF VARIETY WATER USE EFFICIENCY EXPECTS EXPLORING WUE FROM INDIVIDUAL PLANT SCALE

WUE has different definitions depending on the time and space scales of the processes and system aggregation it refers to (Steduto and Albrizio 2005). WUE at the leaf scale ($WUE_l$) or transpiration efficiency ($TE_{leaf}$) is the ratio of the photosynthesis rate by the transpiration rate. The intrinsic WUE ($WUE_i$) is then defined as the photosynthesis rate divided by the stomatal conductance. WUE at the individual plant scale ($WUE_p$) is the ratio of biomass or economic weight/water transpired (van den Boogaard *et al.* 1997). Considering only transpired water, $WUE_p$ is also called plant transpiration efficiency ($TE_p$) in some studies. WUE at field population scale ($WUE_f$) is the economic product or biomass divided by water used through both transpiration from plant and evaporation from soil surfaces.

$WUE_l$ and its related parameters such as the net $CO_2$ assimilation rate and stomatal conductance can be easily measured by gas exchange methods. A large number of studies on genetic variability in $WUE_l$ have been performed in the NCP and other regions of the world (Anyia and Herzog 2004; Dong *et al.* 2008). The instantaneous measurements of $WUE_l$, however, can only provide limited information for characterizing plant performance under water deficit and well-watered conditions. In practical terms, $WUE_f$ represent the WUE of a variety in the field, and therefore deserve most attention. However, its determination is difficult and laborious requiring measurement of the water consumption of the whole crop population. In recent years, some micrometeorological methods such as the eddy-covariance method and the Bowen ratio method have been adopted as the best direct and scale-appropriate methods to assess $WUE_f$ (Wang *et al.* 2001; Guo *et al.* 2006; Zhao *et al.* 2007). However, because of the larger land areas measured, these methods are not suitable for comparative studies between different varieties which require only relatively small plots. Due to the fact that soil evaporation, which accounts for a large amount of water consumed, is influenced largely by agricultural practices, studies on $WUE_f$ were conducted rather more for a guidance of agricultural practices in the NCP.

With soil evaporation being controlled by covering soil surfaces, $WUE_p$ depends on accumulation and partition of photosynthetic assimilates, and transpiration of crops. This implies that varietal variability in $WUE_p$ is derived mainly from differences in inheritable physiological traits of varieties. Therefore exploring physiological factors which closely associate with $WUE_p$ under specific water conditions, and characterizing the contribution of the factors to yield or $WUE_f$ has special implication to variety genetic improvement and to WUE evaluation of crop varieties. In the NCP, the relevant studies around $WUE_p$ are far behind up to now. However, some advanced studies have been conducted in other agricultural regions of the world where the crops share similar needs for an increased $WUE_p$ (Vadez *et al.* 2010a, b; Khazaei *et al.* 2010; Devi *et al.* 2011; Gilbert *et al.* 2011; Belko *et al.* 2012). This review focuses on research progress in the factors affecting $WUE_p$ only to provide some information for WUE improvement of varieties, with special attention being paid to winter wheat, the largest consumer of irrigation water in the NCP.

## ANALYSIS ON PHYSIOLOGICAL FACTORS AFFECTING $WUE_P$

$WUE_p$ has large variability among varieties under both well-watered (van den Boogard *et al.* 1997; Bhatnagar-Mathur *et al.* 2007) and water-deficit conditions (Ratnakumar *et al.* 2009; Devi *et al.* 2011), but have no apparent trend when compared under the both water conditions. Krishnamurthy *et al.* (2007), using a reliable gravimetric method, measured $WUE_p$ of a set of 318 recombinant inbred lines (RILs) of groundnut under progressive soil drying. The frequency distribution of $WUE_p$ indicated that the trait was governed by dominant and additive genes.

### Stomatal conductance relates closely to $WUE_p$ under different conditions of water availability

Many studies have been carried out in recent years to investigate possible relationship between $WUE_p$ and possible proxies. In groundnut, Krishnamurthy *et al.* (2007) explored the possibility of specific leaf area (SLA), SPAD chlorophyll meter readings (SCMR), and carbon isotope discrimination (CID) as $WUE_p$ surrogates. But the stress-dependent relationships and the poor regression coefficients with $WUE_p$ suggested theses surrogates were not robust enough.

Farquhar *et al.* (1982) proposed, based on a theoretical analysis, that CID would normally bear strong negative correlation with $WUE_i$. This relationship has thereafter been proved in a large number of studies in diverse $C_3$ plants (Hubick *et al.* 1986; Hubick and Farquhar 1989; Condon *et al.* 1990; Ehdaie *et al.* 1991; Ehleringer *et al.* 1991). However, no close relationship was reported between CID and $WUE_p$ in more recent studies in legumes (Kashiwagi *et al.* 2006; Krishnamurthy *et al.* 2007; Turner *et al.* 2007; Devi *et al.* 2011). As for cereals, whether CID closely relates to $WUE_p$ may not be asserted arbitrarily. Instead, further studies are expected to bring about distinct results, according to the following reports. Firstly, leaf gas exchange properties of some legumes differ from that of cereals. In some legumes (such as peanut), variation in photosynthesis capacity is known to account for most of the variation in $WUE_i$ (Rao *et al.* 1994), although recent analysis challenge these views (Bhatnagar-Mathur *et al.* 2007; Devi *et al.* 2011). In wheat, however, variation in $WUE_i$ has been shown to be associated rather with variation in stomatal conductance (Condon *et al.* 1990; Morgan and LeCain 1991; Morgan *et al.* 1993; Martin *et al.* 1994; van den Boogard *et al.* 1997), as found for common bean (*Phaseolus vulgaris* Linn.) varieties by Ehleringer *et al.* (1991). Furthermore, high correlations between CID and grain yield, which were either positive or negative, have been reported in wheat. In the environments where crop growth depends much on within-season rainfall, the correlations between CID and grain yield have been mostly positive (Voltas *et al.* 1999; Merah *et al.* 2001; Jiang *et al.* 2006). In the environments where wheat growth depends on stored-moisture, negative correlations between CID and aerial biomass have been found (Anyia *et al*. 2007). Two new wheat genotypes, which were higher yielding than the checks used, have been released by selection for low leaf CID in wheat breeding programs in Australia (Rebetzke *et al*. 2002). Based on these, in cereals, studies on the association between CID and $WUE_p$ need to be performed under specific conditions of water availability for conferring CID as a screening index of $WUE_p$.

Khazaei *et al*. (2010) examined stomata characteristics of 28 Iranian landraces of wheat and found a highly significant negative association between stomatal frequency and size, which indicates a limited variation in stomatal area per unit leaf area. Further they investigated and found no clear association between stomata characteristics and $WUE_p$. In pearl millet (*Pennisetum glaucum* L.), Kholova *et al*. (2010b) found the differences in transpiration rate between genotypes were not related to stomatal density, and proposed that stomatal regulation rather than stomatal density was more important for regulating water loss in pearl millet, as asserted previously in soybean (Liu e*t al*. 2003), and in wheat (Zhang *et al*. 2005). Bhatnagar-Mathur *et al*. (2007) obtained 5 transgenic lines of peanut with increased $WUE_p$, by overexpressing the *AtDREB1A* gene, driven by a stress-inducible promoter (*Atrd29A*). They also ascribed the enhanced $WUE_p$ in the transgenic events to a lower stomatal conductance and an overall lower rate of water loss per unit leaf area. To further verify the association of $WUE_p$ with stomatal conductance in wheat crops, we carried out a pot cultivation experiment with 6 typical wheat varieties of the NCP. Stomatal conductance was found to be positively related with $WUE_p$ under well-watered conditions ($r^2$=0.784), while negatively related with $WUE_p$ under water deficit conditions ($r^2$=0.755). All these results imply that stomatal regulation closely associates with $WUE_p$. Results of those studies in wheat on the relationship between CID and yield virtually agree with stomatal regulation being a determinant factor of $WUE_p$.

## Contribution of stomatal conductance to yield

**Variability in stomatal conductance response to water deficit** Stomata, as the main switch for controlling water efflux, controls water loss through transpiration. Recent studies investigated transpiration rate in response to soil and air drying for exploring crop variety difference in stomatal regulation when exposed to water deficit. Devi *et al*. (2009) examined the soil moisture level (fraction of transpirable soil water, FTSW) at which transpiration rate begins to drop with soil drying, and showed large variability among 17 tested genotypes of peanut (*Arachis hypogea* L.). Devi *et al*. (2010, 2011) also found in peanut that genotypes differ in the pattern that transpiration rate increase with vapor pressure deficit (VPD). Some genotypes showed a breakdown in the transpiration increase once past a certain VPD threshold, above which there was little or no further increase in transpiration rate. This trait would therefore lead to water saving at high VPD. By contrast, other genotypes did not exhibit any breakpoint, and had a linear response in transpiration rate over the whole range of tested VPD instead. Similar findings were obtained in pearl millet (Kholova *et al*. 2010b), where terminal drought tolerant lines also showed a breakdown in the transpiration response to VPD increase. Using 6 wheat varieties of the NCP, we investigated their stomatal conductance trait at jointing stage. The difference in stomatal conductance between well-watered and water deficit condition ranged largely from 0.1614 to 0.3562 mmol $s^{-1}$ $m^{-2}$. These results indicate large difference among varieties in the sensitivity of stomata responding to soil and air drying.

Sensitive stomata would lead to water saving at high VPD and drier soil, while the down side of it would be a lost opportunity for fixing carbon. Therefore, this trait affects plant water relations, depending on the water availability of targeted regions. Genetic variability in stomatal response can be an important source of information to better appreciate the particular capacities of each variety to perform in both well-watered and water-deficit environments. Similar studies in wheat on these responses (to soil drying or to high VPD) thus could be helpful and informative for improving the efficiency of breeding programs aiming at selecting high-WUE varieties.

**Associations of stomatal conductance with yield under different conditions of water availability** As discussed above, stomatal conductance was an important factor that closely associates with $WUE_p$. Characterizing the contribution of stomatal conductance to yield under different water conditions is required for the trait to be an indicator of WUE evaluation and genetic improvement. As the main switch for water efflux and $CO_2$ influx, stomatal conductance controls both photosynthetic assimilation and water loss through transpiration. And therefore, there are clear trade-off to be expected between high biomass/yield potential and water use. Indeed, high stomatal conductance favors high biomass/yield formation, in particular under well-watered conditions, as reported by Bota *et al.* (2001). We also found in wheat crops that varieties with higher stomatal conductance were more productive than those with lower stomatal conductance. On the other hand, high stomatal conductance leads to large water consumption. In the NCP, variety with medium stomatal conductance of 0.35 mmol $H_2O$ $m^{-2}$ $s^{-1}$ or so, such as Zhengmai 9023, is considered to be more feasible for water saving. Yield loss due to the lower stomatal conductance can be offset, to some extent, by improving carboxylation and harvest index genetically or by agricultural practices.

Under water deficit conditions, stomatal conductance of a variety was found to be partly determined by the stomata sensitivity to soil and air drying. The stomatal conductance determines the extent of water extraction, which is considered to be one of the important factors that affect biomass or yield. As Schultz (1996) pointed out in his early studies, the "luxurious" varieties (with low sensitivity of stomata to water stress) tend to maximize production, though they do not survive well under prolonged drought; meanwhile the "alarmist" varieties (with sensitive stomata to water stress) are less productive but are much more resistant to drought. In stored-moisture environments, in particular late-season water deficit occurs frequently, a variety with sensitive stomata to drought has the possibility of using the conserved soil water to generate a greater yield. This was proved by subsequent studies. van den Boogaard *et al.* (1997) found, under rain-fed conditions, the varieties with the lowest stomatal conductance had, on average, a 20% higher crop $WUE_f$ than those varieties with higher stomatal conductance. But as discussed above, no trend was found under irrigated conditions. Consistent with this, experiments carried out by Condon *et al.* (2002), using two winter wheat varieties with different stomatal conductance, showed that low stomatal conductance resulted in yield gain and a higher $WUE_f$ in drier "stored-moisture" environments. Similar results have been recently found in pearl millet (*Pennisetum glaucum* (L.) R. Br.) (Kholova *et al.* 2010a, b), chickpea (Zaman-Allah *et al.* 2011a, b) and cowpea (Belko *et al.* 2012) where the decrease in stomata conductance under water deficit condition decrease transpiration rate, also result in water savings in the soil. Based on this, in the drought-prone rainfed areas of the NCP, varieties of low stomatal conductance, like Yumai 18, are recommended. These varieties can generate higher yield by largely reducing their stomatal conductance at drought to reserve soil water for grain filling.

No matter under what kind of water conditions, biomass/yield differences among varieties were mostly driven by plant water use. The relation of stomatal conductance with yield is complicated by the fact that it is the water conditions of the whole life cycle that affects crop yield formation. In general, in favorable environments where crop yield depends on current irrigation or on within-season rainfall, high stomatal conductance would undoubtedly favor a high yield formation. In contrast, low stomatal conductance associated with more sensitive stomata to drought could result in considerable yield reductions as well as in a low $WUE_f$ in favorable environments. On the other hand, in stored-moisture environments, in particular late-season water deficit occurs frequently, a low stomatal conductance cultivar has the possibility of using the conserved soil water to generate a greater yield.

## CONCLUSION AND RECOMMENDATION

Breeding programs aiming at high yield have brought about WUE improvement indirectly. However, the yield increase have also been at the expense of using more water and therefore, work is now needed to reduce water use while attempting to preserve yield at high levels. This would in part solve the water resource crisis in the NCP.

$WUE_p$ has large variability among varieties under different water conditions. Stomatal conductance, which controls both photosynthetic assimilation and transpiration, is a main factor that affects $WUE_p$, based on the studies performed up to date. Among varieties, the trait has large variability under well-watered conditions, and differed more largely under water deficit conditions due to varietal difference in the sensitivity of stomata to soil and air drying. The levels of stomata conductance needed to maximize yields depend on water conditions of the whole growing period. Under well-watered conditions, large stomatal conductance results in a high yield gain. While under stored-moisture conditions, low stomatal conductance benefits yield formation.

Therefore, to solve the water crisis in the NCP, for the well-irrigated areas where groundwater is excessively used, a high WUE breeding program should aim to combine medium stomatal conductance (0.35 mmol $H_2O$ $m^{-2}$ $s^{-1}$ or so), high carboxylation efficiency, and high harvest index. Reducing stomatal conductance is expected to be able to efficiently control water consumption of wheat crop population through transpiration. Yield decrease resulting from reduced stomatal conductance can be in part offset by improving the efficiency of photosynthetic assimilation and assimilate allocation. For the areas under limited irrigation, where long term or serious drought seldom occurs, varieties with low stomata sensitivity to soil drying and larger stomatal conductance when released from water stress at irrigation or rain may maximize water use and gain high yield. For the drought-prone rain-fed areas, where wheat crop grows partly depending on the stored moisture, lower stomatal conductance under no water stress and higher stomata sensitivity to soil drying may benefit the growth of later stages in particular grain filling and result in a higher yield gain.

Researches for developing a kind of rapid evaluation method for $WUE_p$ by using robust surrogate traits are ongoing. Up to date, the direct gravimetric evaluation for $WUE_p$ appeared to be more reliable, though more time consuming. In International Crop Research Institute for the Semi-Arid Tropics (ICRISAT), a lysimeter system was developed recently to assess $WUE_p$ over a long period of time in plants that are cultivated in field populations, where drainage is avoided and where yield is measured. Though the method is utilized now in legumes, it is recommended to introduce and modify the method for both $WUE_p$ and $WUE_f$ evaluation of wheat in the NCP. Screening with stomatal conductance trait combining with precise determination of $WUE_p$ with gravimetric method can improve efficiency and reliability of WUE evaluation. Studies on the mechanism about how crops gain high WUE under different water conditions, and the mechanism of stomata regulation under water deficit conditions need further study to find more efficient WUE surrogates traits, and to provide key genes of high WUE. In possession of efficient index and key genes of high WUE, combination of conventional breeding and biotechnological breeding is hopeful to improve WUE of varieties significantly.

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