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Review

Effective use of water (EUW) and not water-use efficiency (WUE) is the target of crop yield improvement under drought stress

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ABSTRACT

Water-use efficiency (WUE) is often considered an important determinant of yield under stress and even as a component of crop drought resistance. It has been used to imply that rainfed plant production can be increased per unit water used, resulting in “more crop per drop”.

This opinionated review argues that selection for high WUE in breeding for water-limited conditions will most likely lead, under most conditions, to reduced yield and reduced drought resistance. As long as the biochemistry of photosynthesis cannot be improved genetically, greater genotypic transpiration efficiency (TE) and WUE are driven mainly by plant traits that reduce transpiration and crop water-use, processes which are crucially important for plant production. Since biomass production is tightly linked to transpiration, breeding for maximized soil moisture capture for transpiration is the most important target for yield improvement under drought stress. Effective use of water (EUW) implies maximal soil moisture capture for transpiration which also involves reduced non-stomatal transpiration and minimal water loss by soil evaporation. Even osmotic adjustment which is a major stress adaptive trait in crop plants is recognized as enhancing soil moisture capture and transpiration. High harvest index (HI) expresses successful plant reproduction and yield in terms of reproductive functions and assimilate partitioning towards reproduction. In most rainfed environments crop water deficit develops during the reproductive growth stage thus reducing HI. EUW by way of improving plant water status helps sustain assimilate partitions and reproductive success. It is concluded that EUW is a major target for yield improvement in water-limited environments. It is not a coincidence that EUW is an inverse acronym of WUE because very often high WUE is achieved at the expense of reduced EUW.

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The coined slogan “more crop per drop” (Kijne et al., 2003) as a target for crop improvement in water-limited environments emerged in recent years in the press and among research administrators and sponsors. It is a very catchy slogan indeed, but also a misleading one. It does not serve well the cause of breeding for water-limited environments, especially rainfed conditions. It led breeders to believe that crop production under water-limited conditions can be genetically improved by increasing plant production per given amount of water used by the crop. A misconception also developed that improved water-use efficiency (WUE) is synonymous with drought resistance and high yield under drought stress. It is possible to achieve “more crop per drop” by certain crop and soil management practices (e.g. plant nutrition). However, this review concentrates on genetic improvement. It is not a comprehensive review of WUE.

This paper is therefore designed to clarify the meaning and consequences of WUE if used in breeding either in practice or in

concept. It raises the argument that the important determinant of plant production under most conditions of limited water supply is the effective use of water (EUW) and not high WUE.

Passioura (1996) proposed to view grain yield as a partial function of WUE:

$$Y = WU \times WUE \times HI \quad (1)$$

where Y is grain yield, WU is water-use, and HI is harvest index.

While Passioura shifted in opinion towards “water productivity” as a prime consideration in dryland crop production (Passioura, 2006), Eq. (1) remains quite popular among breeders (e.g. Reynolds and Tuberosa, 2008) and in training courses since it is simple and has some educational merit. Here it is used only as a gateway for explaining the main message of this review.

The equation implies that WUE is an independent variable in affecting grain yield. In this expression WUE equals B/WU , where B is biomass, therefore:

$$Y = WU \times \left(\frac{B}{WU} \right) \times HI \quad (2)$$

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In Eq. (2) WU can be cancelled out and then we return to the basics (Donald and Hamblin, 1976), namely:

$$Y = B \times HI \quad (3)$$

de Wit (1958) set the cornerstone for relating plant production to water-use:

$$B = \frac{mT}{E_0} \quad (4)$$

where B is crop biomass, m is a crop constant, T is crop transpiration and E_0 is free water (potential) evaporation. This relationship is very solid and has stood the test of time. For genotypic comparisons E_0 is common and can be removed from Eq. (4). Thus for genotypic comparisons, biomass of a genotype is a function of crop transpiration and a crop constant which is independent of T . A comparison of m constants received in various experiments (Hanks, 1983) confirmed their reasonable consistency from one species to another. However it was noted that the m constant may vary with varieties within a species. It was pointed out by Fischer and Turner (1978) that m diverged significantly between C_3 and C_4 species, indicating the evident importance of the photosynthetic pathway in determining m . Since the basic biochemistry of photosynthesis has not yet been genetically improved within a crop species (Horton, 2000; Parry et al., 2007; Sheehy et al., 2000), m offers limited scope for significant genetic improvement in biomass at present. The remaining practical and quantitatively effective option for biomass improvement under drought stress is an increase in T or its seasonal manipulation with respect to plant development and a predictable water supply (see below).

Transpiration efficiency (TE) which is WUE at the leaf level is determined by the delicate interplay between transient photosystem activity, substomatal cavity CO_2 concentration and stomatal activity (Farquhar et al., 1989). Carbon isotope discrimination (δ) measurement in stover or grain has been developed as a method for estimating seasonal plant TE as affected by these transients. Low δ is reasonably correlated with high TE (e.g. Hall et al., 1994). δ was therefore taken to represent crop WUE (e.g. Condon et al., 2002).

The amount of water transpired per given unit of CO_2 fixation (TE) is an interesting physiological yardstick but our interest here is in maximizing CO_2 fixation under drought stress per plant and per unit land area as an engine of biomass production. Stomatal closure, which is a generally negative response in this respect (not considering survival under severe drought), can be driven by a variety of determinants such as internal leaf CO_2 concentration, cellular solutes, specific ions, pH and ABA produced in the leaf or imported from the root. Higher yielding genotypes of cotton, wheat and rice have greater stomatal conductance and transpiration under drought stress (Araus et al., 2002; Blum et al., 1982; Izanloo et al., 2008; Sanguineti et al., 1999) or well-watered conditions (Fischer et al., 1998; Horie et al., 2006; Lu et al., 1994; Lu and Zeiger, 1994; Reynolds et al., 1994; Shimshi and Ephrat, 1975) as indicated by leaf gas exchange measurements or canopy temperature measurements. Therefore high plant production requires high stomatal conductance over time, to allow greater CO_2 fixation per unit land area, under different conditions. This translates into maximized soil water-use for transpiration. In most cases as will be seen further on, higher T and high stomatal conductance under drought stress will express lower TE or WUE.

The delicate interplay between transient photosystem activity, substomatal cavity CO_2 concentration and stomatal activity is not the only determinant of plant transpiration and WU at the whole plant and crop level. Since drought stress is the issue here, interest is in plant water-use for stomatal transpiration at given soil

moisture content. Various plant constitutive and stress-adaptive traits have a role in this respect, namely in enhancing an effective use of water (EUW) for transpiration.

Synchronizing growth duration with the expected or the predicted seasonal soil moisture supply is often the first and foremost step in breeding for water-limited environments. Two major considerations are important in this respect: (a) short growth duration dictates moderate water-use and the escape of terminal (reproductive stage) drought stress; and (b) long duration genotypes generally have a greater water-use and larger and deeper root systems that allow deep soil moisture extraction—if indeed deep soil moisture is available (Mitchell et al., 1996).

Leaf permeability is crucial. Leaves can lose water through the cuticle. This non-stomatal “leak” increases crop transpiration without an associated benefit in CO_2 fixation. For example, rice has a highly conductive cuticle while the drought resistant sorghum has a relatively impermeable cuticle. Eliminating this leak by higher epicuticular wax deposition will increase stomatal transpiration (Kerstiens, 1997, 2006). Stomata leakiness at night can also add to water loss without any advantage in CO_2 assimilation. Nocturnal transpiration can be significant (Caird et al., 2007).

Accelerated leaf desiccation and death is a means by which plants reduce water requirement under drought stress. Plant foliage desiccates in a progressive manner from lower (older) leaves to upper (younger) leaves, despite the fact that lower leaves are generally at a better water status than upper leaves. It has been found in sorghum that this strategy reduces transpiration in older and less productive leaves while deviating water-use to younger, fully productive ones (Blum and Arkin, 1984).

An important part of soil moisture available for transpiration is evaporated directly from soil to the atmosphere without taking part in transpiration. For example, up to 40% of the total available soil water was found to be lost by soil evaporation in wheat in Australia (French and Schultz, 1984; Siddique et al., 1990). Soil surface shading by the crop canopy is crucial for reducing this water loss. Reduced soil evaporation by fast vigorous seedling growth is therefore a target in an Australian wheat breeding program (Rebetzke and Richards, 1999) which is actually directed at increasing T .

The major plant adaptive response to drought at the cellular level which has a proven effect on yield under drought stress is osmotic adjustment (OA) (Blum, 2005). It has been repeatedly demonstrated that OA has two major functions in plant production under drought stress: (a) it enables leaf turgor maintenance for the same leaf water potential thus supporting stomatal conductance under lower leaf water status (e.g. Ali et al., 1999; Sellin, 2001), and (b) it improves root capacity for water uptake (e.g. Chimenti et al., 2006; Tangpremsri et al., 1991).

Therefore the enhancement of biomass production under drought stress can be achieved primarily by maximizing soil water capture while diverting the largest part of the available soil moisture towards stomatal transpiration. This is defined as effective use of water (EUW) and it is the major engine for agronomic or genetic enhancement of crop production under a limited water regime.

There is a wide consensus that the reproductive growth stage is the most sensitive to water deficit. This is well depicted by the classical and widely used example in rice (O'Toole, 1982; Fig. 6). It is also recognized that drought stress at the reproductive stage is the most prevalent problem in rainfed drought prone agriculture, at least simply because in most rainfed ecosystem the crop season's rains diminish towards flowering and harvest time. Therefore, irrespective of biomass production up to flowering, sustained WU and T into the reproductive growth stage is crucial for reproductive success (e.g. Merah, 2001; Kato et al., 2008). An effective means of achieving reproductive success under drought

stress is soil moisture capture by deep root system where deep soil moisture is available (e.g. Kirkegaard et al., 2007). ABA production in the shoot or the root under stress may also impede reproductive processes (e.g. Davies and Jones, 1991), but ABA accumulation might be at least partly repressed by higher WU and the resultant improvement of plant water status (Westgate et al., 1996).

Ample information has been developed by carbon isotope discrimination analysis of plants done in order to understand the relationship between TE, WUE and yield under different water-regimes (e.g. Hall et al., 1994). It should be noted here that delta estimates TE at the leaf level which is not crop WUE. However in most studies where delta (TE) was found to be related to yield then the term WUE is used in the report. Following are some major conclusions which serve to reject the notion that high WUE can be equated with drought resistance or the improvement of yield under water-limited conditions (with the exception of crops grown on stored soil moisture (see below).

1. Conflicting results were obtained in various crops under different growing conditions on the association between delta and yield (Hall et al., 1994; Matus et al., 1996; Monneveux et al., 2007; Morgan et al., 1993; Munoz et al., 1998; Ngugi et al., 1994, 1996; Read et al., 1991; Saranga et al., 2004; Sayre et al., 1995; Specht et al., 2001). These range from no relationship between delta and yield to negative or positive relationships, depending on the crop and the environment. Sometimes the relationship was biased by phenology or plant height (or perhaps HI) (e.g. Rebetzke et al., 2008; Sayre et al., 1995). It appears that the association between WUE and plant production as a biologically legitimate variable across species and environments is very elusive. If solid relationships were found they were limited to narrow environmental conditions within a given crop phenology. In this sense WUE in rainfed agriculture is an intangible index. On the other hand its value in economizing the use of expensive irrigation water is well established.
2. Deep or dense root system which would promote soil moisture capture and WU is correlated across genotypes with low WUE (Pinheiro et al., 2005; Kobata et al., 1996) concluded that “the high dry matter production of those rice cultivars known to be drought resistant under field conditions is caused not by high WUE, but by high ability to maintain transpiration, which is supported by deep root systems.”
3. Thus, it is not surprising that favorable genotypic plant water status under drought stress as reflected in measurements of relative water content or canopy temperature is correlated with low WUE across genotypes (Araus et al., 1993; Frank et al., 1997; Read et al., 1991; Zong et al., 2008).
4. Genotypic variation in WUE under limited water regimes is affected more by variation in the denominator (WU) rather than by variation in the nominator (biomass) (Blum, 2005). This has also been determined for TE and stomatal conductance at the single leaf level (e.g. Juenger et al., 2005; Monclus et al., 2006; Monneveux et al., 2006). Hence, selection for high WUE under limited water supply tends to result in a genetic shift towards plant traits that limit crop WU, such as early flowering and smaller leaf area (Martin et al., 1999; Menendez and Hall, 1995; Ngugi et al., 1994; Sayre et al., 1995; White et al., 1990). The successful and widely cited case for dryland wheat grain yield improvement with selection for high WUE (low carbon isotope discrimination) in NSW Australia (Condon et al., 2002) can be explained by the fact that wheat is grown there mainly on stored soil moisture. A major avenue for yield improvement is the control of WU during the earlier part of the growing season in order to avoid lack of soil moisture during reproduction. This was earlier attempted by selection for reduced root xylem diameter (Richards and Passioura, 1989) and it can also be

achieved by reduced leaf area and growth duration as done in the past in sorghum grown under stored soil moisture conditions (Blum, 1970, 1972; Blum and Naveh, 1976). Such plants that allow optimized seasonal distribution of soil moisture use express high WUE for grain yield due to their relative moderate WU and high HI. The same genetic materials, selected for high WUE were not successful in Western Australia where rainfed wheat does not grow on stored soil moisture (Fig. 6 in Condon et al., 2002).

5. Considering all of the above (1 through 4), it is not surprising that drought resistance was found to be associated with low WUE when analyzed by delta under limited water supply (e.g. Araus et al., 2003; Morgan et al., 1993; Ngugi et al., 1994; Solomon and Labuschagne, 2004). A drought resistant *Coffea canephora* clone had relatively lower WUE than a drought susceptible one, where resistance was associated with deeper roots and presumably greater WU (Pinheiro et al., 2005).
6. Finally, crop WUE has long been known to increase with increasing drought stress and reduced water supply (e.g. Meyers et al., 1984). This has been more recently confirmed with delta analysis (Craufurd et al., 1999; Ismail et al., 1994; Li et al., 2000; Peuke et al., 2006). It corresponds well with the fact that plant water deficit result in high WUE (#3 above). Assume therefore that two different cultivars are planted side by side and exposed to drought stress. If the one with higher WUE is selected it will most likely to be the one relatively more stressed and at a lower plant water status, namely the drought susceptible one.

Therefore, for all practical purposes plant breeders targeting water-limited environments should consider skipping the use and reference to WUE and consider plant constitutive and adaptive traits which drive the effective use of water (EUW) and the resultant dehydration avoidance as major traits for yield improvement in drought prone environments (with one exception per #4 above). This discussion does not refer to very shallow soils with very limited soil water holding capacity. These extremely difficult conditions require another discussion on plant survival and recovery and not plant production.

In conclusion, crop WUE as estimated under rainfed conditions by carbon isotope discrimination analysis or any other method is an elusive ratio. Reynolds and Tuberosa (2008) concluded in tune with the original expression of Passioura (1996) that “water uptake (WU), water-use efficiency (WUE), and harvest index (HI) are drivers of yield.” Indeed WU and HI are drivers of yield but I suggest that WUE is just a passenger. Whereas HI (in terms of assimilate partitioning and reproductive success under drought stress) is also largely influenced by WU and plant water status, it can be concluded that WU alone is the main (not the exclusive) driver of yield under drought stress.

Therefore, it is not a coincidence that EUW is an inverse acronym of WUE whereas very often high WUE is achieved at the expense of reduced EUW, and *vice versa*.

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