

## Water: the most important ‘molecular’ component of water stress tolerance research

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**Abstract.** Water deficit is the main yield-limiting factor across the Asian and African semi-arid tropics and a basic consideration when developing crop cultivars for water-limited conditions is to ensure that crop water demand matches season water supply. Conventional breeding has contributed to the development of varieties that are better adapted to water stress, such as early maturing cultivars that match water supply and demand and then escape terminal water stress. However, an optimisation of this match is possible. Also, further progress in breeding varieties that cope with water stress is hampered by the typically large genotype × environment interactions in most field studies. Therefore, a more comprehensive approach is required to revitalise the development of materials that are adapted to water stress. In the past two decades, transgenic and candidate gene approaches have been proposed for improving crop productivity under water stress, but have had limited real success. The major drawback of these approaches has been their failure to consider realistic water limitations and their link to yield when designing biotechnological experiments. Although the genes are many, the plant traits contributing to crop adaptation to water limitation are few and revolve around the critical need to match water supply and demand. We focus here on the genetic aspects of this, although we acknowledge that crop management options also have a role to play. These traits are related in part to increased, better or more conservative uses of soil water. However, the traits themselves are highly dynamic during crop development: they interact with each other and with the environment. Hence, success in breeding cultivars that are more resilient under water stress requires an understanding of plant traits affecting yield under water deficit as well as an understanding of their mutual and environmental interactions. Given that the phenotypic evaluation of germplasm/breeding material is limited by the number of locations and years of testing, crop simulation modelling then becomes a powerful tool for navigating the complexity of biological systems, for predicting the effects on yield and for determining the probability of success of specific traits or trait combinations across water stress scenarios.

**Additional keywords:** hydraulics, lysimeters, roots, vapour pressure deficit.

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### Introduction

Water stress is the most important abiotic factor limiting crop yields worldwide. This is because of the photosynthesis-driven plant growth trade-off between carbon dioxide and water at the stomata level. Water stress occurs in all situations where plant water demand for growth is not met by water supply. Therefore, matching water supply to water demand is a key consideration to keep in mind when developing crop cultivars that are adapted to water stress. There has been a considerable quantity of research

on water stress, but it appears that in many cases the essentiality of matching water supply and demand did not appear to be an important aspect. For example, cell protection homeostasis mechanisms (e.g. antioxidant enzyme, osmolytes) were shown to be beneficially involved in the water stress response by delaying death and improving survival under fairly unrealistic stress conditions (Bohnert and Shen 1998; Mittler 2002). Although considerable biotechnological research investments have been made to harness these properties (reviewed by

Bhatnagar-Mathur *et al.* 2008), there has been no applied outcome thus far, most probably because plant survival has little economic value to farmers. Similarly, osmotic adjustment has long been viewed as a means of keeping stomata open and sustaining growth under water limited conditions (e.g. Blum *et al.* 1999), although keeping stomata open would also sustain water losses and could be detrimental in many situations. A review on osmotic adjustment later showed that this mechanism had virtually no effect on crop yield in most situations (Serraj and Sinclair 2002) like in chickpea (Turner *et al.* 2007) under water stress, with a few exceptions. Therefore, in this review we argue that research on water deficit must be indeed re-centred on water and we focus our attention on plant strategies that facilitate an economical yield under water-limited conditions. Such strategies revolve around two crucial aspects of the plant water budget: (i) the ability to capture more water; and (ii) the ability to conserve and use captured water more efficiently.

Several studies across crop species indicate that 'superior' structural root traits contribute to better performance of genotypes under water-limited conditions (e.g. Silim and Saxena 1993; Tuberosa *et al.* 2002; Matsui and Singh 2003; Ober *et al.* 2005; Sarker *et al.* 2005; Kashiwagi *et al.* 2006). Most of these studies assume that rooting traits relate to water uptake. However, the link between better rooting and plant performance lacks crucial information on how roots contribute to water extraction, with respect to quantity and timing, in ways that lead to higher grain yield. Therefore, although the assessment of roots provides valuable information on the potential of genotypes to cope with water limitation, this information remains static and sheds little light on the actual water contribution of the roots and on the timing of water uptake. In this review, we address the importance of looking at root functionality rather than structure or architecture, by measuring the volume of water taken up by roots, rather than roots themselves. We highlight the need to develop methods that allow a precise and dynamic measurement of water uptake at key times, together with relevant agronomic evaluations of plant materials, to critically assess relationships between water extraction patterns and grain yield.

The second part of this review relates to plant water conservation and efficient use. Biomass production is water use, thus, biomass production and water conservation are antagonistic features in nature. In other words, under water limitation, biomass production needs to match water availability in a way that allows plants to fulfil their life cycle (Passioura 2012). Here, we review the genetic options that plants have for optimising biomass production per unit of water use and to complete their life cycle. Because part of our current focus is on crops that grow in semiarid tropical conditions, we have a particular interest in water conservation mechanisms. However, we also discuss the trade-off between water conservation and biomass accumulation, and we address the need to maximise water utilisation from the soil profile so that no water remains available in the soil profile once the crop has matured. We note also that there are important management options that can reduce the water use of a crop canopy (e.g. alterations in nitrogen fertilisation or planting densities). These practices are also essential to improve crop productivity under water limitation and are the object of extensive recent reviews

(Kirkegaard and Hunt 2010; Passioura and Angus 2010). In this paper we chose to focus only on the genetic aspects of plant water budget, although management aspects are briefly examined in the last section.

Manipulating these strategies towards genetic improvement is complicated by the fact that crop success under water-limited conditions is not dependent solely on capturing more water or conserving/using it better. Genotypes that are successful under water-limited conditions are those that are capable of both maximising biomass production while securing maximum partitioning to grains. Therefore, in this review, we advocate the need for tools and methods for comprehensive (rather than individual) assessment of these closely related strategies. Additionally, these strategies are over-ridden by the importance of plant phenology and crop duration, which, in turn, depend on the environment (and particularly on the weather). Thus, the third part of this review addresses the methodological requirements for undertaking such efforts. Crop simulation modelling is a powerful tool that helps predict how plant traits related to water capture and use/conservation interact with one another and how this interaction would lead to an increase in yield across the varying weather conditions in a given environment. Here also, we focus mostly on the modelling of the genetic aspects, although crop modelling also allows simulating the effect of management practices. In particular, we discuss the need for a plant breeding-based approach to crop improvement from an environmental perspective, and we postulate that future breeding is likely to become environment-specific, with the genetic gain of improved varieties driven by probability scenarios that are linked to weather conditions.

## Root and water capture

### *Usual assumptions about roots under water-limited conditions*

Roots are often viewed as the key to solving water stress issues, therefore, 'structural root traits' are often assimilated with 'water stress tolerance traits'. A recent work supports the idea that roots will be the basis for a new green revolution (Gewin 2010). In a 2 year study of chickpea, Kashiwagi *et al.* (2006) showed that the root length density was indeed significantly correlated with higher seed yield under terminal water stress, although the 12 genotype experiment was strongly biased by one genotype with poor roots and good yield and one genotype with good roots and poor yield. However, in another experiment within the same study, the yield reduction caused by water stress was less severe, and there was no significant relationship between root length density and seed yield. Similar results were recently obtained in lentils, where root traits and grain yield were not significantly related in a rain-fed situation (Kumar *et al.* 2012). Ratnakumar and Vadez (2011) compared the root systems of 20 groundnut genotypes with variable yields under a range of water stress conditions and showed that the yield differences under stress were not related to differences in rooting depth or root length density at different depths. Zaman-Allah and colleagues (2011a) reached the same conclusion with twenty chickpea genotypes contrasting for terminal water stress tolerance. Nevertheless, the benefit of deeper root systems has been shown in other studies (Kirkegaard *et al.* 2007; Christopher

*et al.* 2008; Hund *et al.* 2009). For example, a simulation study indicated that maize yields would increase if the root depth increased (Sinclair and Muchow 2001). Hammer *et al.* (2009) postulated that changes in root architecture contributed to maize yield increases in the USA. These examples illustrate that roots may not be the answer to all water stress scenarios and that their contribution to yield increases in water-limited environments depends on the crop and the stress conditions (Palta *et al.* 2011). In summary, although there is no doubt that roots are important, their role in adapting to water stress might have been overstated. This may have occurred in part because roots are not akin to water, and it is too often assumed that additional roots lead to additional water extraction. Of course, water extraction is determined by both the water availability in the soil profile and the capacity of roots to access it. Therefore, although roots (deep, profuse at depth) are necessary structures for water extraction, they are by no means a sufficient condition for adapting to water stress.

#### *Do differences in root length density and water uptake relate?*

The fact that a deeper or more profuse rooting system does not always lead to increased yield under water stress conditions is indeed partially because roots and water extraction are not necessarily related. Some studies have shown that an increase in root length density (RLD) leads to additional water extraction (Passioura 1983; Monteith and Greenwood 1986; Lafolie *et al.* 1991; Hund *et al.* 2009; Vadez *et al.* 2013a). In contrast, other studies have shown poor relationships between water uptake and RLD across several cereals and legumes (Hamblin and Tennant 1987; Dardanelli *et al.* 1997; Katayama *et al.* 2000; Amato and Ritchie 2002; Ratnakumar and Vadez 2011; Zaman-Allah *et al.* 2011a). Therefore, whether RLD and water uptake are related is still a subject of debate. Part of the controversy is due to (i) the limited knowledge of the minimum RLD required to fully extract water from a given soil volume, (ii) the limited knowledge of how roots are distributed at a given soil depth, (iii) the fact that the soil profile depth may vary, and (iv) simply that the roots have reached layers where there is no water or limited water for uptake. Relatively few roots in deep layers would be sufficient to supply an ample amount of water to the plant when the topsoil is dry, provided that water is available at this depth (Gregory *et al.* 1978; Sharp and Davies 1985). Indeed, the development of a larger proportion of the root structure at depth has been shown to contribute to higher grain yield in peanut (Jongrungrklang *et al.* 2011), more so than the RLD. Similarly, the extraction of more water in water stressed DREB1A transgenic peanut plants was related to higher root length density at depth (Vadez *et al.* 2013a). Thus, progress will be achieved by putting more focus on the distribution of roots in the soil profile, and an investigation of the role of roots in water stress adaptation may involve tomographic measurements of the root system *in situ* (e.g. Mooney *et al.* 2012) or an examination of root models that take into account rooting architecture (Lobet *et al.* 2011). However, measuring such a fine rooting differences at depth is a challenge, and although destructive measurements provide static data, they do not provide data on the quantities or kinetics of water extraction. Therefore, until there is a means of accessing root growth *in situ* and possibly

under natural conditions, we argue that destructive root measurements provide only an indirect assessment of the potential of a given genotype to cope with water stress via its root system. Until then, the measurement of water uptake at different times during the cropping cycle might be an easier target for future research on the contribution of roots to water stress adaptation, as suggested previously (McIntyre *et al.* 1995; Dardanelli *et al.* 1997; Vadez *et al.* 2008; Zaman-Allah *et al.* 2011a; Vadez *et al.* 2013b).

#### *The need for dynamic measurements of water extraction at key times*

Thus far, we have discussed the need for a shift away from destructive root measurements and towards water uptake measurements to better understand differences in genotype adaptation to water deficit. Several authors have argued that the presence of small amounts of water during key crop stages such as the grain filling period would confer a major benefit (Ketring and Reid 1993; Christopher *et al.* 2008; van Oosterom *et al.* 2011). Unfortunately, it is difficult to measure water extraction precisely in the field, especially the small but key amounts that may be extracted during the grain filling period; however, a lysimetric method now exists in which a precise water extraction measurement is possible at all crop stages (e.g. Payne *et al.* 1992; Vadez *et al.* 2008). This method indeed confirms that the extraction of small amounts of water at key stages is critical and likely more informative than measuring total water extraction (Ratnakumar *et al.* 2009; Zaman-Allah *et al.* 2011a; Vadez *et al.* 2013b). Manschadi *et al.* (2006) also showed that each mm of water provided during grain filling would contribute a 55 kg ha<sup>-1</sup> yield increase. Similar data were provided by Kirkegaard *et al.* (2007) in wheat (59 kg ha<sup>-1</sup> yield increase mm<sup>-1</sup> water), and these data are in line with those obtained from lysimeter experiments in pearl millet (Vadez *et al.* 2013b; 37–45 kg ha<sup>-1</sup> yield increase mm<sup>-1</sup> water). In chickpea, each additional mm of water would lead to a 40 kg ha<sup>-1</sup> increase in grain yield, and the water extraction differences between tolerant and sensitive entries extrapolated to field conditions were only on the order of 25 mm (Zaman-Allah *et al.* 2011a).

The continued extraction of water at late crop stages would be possible if the roots continued to grow during these stages, as was shown earlier, especially under different conditions such as water stress (Chopart 1983; Hafner *et al.* 1993; Ketring and Reid 1993), thus, it might be valuable to screen for such a trait. Of course, the continued growth of the roots during the grain filling stage would be useful only if the soil profile were deep enough and had water available. Importantly, genotypes that extract more water during the grain filling period extract less water during the vegetative stage (e.g. Vadez *et al.* 2011b, 2013a; Zaman-Allah *et al.* 2011a). The continued extraction of water at later stages therefore appears to depend on water-saving mechanisms functioning at earlier stages, and water extraction by the root at key stages is a dynamic process that does not depend only on the root tapping more water at depth. This process is also the consequence of differences in the shoot water demand at earlier stages. The next section explores the reasons for the variations in this demand, wherein the important factors are canopy size and conductance. Therefore, we believe that an

understanding of the role of root traits in water stress adaptation also involves an understanding of how traits interact at different levels of plant organisation (Kudoyarova *et al.* 2013) and also raises the question of how root and shoot traits are coordinated.

#### *Are root and shoot growth under common or independent genetic control?*

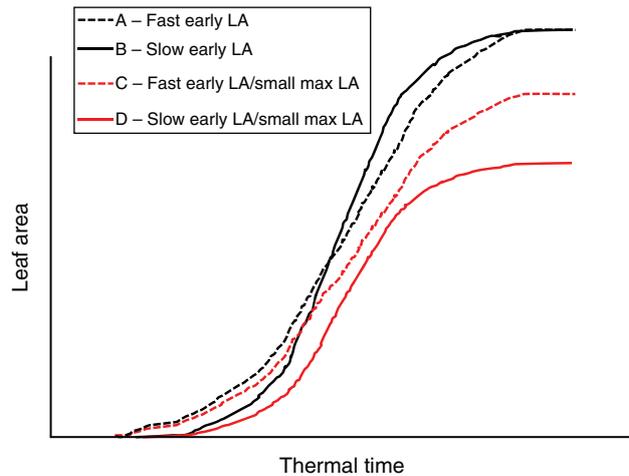
Under water limitation, larger, longer and deeper roots could confer a major benefit if water were available in the soil profile and if the roots were able to tap that water to substantially increase the water supply. However, enhanced root traits might provide little advantage to the plant if such characteristics are paralleled by a larger shoot that consumes more water. This raises the question as to whether root and shoot growth are under independent or coordinated genetic controls. Root and shoot growth is indeed closely coordinated (Jackson 1993; Palta *et al.* 2011), and abscisic acid (ABA) likely plays a major role in that regulation (Munns and Cramer 1996). It is, in fact, critical for plants to maintain a hydraulic integrity in the soil–root–xylem–leaf–atmosphere continuum to maintain water fluxes (Kudoyarova *et al.* 2013). A major quantitative trait locus (QTL) was identified for root length density and root depth in chickpea (Chandra *et al.* 2004), explaining ~35% of the phenotypic variation. However, this locus was also a QTL for shoot growth, explaining more than 50% of the shoot biomass. Recent work examining *Arabidopsis thaliana* showed that shoot and root growth are indeed under the same genetic control (Bouteillé *et al.* 2012; and references therein). These results suggest that any advantages conferred by bigger root systems in terms of additional water extraction might be offset by the presence of a larger shoot consuming the extra water (Palta *et al.* 2011). Two recent modelling studies showed exactly that: faster root growth generally led to faster soil water depletion, which subsequently led to yield penalties in soybean (Sinclair *et al.* 2010) and chickpea (Vadez *et al.* 2012).

In summary, although roots can play an important role in water stress adaptation, the focus on faster root growth and more profuse rooting risks the generation of plant types that exploit soil water quickly. However, faster root growth could still be important in specific conditions such as areas in which rainfall occurs over short durations, where slower root growth would not allow early maturity genotypes to extract all the water available from the soil profile (Vadez *et al.* 2012), or in areas where the soil depth is high and water is available at that depth (Sinclair *et al.* 2010).

### Water use and conservation

#### *Leaf canopy development*

Plants use water to produce biomass for the development of leaf area. Because species or genotypes within species have different leaf areas, they have different water uses. Fig. 1 shows the typical sigmoid shape of the leaf area development curve as a function of thermal time. In the left part of the curve, the leaf area of two hypothetical genotypes, A and B, is represented. Genotype A shows faster leaf area development at earlier stages compared with genotype B, although both genotypes eventually reach a similar leaf area. For breeders, genotype A represents a high-vigour phenotype compared with B. The differences in area between the two curves of genotypes A and B represent the



**Fig. 1.** Typical sigmoid curve of leaf canopy development as a function of thermal time (in degree-days). Genotypes represent a factorial of cases combining slow/fast early leaf area (LA) development and small/large maximum leaf area.

leaf area differences between the two genotypes. Assuming similar leaf conductance, these leaf area differences therefore represent differences in water use. Several genetic factors can contribute to these differences, including the rate of leaf appearance, or simply the size of individual leaves appearing at different stages. When the leaf area of the canopy reaches a hypothetical maximum, several situations can arise. Fig. 1 shows the case of genotypes A and C, which have similar initial kinetics of canopy development, but eventually differ in their maximum leaf areas. Genotypes A and D differ for both the initial rate of leaf area development and for the maximum leaf area. In addition to the genetic factors mentioned above that can contribute to these differences, the level of branching (or tillering for cereals) is important. Therefore, Fig. 1 illustrates four different hypothetical situations and is essentially a factorial of slow/fast canopy development with small/large canopies. Differences between the curves indicate differences in leaf area; however, at the same leaf conductance levels, these differences represent differences in water usage over the course of leaf area development. Therefore, every factor that affects how rapidly and how large the canopy develops is bound to affect how much water a given genotype will use before anthesis, and this would have significant implications in a water-limited context.

These theoretical differences are illustrated by several experimental results in different crops. Chickpea genotypes that were tolerant to terminal water stress conditions tended to have a smaller leaf canopy at the vegetative stage than sensitive genotypes (Zaman-Allah *et al.* 2011b). This partially explained the smaller plant water use at the vegetative stage in these genotypes (Zaman-Allah *et al.* 2011a). A similar observation was noted in peanut genotypes exposed to three different intermittent water stress treatments varying in intensity where the tolerance index was negatively related to the leaf area and the leaf dry weight, i.e. genotypes with a small canopy maintained their yield under water stress at levels closer to that of the fully irrigated control (Ratnakumar and Vadez 2011). Further, recent data have shown that the coefficients of an exponential function

linking the node number on the main stem to the leaf area of plants (a function used in a family of robust legume crop models (Soltani and Sinclair 2011)) vary between genotypes and lead to different leaf area indices in peanut (O Halilou, TR Sinclair, F Hamidou, V Vadez, unpubl. data) and chickpea (V Vadez, R Wangari, P Murthy, unpubl. data). A set of contrasting cowpea genotypes, selected for differences in grain yield under terminal water stress across field conditions, also contrasted for leaf area at the time of flowering, with tolerant genotypes exhibiting less leaf area (Belko *et al.* 2012). Anyia and Herzog (2004) also showed that genotypes with larger leaf areas showed lower water stress avoidance. Similar examples can be found outside of legume crops. For example, in sorghum, hybrids with a higher leaf appearance rate showed reduced tillering, which led to both a reduced leaf area around anthesis and increased yield under water stress (van Oosterom *et al.* 2011). Of course, a smaller canopy would also restrict light capture and limit yield under certain conditions or crops (Sinclair and Muchow 2001).

Above, we noted that differences in the rate of leaf canopy development and in the maximum leaf area around anthesis. Some of these differences are genetic; however, environmental conditions are also known to play an important role in leaf area development through a combination of hydraulic and metabolic controls (Pantin *et al.* 2011, 2012; Kudoyarova *et al.* 2013). For example, maize leaf development varied among genotypes when plants were exposed to either a high vapour pressure deficit (VPD) or a low soil water potential (Reymond *et al.* 2003). Thus, genotypes that exhibit sensitivity to a high VPD with respect to their leaf area development would have smaller leaf areas than insensitive genotypes if grown under such conditions. It is indeed quite clear that leaf development is under hydraulic control (Munns and Cramer 1996; Tardieu *et al.* 2010; Pantin *et al.* 2012). Leaf development is also sensitive to soil drying, and the termination of leaf growth occurs before termination of transpiration (Sadras and Milroy 1996; Soltani *et al.* 2001; Reymond *et al.* 2003; Parent *et al.* 2009; Tardieu *et al.* 2010). Depending on the water stress scenario, limiting leaf development under water stress could limit productivity. QTLs for sustained leaf growth under a high VPD or soil drying were identified in maize, with beneficial alleles originating from water stress tolerant parents (Welcker *et al.* 2011). In other crops, as observed above, limiting leaf growth or decreasing it at higher soil water potentials could be beneficial (Lawlor and Tezara 2009; Ratnakumar and Vadez 2011). In any case, it will be important to harness the genetic determinants of leaf area development (both the inherent characteristics and the genetic responses to environmental conditions) to subsequently tailor cultivars with a trait makeup that fits specific conditions.

#### Leaf canopy conductance

Whereas limiting the size of the transpiring leaves is one way to control plant water losses, limiting the conductance of the leaf canopy is another point of control. Indeed, under similar environmental conditions, two genotypes with the same leaf area exhibiting differences in leaf canopy conductance would lose different amounts of water. For example, pearl millet genotypes varied with respect to leaf canopy conductance

under fully irrigated conditions despite exhibiting a similar leaf area (Kholová *et al.* 2010a), and this appeared to be related to higher leaf ABA content in genotypes with low leaf canopy conductance (Kholová *et al.* 2010b). Similar results were obtained in chickpea (Zaman-Allah *et al.* 2011b) and cowpea (Belko *et al.* 2012), where the canopy conductance differed among genotypes. In the research reported by Kholová *et al.* (2010b), Zaman-Allah *et al.* (2011b) and Belko *et al.* (2012), the leaf canopy conductance was calculated as the ratio of gravimetric transpiration measurements at the whole-plant level divided by the leaf area and the time that plants were allowed to transpire (either an entire day or one-hour time periods across an entire day). Thus, it was ensured that the leaf area index of the plants was <1, such that there was a lack of (or limited) mutual shading of leaves. Leaf conductance measurements using gravimetric methods have a throughput that makes them suitable for breeding programs. These measurements were robust, and they were preferred over porometric measurements, which have several drawbacks (Turner 1991), including sampling (choice of leaf or choice of leaf section), time of sampling (possible changes in light or VPD conditions), and throughput. Porometric measurements would also not be able to cope with the possibility of stomatal patchiness (Buckley and Mott 2000). Using these methods, chickpea genotypes that were tolerant to terminal water stress were found to have a lower leaf canopy conductance at the vegetative stage and under fully irrigated conditions (Zaman-Allah *et al.* 2011b). Higher yielding chickpea genotypes also had a lower index of leaf canopy conductance, measured using canopy temperature data obtained from infrared images, than lower yielding genotypes, and this water saving feature led to a lower plant water use in tolerant genotypes at the vegetative stage (Zaman-Allah *et al.* 2011a). Similarly, in cowpea a majority of terminal water stress tolerant germplasms also had a lower leaf canopy conductance than sensitive germplasm (Belko *et al.* 2013). DREB1A groundnut, which has high transpiration efficiency (TE), also exhibited low stomatal conductance (Bhatnagar-Mathur *et al.* 2007). Transgenic tomatoes with high levels of ABA also showed reduced leaf conductance, which also led to a higher TE (Thompson *et al.* 2007). A similar situation was observed in wheat (Condon *et al.* 2002).

Stomatal opening is sensitive to the evaporative demand, and a high VPD reduces stomatal aperture to restrict water losses. This phenomenon has long been reported in different crop species (e.g. Squire 1979; Turner *et al.* 1984; Grantz 1990), and it ensures maximum transpiration at times of the day when the VPD crosses a threshold. However, genotypic variation has only recently been revealed in different species such as soybean (Fletcher *et al.* 2007; Sadok and Sinclair 2009), chickpea (Zaman-Allah *et al.* 2011b), cowpea (Belko *et al.* 2012), peanut (Devi *et al.* 2010) and cereals such as sorghum (Gholipour *et al.* 2010) and pearl millet (Kholová *et al.* 2010b). Crop simulation analysis has shown that this maximum rate of transpiration would have a beneficial effect on yield and also that it would lead to water saving and a higher TE (Sinclair *et al.* 2005). In the case of cowpea, this trait was used to discriminate terminal water stress-tolerant from sensitive entries (Belko *et al.* 2012). More recently, a QTL for lower leaf canopy conductance under high VPD was identified in pearl millet (Kholová *et al.* 2012), and genotypes with VPD-responsive traits had higher yields under

terminal water stress conditions. The method developed in that research was also designed in a way it can be used by a breeding program.

Fig. 2 synthesises the characteristics of leaf conductance that can affect plant water use: (i) high leaf conductance under low or moderate VPD conditions and insensitivity to the high VPD conditions in genotype A; (ii) high leaf conductance under low or moderate VPD conditions but sensitivity to the high VPD conditions in genotype B; (iii) low leaf canopy conductance under low or moderate VPD conditions and sensitivity to high VPD conditions in genotype C; and (iv) low leaf conductance under low VPD and a small positive slope for leaf conductance in response to VPD increase, leading to a low leaf canopy conductance at a high VPD but no VPD breakpoint in the case of genotype D. Genotypes A and D are illustrated by the chickpea genotypes ICC8058 and ICC14799 (Zaman-Allah et al. 2011b) and the cowpea genotypes UC-CB46 and IT93K-503-1 (Belko et al. 2013). Genotypes A and C are illustrated by the pearl millet genotypes H77/833-2 and PRLT-2/89-33 (Kholová et al. 2010b) and the cowpea genotypes IT82E-18 and IT93K-693-2 (Belko et al. 2013). Practically, genotype B saves more water compared with genotype A when the VPD is above the breakpoint value, whereas genotypes C and D save more water compared with genotype A under all VPD conditions. Therefore, genotypes C and D can be considered as ‘water savers’, and although this feature can be beneficial under water-limited conditions, it can also limit carbon fixation under moderate or no water limitation. However, Gilbert et al. (2011a, 2011b) have shown that slow wilting soybean, which displays the typical phenotype of genotypes B or C (Fig. 2), has a photosynthetic rate capable of compensating for a slight reduction in stomatal opening due to the sensitivity to high VPD. Indeed, the relationship between the photosynthetic rate and stomatal conductance has a logarithmic shape (Wong et al. 1979) such that above a certain stomatal conductance, any additional increase in stomatal conductance

only leads to a marginal increase in the photosynthetic rate. In summary, the control of leaf water losses, especially under high VPD conditions, appears to be a major avenue for increasing the performance of crops grown under high VPD conditions, and this control mechanism likely leads to increases in TE.

Transpiration response to soil humidity

Upon progressive exposure to water deficit, stress-exposed plants reach a soil moisture level at which the root cannot support the full transpirational demand, and the plants must initiate stomatal closure to avoid shoot desiccation. It has long been believed that transpiration would start declining at a fraction of transpirable soil water (FTSW, i.e. the portion of the soil water that plants can take up to support transpiration) on the order of 30–40% regardless of plant species or genotypes within species (e.g. Sinclair and Ludlow 1986; Sinclair et al. 1998). The FTSW thresholds at which leaf expansion starts to decline are known to be higher than those at which transpiration declines; in other words, the leaf expansion processes are more sensitive than transpiration (Sadras and Milroy 1996). Fig. 3 represents the typical curve of the transpiration response of genotype A to soil drying, normalised to a fully irrigated control. This curve shows that the normalised transpiration rate (NTR) remains at a value of 1.0 until the FTSW has dropped below ~0.40 (i.e. 40% of the soil water available for transpiration remains). This also indicates that the leaf gas exchange of the stress-exposed plant is similar to that of a non-stressed plant until 60% of the soil moisture is depleted, i.e. there is no stress in terms of leaf gas exchange as long as the NTR remains at ~1.0. However, in more recent experiments, a large genotypic variation in these FTSW thresholds for transpiration decline was identified. For example, in soybean, differences in the FTSW thresholds were reported among different soil-applied manganese treatments (Vadez et al. 2000), and genetic differences were reported later (Sinclair et al. 2003). Genetic differences in these FTSW thresholds have been reported in groundnut (Devi et al. 2009;

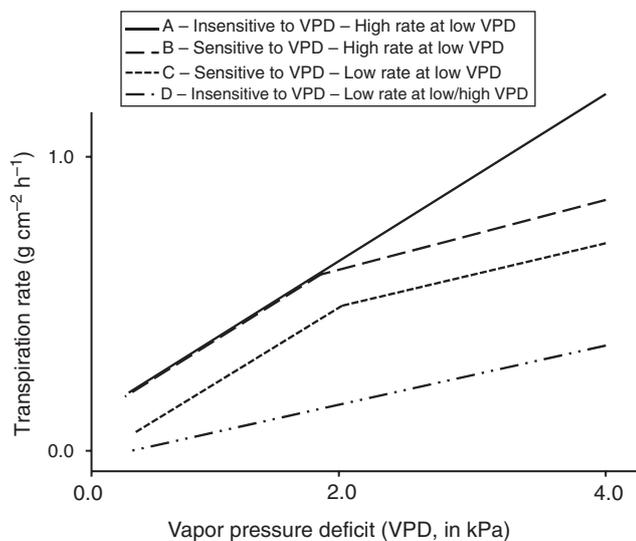


Fig. 2. Potential cases illustrating the transpiration rate ( $\text{g cm}^{-2} \text{h}^{-1}$ ) response to increases in the vapour pressure deficit (VPD). The transpiration rate is used as a proxy for leaf canopy conductance.

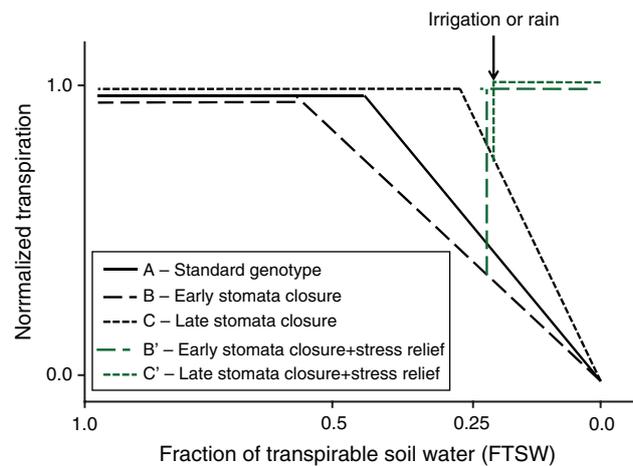


Fig. 3. Transpiration response to soil drying in different hypothetical genotypes displaying a drop in the normalised transpiration at high and low FTSW (genotypes B and C respectively). Curves B' and C' depict the potential losses in terms of NTR if irrigation is given or rainfall occurs when the FTSW reaches ~0.25.

Leal-Bertioli *et al.* 2012), chickpea (Zaman-Allah *et al.* 2011b), cowpea (Belko *et al.* 2012) and other non-legume crops such as sorghum (Gholipour *et al.* 2010) and pearl millet (Kholová *et al.* 2010a). This trait is important because genotypes with high FTSW thresholds begin to partially close their stomata at a relatively high soil water content and hence save water. A simulation study has shown that this trait would lead to a significant soybean yield increase in the USA, especially in years classified as dry (Sinclair *et al.* 2010), although the same trait has been reported to have only a limited impact on chickpea yields (Soltani *et al.* 2000).

Fig. 3 illustrates different potential cases of genotypic variation in FTSW thresholds. Genotype B has a high FTSW threshold value; therefore, it saves water early and has a 'conservative' behaviour with regard to plant water use. This phenotype could be advantageous under severe stress conditions such as long-terminal water stress or intermittent water stress with long gaps between rains and is illustrated by the peanut genotype ICGV86015 as described by Devi *et al.* (2009). Genotype C has a very low FTSW threshold, and its transpiration relative to a fully irrigated control drops at low soil moisture and declines rapidly thereafter. These characteristics are illustrated by the peanut genotypes TMV2 and ICGV86699 described by Devi *et al.* (2009) and the cowpea genotypes IT84S-2049, Mouride and Suvita 2, which are all terminal water stress tolerant (Belko *et al.* 2012). Such genotypes exhibit 'opportunistic' behaviour with regard to plant water use and would perform well under late terminal water stress or intermittent stress conditions with frequent relief from water stress by irrigation or rain. We recognise that a high FTSW threshold for transpiration decline would also bear negative consequences under intermittent stress conditions, in which there is frequent alleviation of stress and where genotypes with a high FTSW threshold would perform limited carbon fixation between the time when the FTSW threshold value is reached (~0.60 in Fig. 3) and relief of stress. The transpiration of genotype B' illustrates such a case, whereas genotype C', with a low FTSW threshold, would barely be affected by the stress before stress relief (Fig. 3).

#### *Regulation of plant water loss: plant hydraulics and hormonal regulation*

The sections above highlight the importance of canopy size, kinetics of canopy development, canopy conductance, environmental responses and combinations of these aspects in canopy water use. A considerable body of knowledge exists regarding the individual regulation of some of these factors; however, the co-ordination and integration of their regulation at the organ and plant level are very complex processes that are not yet understood.

Stomatal closure is partially under the control of ABA, which is produced in the roots and transported to the shoot where it targets stomatal guard cells (Zhang and Davies 1991; Tardieu *et al.* 2010). Evidence for the role of ABA in stomatal closure was obtained from partial root drying experiments, wherein half of the root system was partially dried, and the other half was kept fully irrigated. Although the leaf water potential of the plant exposed to the partial root drying treatment was similar to that

of the fully irrigated control, its leaf conductance was reduced (Gowing *et al.* 1990). Several papers have reviewed the role of ABA in stomatal signalling (Zhang and Davies 1991; Davies *et al.* 2002; Buckley 2005). Part of the complication arises from the fact that ABA is also known to positively influence the hydraulic conductivity of the roots, which in turn influences the rate of transpiration under high VPD in tomato (Thompson *et al.* 2007). Comstock (2002) reviewed the possible role of both hydraulic and chemical signals on the control of stomata, providing evidence for both types of regulation. In fact, the question of whether signalling molecules control stomatal movements raises the question of how the rapid changes in stomatal closure can be explained (e.g. those recorded when transpiring plants were exposed to a gradient of increasing VPD conditions). The transpiration responses to VPD reported above indeed imply relatively rapid changes in transpiration, which is hypothesised to be hydraulic in nature (Sinclair *et al.* 2008; Kholová *et al.* 2010b). The hypothesis that a hydraulic signal controls stomatal aperture has indeed been proposed and offers an elegant and sensible model for the regulation of stomatal opening (e.g. Sperry *et al.* 2002). Indeed, it is accepted that some aspects of stomatal regulation are under hydraulic control, at least under a high VPD (Mott 2007).

A consensus has been reached regarding the hydraulic control of leaf development, and there is much evidence for hydraulic regulation (Salah and Tardieu 1996; Thompson *et al.* 2007; Ehlert *et al.* 2009; Pantin *et al.* 2011). However, leaf development is also influenced by ABA via several direct and indirect means (Tardieu *et al.* 2010), including its effect on root hydraulic conductance via the stimulation of aquaporin (AQP) transcription (Ehlert *et al.* 2009; Parent *et al.* 2009). A recent genetic analysis also showed that the sensitivity of leaf development to VPD is controlled by the same genomic regions that control the sensitivity to soil drying in ~75% of cases (Welcker *et al.* 2011). Given that the sensitivity of the leaf growth rate to VPD is under clear hydraulic control (Reymond *et al.* 2003; Sadok *et al.* 2007; Ehlert *et al.* 2009; Parent *et al.* 2009), this represents strong evidence that the leaf development response to soil drying is also under hydraulic control.

These examples illustrate the complexity of the regulation of two critical aspects of plant water use, i.e. leaf conductance and leaf development, and clearly show a central role for hydraulics in these processes. In summary, both hydraulic and chemical regulation appear to be playing a role in the control of stomatal aperture and in leaf development. We argue that hydraulic and chemical signalling need to be observed from two angles: first, in the short term control of stomatal aperture, where a hydraulic signal would likely have a prominent influence, although the 'biochemical environment' might be playing a role that is still not understood. For example, it was intriguing that pearl millet genotypes with contrasting VPD responses also contrasted with respect to their leaf ABA content (Kholová *et al.* 2010b). Several studies have also reported that ABA affects the level of AQP in different plant tissues, and this leads to differences in the hydraulic conductivity of tissues (Thompson *et al.* 2007; Ehlert *et al.* 2009). Therefore, even under the short-term time frame of stomatal aperture control, both hydraulic and chemical signalling are likely to be intertwined. Second, the long-term control of leaf water loss

via the control of leaf development is under both biochemical and hydraulic control; however, it is becoming increasingly clear that the long-term growth environment eventually conditions a short-term leaf conductance response to VPD (Sermons *et al.* 2012; Schoppach and Sadok 2013).

### What progress is needed in ‘water stress’ research?

#### *The need to comprehensively understand root water uptake and shoot water loss/use*

Summarising the sections above, we understand that under water limitation conditions plants have different means of either increasing access to water or optimising water use by rationing it for use during critical periods of the developmental cycle. These strategies are related to water input. In contrast, a plant loses water depending on the size of its canopy, the speed of its development, and its conductance (especially conductance under particular atmospheric conditions). These situations are related to water output. Water stress ‘tolerance’ therefore results from a complex combination of traits that influence supply and demand for water (Passioura 2012). The ability of a genotype to adapt to a particular water availability level eventually determines the level of ‘tolerance’ of that genotype. Therefore, to understand these complex interactions, methods are needed that can be used to analyse as many components as possible related to plant water balance such that a comprehensive understanding can be achieved. Recently, a lysimetric system has been developed (Vadez *et al.* 2008), in which plant water use can be monitored from a very early growth stage until maturity and highly relevant agronomic assessments can be performed in conditions that mimic field situations at least in terms of plant density and the soil and water volume available to each plant (Ratnakumar and Vadez 2011; Vadez *et al.* 2011a, 2011b, 2013b; Zaman-Allah *et al.* 2011a). In particular, this system allows the measurement of water extraction at key stages, especially the grain filling period, and it can be used to assess leaf conductance using the index of stomatal conductance (Zaman-Allah *et al.* 2011a).

The system also has the advantage of providing a means of stress response assessment via comparisons between the transpiration of water stressed plants and that of fully irrigated controls. For example, under terminal stress conditions, sorghum transpiration remained at the level of fully irrigated controls for approximately four weeks after stress imposition, after which the transpiration declined sharply (Vadez *et al.* 2011b). Similarly, in chickpea plants exposed to terminal water stress, the average transpiration of 20 genotypes remained at the level of fully irrigated controls for ~22 days after stress initiation (Zaman-Allah *et al.* 2011a). This finding provides better knowledge regarding the physiological stages of the plants that are affected by stress. In a recent study, the levels of antioxidant enzymes in water stress tolerant and water stress sensitive pearl millet genotypes were measured and were found to differ between genotypes. However, these differences were the consequence of the soil water status (FTSW) (Kholová and Vadez 2013). Further improvement of the system, which is currently ongoing, will allow for measurements of the kinetics of leaf canopy development in plants within which water uptake is also monitored. This will allow dynamic measurement of leaf

area development together with the evolution of leaf canopy conductance over time.

#### *Modelling as a tool to integrate the different water stress components*

Once traits contributing to certain water stress patterns for any given crop have been identified, the evaluation of their effects remains difficult because several traits can play roles, and these traits are likely to interact with one another and with the environment. In summary, testing the effects of traits via experimental means is bound to be restricted to a few traits at a time and a few environmental and climatic scenarios. It is indeed becoming very clear that much of the complexity originates from the interaction among traits and from their interactions with the environment (Buckler *et al.* 2009; Schuster 2011). Therefore, a tool is needed that can artificially simulate the effect of a given trait across different layers of complexity. Crop models can serve to ‘integrate’ complex behavioural/developmental processes of plants that are all related through water need/use. Not all models are suitable for this purpose, and those that are suitable must be designed such that the algorithms that are part of the model structure reflect observable and quantifiable biological observations (Sinclair and Seligman 2000; Hammer *et al.* 2010). Only then can the model be sensitive to changes in the conditions and accurately predict effects.

A large body of convincing evidence has been gathered regarding the relevance of crop models in the guidance of breeding targets. Water use/conservation and water capture are composed of several ‘pieces’, and the effects of these pieces are more easily modelled than assessed. For example, using a robust crop model for chickpea, Soltani *et al.* (1999) showed that an early decline in leaf expansion and transpiration upon soil drying led to yield improvement under water stress conditions, although the yield improvements obtained were <5%. Although these two traits were discussed in earlier sections as potential key water saving traits, this example illustrates that under the geographical conditions in which the model was used, these traits had only limited interest, and making an investment in breeding them was not a priority. In other simulations with chickpea, a rapid root growth rate was shown to decrease yield by an average of 5%, whereas an increase in the depth of root water extraction by 20 cm increased yield by an average of 10%, therefore, among all the genetic traits tested, this trait conferred the largest yield benefit (Vadez *et al.* 2012). We note that this study also modelled the effect of management options and showed that a 40% yield improvement was derived from providing a 30 mm irrigation at the beginning of seed growth, which is in full agreement with previous results (Soltani *et al.* 2001). Therefore, these data show the efficacy of a model for comparing both genetic and management options. For example, crop simulation allowed the optimisation of sorghum planting density in a low rainfall environment (Hammer 2006). Simulations have been utilised for maize, in which different genetic traits of the maize cultivar were given values of sorghum cultivars. The results showed that increasing the depth of soil water access led to yield increases of ~20%, whereas the other traits either had no effect (e.g. early or a late decline of transpiration upon progressive water stress imposition) or a negative effect (e.g. the development of smaller

leaves) (Sinclair and Muchow 2001). The modelling approach is powerful because it is now possible to simulate the effects of certain QTLs on yield based on the percentage effect of a given QTL on particular traits (Chapman *et al.* 2003; Welcker *et al.* 2007; Chenu *et al.* 2009). It should be noted that in these examples, the effects on yield are the results of single traits tested in isolation from others, whereas the use of a model allows for the assessment of trait combinations, which has been initiated recently (Vadez *et al.* 2013b).

#### *'Environment-specific' breeding and probabilistic estimation of potential gains*

The few examples provided in the last section illustrate the potential of crop models for predicting the value of specific traits. These examples also show that, depending on the regions targeted by the modelling exercise, the effects of traits on yield are often counterintuitive. Specifically, some traits can have either less of an effect than expected, a negative effect, or an unexpected effect. This illustrates the role of crop simulation as a critical pre-screening technique for the many traits that can be bred for and its role as a means of generating a yield-trait performance landscape (Messina *et al.* 2011). At the same time, it demonstrates the potential of crop simulation as a tool for deciphering the complexity of biological responses.

An important application of crop models is therefore to provide a geographical dimension for possible trait effects along with a stochastic measurement of the probability of success of a given trait in a given environment. This approach is still in its early stages, and we argue that it will have great potential for use in breeding programs. For example, the enormous benefit of the sensitivity of transpiration to high VPD on soybean yield in the USA has been recently shown (Sinclair *et al.* 2010). Moreover, the yield improvements were greater in the driest years, and there was no yield penalty in the wettest years. Finally, although the overall effect of this trait is highly beneficial, the model also provides the probability of trait success. In other words, although a given trait could have an overall positive effect on yield, the environmental variability is such that yield could be decreased in a substantial number of cases, whereas it would be increased in other cases. Unless there is a clear geographical zonation of these scenarios, a trait that would not lead to a majority of success cases would likely generate little interest among breeders for use in their program. Therefore, we argue that crop modelling will be increasingly used as a stochastic tool to predict trait effects and to assess the percentage of expected yield increase and the probability of trait success.

#### *Engaging the breeding community*

The different aspects covered in the present paper give a lot of insights on what traits potentially matter for water stress adaptation and on methods that can be applied by the breeding community to use these traits. We present traits but also trait responses to the environment, which also gives insight and possible explanations for the high levels of interactions between genotype and environment in the yield expression, i.e. one of the main challenge of breeding programs. The information presented in this paper offers direct possible

applications by the breeding community. For instance, the gravimetric measurement of the transpiration rate under high VPD, a trait that leads to better adaptation to water stress in several crops and at least in some environment, can be measured at a fairly high throughput level (e.g. Kholová *et al.* 2012). The use of lysimetric measurements of the pattern of water extraction, or of long-term transpiration efficiency measurement, provides other examples of tools, methods and approach that breeding program can use. Moreover, we believe that the engagement of the breeding community needs to be around the approach. In the end, tools and methods are only parts of recipes which can only be as good as the approach has been. The examples herein give insights of the changes that are needed in the breeding approach. First, we talk about trait measurements. These imply new experimental setups that are not only fields, even well equipped fields, but specialised facilities towards specific measurements. These can be automatic setups to measure traits such as transpiration and leaf area, in which there is currently a technological revolution taking place. Second, we have seen the large influence of the environment on traits. Therefore, breeding is not only about understanding the genetic of the traits, but, in many cases, the genetics of the response of the trait to the environment. Recent work on maize leaf development gives us outstanding example of how an eco-physiological approach needs to be embraced by the breeding program (Welcker *et al.* 2011). Third, we provide examples of how crop modelling can assist the breeding program. Indeed increasingly, and especially for complex issues such as water stress, breeding programs will need to embrace a component of modelling to guide their target. Some companies and breeding program have already made this fully operational. Last, but not least, we believe that the engagement of the breeding community is about the integration of other disciplines in the breeding approach and process, namely physiology, genetics, and modelling, as far as this paper is concerned, but also of agronomy.

#### **Conclusion**

Plant adaptation to water deficit is not likely to depend on 'water stress tolerance genes' but rather, on both the inherent and adaptive characteristics that condition water supply and demand. The resulting 'tolerance' of a plant depends on the degree of fitness, i.e. how close the matching of water supply and demand is achieved in a given water stress scenario (Tardieu 2012). Among these characteristics, the speed and extent of canopy development, the water conductivity, and the sensitivity of plants to soil drying are important factors that influence plant fitness in a particular water stress environment. Here, we advocate that further progress in water stress research needs to place water at the centre of all considerations. Further progress will be made by harnessing the genetics of these traits, and particularly the genetics of ecophysiological responses to environmental cues. Given the complexity of the interactions between these characteristics and with the environment, crop modelling will become an increasingly critical tool for navigating the complexity of these numerous interactions. Breeding will then be no longer limited to field experimentation but will involve both precise phenotyping under specific conditions to target critical traits and utilisation of the simulation outputs to

guide breeding targets. The research cited in this review also highlights the critical need for a close and equal collaboration between disciplines.

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