

# Coping with drought: Resilience *versus* risk. Targeting the most suitable G\*E\*M options by crop simulation modeling\*

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## Abstract

Crop production is axiomatically related to water consumption of transpiring leaves. Crop adaptation to water limitation then becomes an exercise of matching water supply and demand in a way that the crop has enough water to complete its cropping cycle. Weather conditions vary greatly across years within environments while both weather and soil conditions vary across locations, which means that drought scenario are extremely variable and these need to be properly characterized as a pre-requisite to undertake drought research. Once the weather scenarios are defined, traits contributing to the crop adaptation to any of these scenarios need to be identified. We believe that much of these traits revolve around the need to optimize plant water use and make it efficient, together with the need to maximize water capture from the soil. Optimization of plant water use consist in identifying traits that will ensure maximum crop growth while keeping sufficient water for the grain filling period, and it deals with controlling water losses, and minimizing leaf canopy development. While tapping more water is surely important, the timing of water extraction to critical crop stages, e.g. the grain filling stage, is even more critical. It depends in great part on the way water has been managed by the plant at earlier stages, in particular to the capacity to develop a smaller crop canopy, or the capacity to restrict plant transpiration, especially under high evaporative demand. Clearly, the development of cultivars capable of better performance under water limited conditions is the result of many possible characteristics that interact with one another and with the environment, and it is difficult to experimentally determine which among these traits has a predominant effect on yield in a given situation. Crop simulation modeling comes in to help to navigate biological complexity by allowing to test the effect of traits on yield across many years of weather and many locations. It also helps combining both agronomic and genetic options to maximize crop production at the plot level.

**Key words :** aquaporin, lysimeters, vapor pressure deficit, water saving traits.

\*G\*E\*M: Genotype, Environment and Management.

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## Résumé

### **S'adapter à la sécheresse: résilience ou risque. Cibler les meilleures options G\*E\*M par simulation**

La production des cultures est invariablement liée à la consommation d'eau pour la transpiration des feuilles. L'adaptation des cultures au déficit hydrique devient donc un exercice d'équilibre entre la demande et la disponibilité en eau, de manière à ce que la culture ait suffisamment d'eau pour terminer son cycle. Le climat varie beaucoup au travers des années et des environnements, de même que le sol, ce qui veut dire que les scénarios de sécheresse sont extrêmement variables et qu'il faut en premier les caractériser avant d'entreprendre la recherche sur l'adaptation au stress. Une fois les scénarios définis, les caractères contribuant à l'adaptation des plantes peuvent être identifiés. Nous pensons que ces caractères sont ceux qui contribuent à maximiser la capture en eau et une utilisation raisonnée et efficace de l'eau. Si la maximisation de la capture en eau par les racines est évidemment un caractère important, le fait d'avoir de l'eau disponible pour des stades critiques du cycle de la plante, comme le remplissage des grains, est absolument essentiel. Cela dépend beaucoup de la façon dont les plantes ont géré l'eau à des stades plus précoces, par exemple en développant une canopée plus petite ou en restreignant la transpiration sous conditions de forte demande évaporatoire. Clairement, le développement de variétés adaptées à la sécheresse est le résultat de plusieurs adaptations possibles, qui peuvent interagir les unes avec les autres, avec l'environnement, et il est alors difficile de déterminer expérimentalement laquelle de ces caractéristiques a un rôle prédominant dans une condition donnée. La simulation des rendements vient alors en appui pour aider à déchiffrer la complexité des systèmes biologiques, et permet d'évaluer les effets de ces caractéristiques sur le rendement. La simulation permet aussi de combiner des caractéristiques agronomiques et génétiques au niveau de la parcelle.

**Mots clés :** aquaporine, contrôle de l'eau, demande évaporative, lysimètres.

**W**ater limitation is bound to be a central issue in the 21st century because of an increasing demand from competing sectors, namely industrial, domestic, and agricultural. In that context, producing more crops with less water is going to be a must and breeding efforts are needed to develop water efficient crops. However, for much of the agriculture area facing water limitation in the world, the main issue is not only about producing more crops but to ensure that crop production is resilient to ensure food security year after year. So, in this paper we want to discuss ways to both optimize crop production under limited water while minimizing the risk of crop failure under particularly harsh conditions.

The first entry point to develop crops adapted to water limitation is to match water supply and demand. Crops species are usually well spread along gradients of rainfall conditions (FAO, doc number 56) which is in most part for that very need to match water demand of a given species and the water available in a given region. The same applies within species and breeders have long used that principle to breed cultivars whose duration fits specific length of growing period. However, beyond the regional rainfall trends, year to year and location to location variations remain very high within a given region, leading

to very different patterns of water stress. Therefore, a first step consists in a thorough characterization of the environment to clearly define stress patterns (intensity, duration) and their frequency of occurrence in a given region (e.g. Kholová *et al.*, 2013) and this will be the object of a first section. In that context, a successful genotype in any given drought scenario is one that has sufficient water to fill up grains and one that has used all the available water once reaching maturity. In contrast, an unsuccessful genotype would be one using most available water before anthesis, leaving insufficient water for the reproductive period, or the complete opposite, *i.e.* a genotype that would grow too small to fully benefit from the water available. Therefore, a lot of recent work on drought adaptation deals with the need to ensure water availability for the critical period of grain setting and grain filling, and on maximizing water extraction from the soil. The following section will then set a framework around water use, based on Passioura's equation ( $Y = T \times TE \times HI$ ; 1977), and will discuss recent re-evaluations of that equation and of its components, in particular by paying attention to particular time patterns of water extraction (the T component).

The next area of research on crop adaptation to water limitation deals with

the possible genetic alterations that can bring a better fit between water demand and supply and ensure that maximum water is available for critical periods. One section will review recent work on traits that affect water use, including water saving traits. Transpiration of pearl millet genotypes is sensitive to exposure to high vapour pressure deficit but this sensitivity differs among genotype (Kholová *et al.*, 2010). Plants can save water by developing leaves more slowly or smaller, while at plot scale water saving can be achieved by reducing sowing density (van Oosterom *et al.*, 2011). The following section will review the role of the underground part of the plant for drought adaptation, by mostly focusing on water capture and the need for water capture at critical times (e.g. Zaman-Allah *et al.*, 2011a; Vadez *et al.*, 2013a). A last section on these water supply/demand aspects will then present the concept of "genetic ideotypes", where the idea is first to decipher the genetic components of individual traits affecting plant water use and capture, their mutual interaction, and their interactions with the environment, and then to design specific ideotypes having varying water use/capture attributes depending on their genetic makeup.

Once the target environment is characterized and the genetic component of adaption are known, a third major area

is to tackle the complex inter-relations between genetic, management and environmental factors that contribute to crop adaptation to drought. Plant traits have a high degree of interaction with the environment (e.g. Reymond *et al.*, 2003) and a given plant trait will not lead to the same phenotype in different seasons. Therefore complex interactions take place between genetic and environmental effects, and one section will present recent work using crop simulation modeling to resolve multi-factor equations, as a way to pre-empt the effect of modifications at genetic, environmental, or management level.

Therefore the overall objective of this paper is to review three important complementary areas of research toward the development of cultivars adapted to water limitation, namely: i) the environmental characterization to better frame the search of genetic traits and management options; ii) the search of genetic traits that contribute to shift water to key periods of the crop cycle and the opportunity that exist to recombine these traits and their genetic determinant in an intelligent way to develop ideotypes targeted to a specific environment target; iii) the integration of the role of the genetics, the environment, and the management taking through crop simulation modeling, used here as the vector to fare through biological complexity.

## Environmental characterization: the key to target breeding efforts

Characterization of the prevalent drought scenarios for sorghum production has been undertaken in India (Kholová *et al.*, 2013) and Australia (Chapman *et al.*, 2003), and similar environmental characterization has been done for maize in Australia (Chenu *et al.*, 2009). The approach uses long term daily weather data and, using crop simulation modeling, assess on a daily basis whether the water availability (or supply) on a given day at a given location-year combination is sufficient to supply water demand of the developing crop. The resulting supply/demand ratio (S/D) is set to 1 when water supply matches or exceeds water demand from the crop. The S/D ratio falls below 1 when the water supply does not match the water demand from the crop, indicating that plants are under stress. Figure 4 in Kholová *et al.* (2013) illustrates the very large variations in the patterns of stress. The purpose of the above cited studies

was then to cluster these different scenarios into groups having similarity. For instance, recent report shows that the post-rainy sorghum area in India (about 5 million hectares) fall into five different stress pattern, ranging from very severe to no stress situation. More importantly, it clearly shows that certain types of stress prevail in specific sub-regions, for example severe to very severe stress in one of the four regions (Kholová *et al.*, 2013), therefore calling for specific breeding target depending on the which type of stress prevails in a given region.

## Setting the framework: matching demand to supply

A simple water-based model has been widely used to decompose plant production into three main components: the water capture for transpiration (T), the conversion of water into biomass through the transpiration stream (transpiration efficiency, TE), and the conversion of biomass into grain through the harvest index (HI). Crop yield (Y) is then a function of the quantity of water that can be extracted to support transpiration (T), of the efficiency to convert transpiration into biomass (TE) and the efficiency of conversion of the biomass into grain (HI), so that  $Y = T \times TE \times HI$  (Passioura, 1977). This model has been widely used and has offered a convenient framework to structure research on crop adaptation to water limitation into relatively simpler components. However, the T and the TE components are difficult to measure under field conditions. The T component is derived from evapotranspiration (ET) data calculation from neutron probe readings. These are prone to error (variability in depth, heterogeneity in the soil profile) and most difficult is to obtain reliable data on the soil evaporation. The TE measurement faces the same issues. A method has been developed to calculate TE under field conditions (Cooper *et al.*, 1983), although the calculation of the T component still relies on many assumptions. In face of this, many have started relying on indirect estimates of these components, such as the specific leaf area (SLA) or the Soil Plant Analysis Development (SPAD) chlorophyll meter reading (SCMR), or the carbon isotope discrimination (CID) to estimate TE (Hubick *et al.*, 1986; Nageswara Rao *et al.*, 1993; Wright *et al.*, 1994). However, more recent re-assessments of these surrogates have shown poor relationship between TE

and some of these traits, questioning therefore its reliability (Krishnamurthy *et al.*, 2007; Turner *et al.*, 2007; Devi *et al.*, 2011).

Recently a method using lysimeters (Vadez *et al.*, 2008) has been developed that allows a direct assessment of the component of the Passioura equation (Passioura, 1977). This method consists of long and large tubes (lysimeters), with soil volume available for water capture and surface area equivalent to the field conditions. This system also allows having a highly relevant agronomic assessment of agronomic parameters such as yield (Zaman-Allah *et al.*, 2011a). The system has now been used to assess genotypic variation for T and TE, the most difficult components of the Passioura equation to measure in the field, for instance in sorghum (Vadez *et al.*, 2011a), peanut (Ratnakumar *et al.*, 2009). We initially hypothesized that the lysimetric system would lead us to identify large variation for the water extraction potential among genotypes in several species. However, while we found differences in total water extraction among germplasm, for instance 3 kg/plant in sorghum (which would represent a 30 mm once extrapolated to a plot level, [Vadez *et al.*, 2011a]), we found that the timing of water extraction around critical stages was more critical (Ratnakumar *et al.*, 2009; Zaman-Allah *et al.*, 2011a; Vadez *et al.*, 2013a). Indeed, the total water extraction has only little bearing on yield (e.g. Vadez *et al.*, 2011a; Vadez *et al.*, 2011b; Vadez *et al.*, 2013a), or no bearing at all (Ratnakumar *et al.*, 2009; Zaman-Allah *et al.*, 2011a). Therefore, while the Passioura equation has offered a very useful network to structure the approaches to resolve drought, the fact that water extraction at key stage is more important than at other stages tells us that at least some terms of the equation are non-linear. This is shown by other work reporting the extremely high water use efficiency of water applied during the grain filling period (*i.e.* 55 kg/ha/mm in wheat (Manschadi *et al.*, 2006); about 40-45 kg/ha/mm in pearl millet (Vadez *et al.*, 2013a), about 40 kg/ha/mm in chickpea (Zaman-Allah *et al.*, 2011a).

## Identification of adaptation traits – water conserving mechanisms

### Leaf canopy development

Plant use water in the process of producing biomass for the development

of more leaf area. Every species varies in the leaf area that a crop canopy develops and therefore there is genotypic difference in water use. Two genotypes can vary in the early stages of leaf development and this is often referred to as “vigour differences”. Of course, if leaf conductance is similar, higher vigour means also higher water use. Several genetic factors can contribute to these differences, one being the rate of leaf appearance, or simply the size of individual leaves appearing at this stage. When leaf area of the canopy reaches an hypothetical optimum, several situations can arise and genotypes can reach different leaf areas. Again, assuming similar leaf conductance, differences in leaf area would mean differences in water use. The leaf appearance rate and the size of individual leaves but also the level of branching (or tillering for cereals) can explain these differences. Therefore, every factor affecting how quick and how large the canopy develops is bound to affect how much water a given genotype will be using and this would have major consequences under water limitation.

Terminal drought tolerant chickpea genotypes had smaller leaf canopy at vegetative stage than sensitive materials (Zaman-Allah *et al.*, 2011b). This explained in part the smaller plant water use at vegetative stage in these genotypes (Zaman-Allah *et al.*, 2011a). Similar observation came from peanut genotypes that were exposed to three different intermittent drought treatments varying in intensity and where the tolerance index was negatively related to the leaf area and the leaf weight, *i.e.* genotypes having a small canopy maintained the yield under drought at levels closer to the fully irrigated control (Ratnakumar and Vadez, 2011). A set of contrasting genotypes of cowpea, selected for differences in terminal drought yield across field conditions, also contrasted for the leaf area at the time of flowering, tolerant one having lower leaf area (Belko *et al.*, 2012). In sorghum, hybrids having a higher leaf appearance rate had reduced tillering and this led to a reduced leaf area around anthesis (van Oosterom *et al.*, 2011). A number of environmental factors also affect the leaf area development. For instance, maize leaf development was shown to vary among genotypes exposed to either high vapour pressure deficit or leaf water potential (Reymond *et al.*, 2003). So that genotypes whose leaf area development is sensitive to high vapour pressure deficit (VPD) would have smaller leaf area than

insensitive genotypes if grown under high VPD conditions.

### Leaf conductance

At similar leaf area, two genotypes differing in leaf canopy conductance would lose different amounts of water. For instance, pearl millet genotypes varied for leaf canopy conductance under fully irrigated conditions despite having similar leaf area (Kholová *et al.*, 2010). Here, 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 left to transpire, either an entire day or one-hour time period across an entire day, and ensuring no or limited mutual shading of leaves. These measurements were preferred to porometric measurements because of sampling issues associated to porometric measurements (what leaf, what portion of a leaf), time of sampling (possible changes in light or VPD conditions), and throughput. Tolerant chickpea genotypes to terminal drought had a lower leaf canopy conductance at vegetative stage and under fully irrigated conditions (Zaman-Allah *et al.*, 2011a). Similarly a majority of terminal drought tolerant cowpea germplasm had a lower leaf canopy conductance than sensitive one. DREB1A groundnut having high transpiration efficiency (TE) also had low stomatal conductance (Bhatnagar-Mathur *et al.*, 2007).

Plants exposed to high vapour pressure deficit (VPD) do reduce stomata aperture to restrict water losses. This is known as the midday stomatal closure and the phenomenon reported in different crops (e.g. Squire, 1979; Turner *et al.*, 1984; Grantz, 1990). However, it is not until recently that genotypic variation has been revealed in soybean (Fletcher *et al.*, 2007). The effect of a maximum rate of transpiration on yield has been simulated in sorghum and it led to higher yield while also increasing transpiration efficiency (Sinclair *et al.*, 2005). Since then, genotypic differences for the capacity of the leaf canopy to restrict transpiration under high VPD conditions have been found in several legume species such as chickpea (Zaman-Allah *et al.*, 2011a), cowpea (Belko *et al.*, 2012), peanut (Devi *et al.*, 2010). In the case of cowpea, this trait discriminated tolerant from sensitive entries (Belko *et al.*, 2012). More recently, QTL for a lower leaf canopy conductance under high VPD was identified in pearl millet (Kholová *et al.*, 2012).

Therefore, there are two ways in which leaf conductance can influence water losses in plants: i) by being low under low to moderate VPD conditions; ii) by restricting water losses under high VPD conditions.

### Transpiration response to soil humidity

Under progressive soil moisture, a stage comes when the root cannot supply all the water needed for transpiration. At this stage, the stomata start to close to avoid desiccation. The fraction of transpirable soil water for transpiration (FTSW), *i.e.* the portion of the soil water that plants can take up to support transpiration, is taken as an index of stress. Values around 30-40% for the beginning of the decline in transpiration are usually reported (Sinclair and Ludlow, 1986; Sinclair *et al.*, 1998; Sadras and Milroy, 1996), although larger genetic variations have recently been found. Genetic differences in these FTSW thresholds have been reported in groundnut (Devi *et al.*, 2009; Leal-Bertioli *et al.*, 2012), soybean (Sinclair *et al.*, 2003), chickpea (Zaman-Allah *et al.*, 2011a), cowpea (Belko *et al.*, 2012), and other non-legume crops such as sorghum (Gholipour *et al.*, 2012) or pearl millet (Kholová *et al.*, 2010). The significance of that trait is that upon progressive exposure to water deficit, genotypes having a high FTSW threshold begin to partially close stomata at relatively high soil water content and hence save water. A simulation study in soybean has shown that this trait would lead to significant yield increase of soybean in the United States, especially in those years classified as dry (Sinclair *et al.*, 2010). A genotype with a high FTSW threshold value would save water early and could be characterized as having a “conservative” behaviour with regards to plant water use. This phenotype could be advantageous under severe stress conditions, either long terminal drought, or intermittent water stresses with long gaps between rains. A genotype with a low FTSW threshold would sustain transpiration to the levels of fully irrigated controls until the soil is fairly dry. This “opportunistic” behaviour with regards to plant water use would fit situations of late terminal drought or intermittent stress conditions with frequent relieve of water stress by irrigation or rain. A high FTSW threshold for transpiration decline would also bear negative consequences under intermittent stress conditions where there is frequent alleviation of stress and where

genotypes with high FTSW threshold would limit carbon fixation between the FTSW threshold values and relief of stress.

## Identification of adaptation traits – water uptake

Roots are often seen as the key to solve drought, and therefore 'root traits' are often assimilated to 'drought tolerance traits' (Silim and Saxena, 1993; Matsui and Singh, 2003; Ober *et al.*, 2005; Sarker *et al.*, 2005; Kashiwagi *et al.*, 2006). However, their contribution is not always proven, like in a two years trial in chickpea where higher grain yield under terminal stress was related to higher root length density in one of the two year, although not in the other one Kashiwagi *et al.* (2006). In this study, the drought intensity was less in that year where no relation was found between yield and roots, and this tells us that the importance of roots to cope with water stress depends on stress intensity at least. Similar results were recently obtained in lentils where root traits and grain yield were not significantly related in a rainfed situation (Kumar *et al.*, 2012). Ratnakumar and Vadez (2011) also compared the root systems of 20 groundnut genotypes varying for yield 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 depth. Zaman-Allah *et al.* (2011a) reached the same conclusion in a similar trial with contrasting chickpea genotypes. Nevertheless, the benefit of deeper root systems has also been shown in different species. For instance a simulation study indicated that maize yields would increase from having the depth of root increased (Sinclair and Muchow, 2001). Hammer *et al.* (2009) also postulated that an increase in root growth must have been part of the reason for the increase in maize yield in the US over the last 30 years. We argue here that the importance of roots for drought adaptation might have been over-inflated because roots are not akin to water and because it is too often assumed that more roots would lead to more water extraction. Water extraction is indeed set both by the water availability of water in the soil profile and the capacity of roots to access it. Therefore, while roots are a necessary condition for water extraction, that condition is by no mean a sufficient condition.

This is in part because root length density and water extraction are not always related. Some studies show that an increase in root length density leads to more water extraction (Passioura, 1983; Monteith, 1986; Lafolie *et al.*, 1991; Vadez *et al.*, 2013b). Others show poor relationships between water uptake and the root length density (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). There is in fact a limited understanding of the root density required to fully extract water from a given soil volume. Relatively small length of roots in deep layers would be sufficient to supply water to the plant when the top soil is dry (Gregory *et al.*, 1978; Sharp and Davies, 1985), and in fact, having a small amount of roots in a deep and wet layer, acting as a wick might be enough to capture much water. However, measuring such a fine rooting differences at depth is a challenge, while such destructive measurements also provide extremely static data. In fact, more than the RLD per se, the proportion of the root being developed at depth has been shown to contribute to higher grain yield in peanut (Jongrunklang *et al.*, 2012). Future progress in using root measurement to investigate their role in drought adaptation may involve measurements of the root architecture *in situ*, for instance using tomographic measurements (Mooney *et al.*, 2012). *In fine*, until there is a mean to access root growth *in situ* and possibly under natural conditions, we argue that water uptake should be a prime target on future research on roots, as suggested previously (McIntyre *et al.*, 1995; Dardanelli *et al.*, 1997). Several authors have argued that small amount of water during the grain filling period would have major effects on the grain filling, and therefore measuring water extraction at certain key times may be more informative than measuring total water extraction. Each additional millimeter equivalent of water provided during grain filling would contribute to 55 kg/ha wheat yield increase Manschadi *et al.* (2006). Similar data have been provided by Kirkegaard *et al.* (2007) and Vadez *et al.* (2011b). In chickpea, each additional mm of water would lead to 40 kg/ha increase in chickpea yield and the water extraction differences between tolerant and sensitive entries extrapolated to a field density were in the order of 25 mm only (Zaman-Allah *et al.*, 2011a). Of course it is difficult to precisely measure water

extraction in the field, especially small but key amounts that would be extracted during the grain filling period. Previous work on roots indicates that root growth can persist at very different stages and under different conditions such as drought (Chopart, 1983; Hafner *et al.*, 1993; Ketring and Reid, 1993).

## Crop ideotypes

In what we have seen before, a number of traits are known whose individual actions would influence plant water use. Of course, none of these traits works in isolation and all are highly inter-dependent. In a recent study in pearl millet a number of traits associated to plant water use in pearl millet (leaf conductance, leaf conductance under high VPD, leaf area, leaf thickness, total shoot biomass, leaf size) have been mapped (Kholová *et al.*, 2012). Interestingly, three of the leaf conductance quantitative trait loci (QTL) co-mapped with an earlier identified QTL for terminal drought tolerance (Yadav *et al.*, 2002). Because that earlier QTL was based on yield assessments, the fact that we find a close co-mapping with explanatory trait QTLs indicates that our initial hypothesis that higher yields under terminal drought were conferred by water saving traits (here low leaf conductance) was correct. Moreover, we also found that several trait QTLs had high levels of interactions and that interaction of two or three QTLs could explain a larger part of the water use variations. More exciting is the fact that the population contains a whole range of recombinants varying in the "content" of these different QTL, which confer them a whole range of plant water use. We are currently in the process of exploiting this variation. We have reselected several recombinants, based on their QTL content, in order to select lines ranging from high to low water users. These will then be tested in the field and in the lysimetric system across a range of water stress treatments ranging from severe to mild. We argue here, assuming our hypothesis is correct, that combinations of loci involved in plant water use can be used toward the tailoring of cultivars fitted to specific drought conditions.

## Crop modeling to fare through complexity

Different traits can individually contribute to a better adaptation to drought.

However, because drought scenarios differ, adaptive traits may also differ depending on the stress scenario. We have seen one such example above (Kashiwagi *et al.*, 2006), where root contributed to higher yields in a fairly severe stress situation, but not under milder stresses. There are countless reports in the literature that report opposite effects of similar traits and all that account for the well know genotype-by-environment interactions, *i.e.* the fact that genotype's behavior changes with the environment in which it is being tested. Genotype-by-Environment interactions (GxE) have long been a major impediment to genetic progress and breeders have dealt with it by having large, but also costly, networks of testing sites, from which highly consistent cultivars could be selected.

GxE interaction could be a major opportunity to further enhance crops productivity, provided the reasons for having these interactions are thoroughly deciphered. We believe GxE interactions are caused by specific interactions between a particular plant trait and the conditions prevailing in a given environment. For instance, the transpiration response to high VPD could be a major trait to save water under conditions only where certain VPD thresholds are crossed. A responsive genotype A would fit better than non-responsive genotype B in an environment where VPD is high, whereas both genotypes might equally fit in an environment where there is low VPD. This only could lead to major yield difference and of course to GxE interactions.

Once traits contributing to certain drought patterns for any given crops have been identified, the difficulty remain in how to evaluate their effects, knowing that several traits can play a role, that these traits likely interact with one another, and most would interact with the environment. In sum, testing their effect through experimental means is bound to be restricted to relatively few testing environments under few climatic scenarios. Therefore, a tool is needed that can artificially simulate the effect of a given trait across different layers of complexity. Crop models are there to "integrate" complex behaviour/development processes of plants parts that are all related through water need/use (Hammer *et al.*, 2010; Sinclair *et al.*, 2010; Messina *et al.*, 2011). Not all models are suitable for that and those suited need to be designed in a way that the algorithms that are part of the model structure reflect observed and quantified biological observations (Sinclair and

Seligman, 2000; Hammer *et al.*, 2010). Only then the model can be sensitive to changes in the conditions and predict effects.

A number of convincing evidences have been gathered of the relevance of using crop models to better guide the breeding targets. The effect of the combination of traits related to water use/conservation and water capture could be modelled better than assessed. For example, Soltani *et al.* (1999) showed that an early decline in leaf expansion and in transpiration upon soil drying did indeed lead to yield improvement under drought conditions, but the yield improvements obtained were less than 5%. While these two traits are discussed in earlier sections as potential key water saving traits, they had limited interest under the geographical conditions in which the model was used. In other simulations with chickpea, a rapid rate of root growth was shown to decrease yield by an average 5% while increase the depth of root water extraction by 20 cm increased yield on average by 10%, this trait being among the genetic trait conferring the largest yield benefit (Vadez *et al.*, 2012). Interestingly, this study also modelled the effect of management options and showed a 40% yield improvement from providing a 30 mm irrigation at the beginning of seed growth, in full agreement with previous results (Soltani *et al.*, 2001). Therefore, models have the capacity to compare both genetic and management options, and were used to optimize planting density in low rainfall environment of sorghum growing areas (Hammer, 2006). The power of the modeling approach is that it is now possible to simulate the effects of certain QTLs on yield, based on a percentage effect of the QTL on particular traits (Chapman *et al.*, 2003; Welcker *et al.*, 2007; Chenu *et al.*, 2009). It should be noticed that in these examples, effect on yield are the results of single traits tested in isolation of others, while the model offers the huge potential to assess trait combinations, as it has been initiated recently (Vadez *et al.*, 2012).

### Crop modeling to fare through complexity: on the best G\*E\*M combinations

The few examples taken in the last section illustrates the potential of crop models to predict the value of the traits. They also show that depending on

regions targeted by the modeling exercise the effects of traits on yield are in a number of case counter-intuitive. Especially, they show that some traits have either less effect than expected or even negative effects, while certain traits can have an unexpected effect. This shows the role of the crop simulation as a critical pre-screen of the many traits that can be bred for, as a mean to generate yield-trait performance landscape (Messina *et al.*, 2011). At the same time, it shows the potential of crop simulation to be used as a tool to decipher the complexity of biological responses.

An important application of crop models is then to give a geographical dimension of 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 infancy and we argue it will have a great potential for breeding programs. For instance, the enormous benefit of the sensitivity of transpiration to high VPD on the yield of soybean across the USA has been recently shown (Sinclair *et al.*, 2010). Moreover, that study also shows that the yield improvements are greater in the driest quartile of weather years, but brings no yield penalty in the wettest years. Finally, while the overall effect of this trait is highly beneficial, it also provides a probability of success of the trait. In other words, while a given trait could have an overall positive effect on yield, the variability in environment is such that yield could be decreased in a substantial number of cases, while 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 raise little interest for breeders to use it in their program. Therefore, we argue that crop modeling will be increasingly used as a tool to predict trait effects, to assess the percentage of expected yield increase, and the probability of success of traits. ■

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