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Any trait or trait-related allele can confer drought tolerance: just design the right drought scenario

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Abstract

Most traits associated with drought tolerance have a dual effect, positive in very severe scenarios and negative in milder scenarios, or the opposite trend. Their effects also depend on other climatic conditions such as evaporative demand or light, and on management practices. This is the case for processes associated with cell protection and with avoidance, but also for the maintenance of growth or photosynthesis, high water use efficiency, large root systems or reduced abortion rate under water deficit. Therefore, spectacular results obtained in one drought scenario may have a limited interest for improving food security in other geographical areas with water scarcity. The most relevant questions on drought tolerance are probably, 'Does a given allele confer a positive effect on yield in an appreciable proportion of years/scenarios in a given area or target population of environment (TPE)?'; 'In a given site or TPE, what is the trade-off between risk avoidance and maintained performance?'; and 'Will a given allele or trait have an increasingly positive effect with climate change?' Considerable progress has already occurred in drought tolerance. Nevertheless, explicitly associating traits for tolerance to drought scenarios may have profound consequences on the genetic strategies, with a necessary involvement of modelling.

Key words: Allele, drought, drought tolerance, trait.

Introduction

The scientific community has a large responsibility when it announces spectacular results on the drought tolerance of plants, a topic with direct consequences on the food security of millions of people. Agriculture is facing a declining water availability, a reduction in arable land, and strongly increasing demand for harvested products. Predictions of climate change indicate an increased variability of rainfall in the next 40 years and an increased risk of high temperature (IPCC, 2007; Battisti and Naylor, 2009), that will cause appreciable limitations of yield (Tebaldi and Lobell, 2008; Brisson *et al.*, 2010). Food security requires investments in this domain, in particular with new genotypes that can at least maintain an acceptable productivity under reduced water availability. During recent decades, an appreciable part of the academic effort and the most spectacular results have been associated with the identification of single genes that would confer drought tolerance, mostly in controlled conditions. Surprisingly, these results have been obtained via a large variety of processes and mechanisms, for example, cell protection mechanisms (Garg *et al.*, 2002; Castiglioni *et al.*, 2008), detoxification of reactive oxygen species (Sunkar *et al.*, 2003; Yang *et al.*, 2007), hormone balance (Iuchi *et al.*, 2001; Rivero *et al.*, 2007) or the manipulation of a transcription factor (Nelson *et al.*, 2007; Oh *et al.*, 2009).

Taken together, these results may either suggest that individual mechanisms acting on very different pathways can bring a spectacular increase in drought tolerance, or that drought tolerance is such a vague concept that very different results can fit into it. It is clear that plant survival and plant performance under water deficit depend on different mechanisms, quantitative trait loci (QTL), and sets of genes (Tardieu, 1996; Skirycz *et al.*, 2011), although they are often grouped under the same concept. Furthermore, an allele associated with a given gene or QTL have different effects depending on environmental scenarios (Chenu *et al.* 2009). A given gene polymorphism may therefore bring spectacular results in a given drought scenario but not in others. In a provocative way, one can argue that any trait-related gene polymorphism can bring drought tolerance, provided that the appropriate scenario to demonstrate this tolerance is identified by model-based reverse engineering.

The most striking example of a contradictory effect is the duration of the plant cycle, largely determined by genes affecting flowering time. Simple computer simulations and agronomic experience show that a long cycle duration tends to improve yield under favourable conditions because it increases the amount of intercepted light (Monteith, 1977), but that it

decreases yield under severe terminal drought because it causes a depletion in soil water before the end of the crop cycle.

The objective of this short review is to contribute to a better definition of 'drought tolerance' in terms of plant performance, by discussing the scenarios of climate, soil, and management in which traits or alleles have either a beneficial or a detrimental effect (Table 1), and to evaluate how often a given drought scenario occurs in a target population of environments (TPE; Loffler *et al.*, 2005).

Avoidance and cell protection: does the ability to survive and grow under extreme stresses provide an avenue for genetic progress of tolerance in field conditions?

Resurrection plants can undergo total dehydration and recover upon rehydration (Phillips *et al.*, 2008). This requires a wide range of mechanisms of detoxification and protection (Smith-Espinoza *et al.*, 2003), which can be transferred to more common plants (Sunkar *et al.*, 2003). It is therefore tempting to consider that the genetic engineering of these mechanisms is a promising avenue for drought tolerance. This would imply that individual cells of droughted plants experience a water stress and have to be

Table 1. Synthesis of the effect of traits under different scenarios of climate, soil or management.

Trait	Abundance of known genes/ alleles affecting the trait	Variable for phenotyping	Positive effect	Drawbacks	Scenario for maximum positive effect	Scenario for maximum negative effect
Short crop cycle	***	Duration (°Cd)	Escape : end of cycle occurs with non-depleted soil water reserve	Lower cumulative photosynthesis during the crop cycle	Very dry year	End of cycle with favourable conditions
Cell protection against stress	***	Aspect, biomass	Controversial[1] probably minor except in very severe stresses	Controversial and variable	Very severe	?[2]
Avoidance via stomatal closure	*	Aspect, biomass gas exchange, thermography	Keep soil water, ↘ hydraulic gradients	↘ photosynthesis ↗ leaf temperature (heat stress)	Terminal severe stress	End of cycle with favourable conditions
Avoidance via reduced leaf area	**	Aspect, biomass	Keep soil water, ↘ hydraulic gradients	↘ photosynthesis	Terminal severe stress	End of cycle with favourable conditions
Water use efficiency	**	$\triangle^{13}C$, ratio biomass/ transpiration	↗ Crop for drop ; Avoidance	↘ photosynthesis	Terminal severe stress	End of cycle with favourable conditions
Maintained photosynthesis /stomatal conductance	*	Gas exchange thermography[3]	↗ biomass	↗ risk of stress at end of cycle	Medium/mild stress	Terminal severe stress
Maintained vegetative growth	**	NDVI, proxidetection[4]	↗ biomass	↗ risk of stress at end of cycle	Medium/mild stress	Terminal severe stress
Increased root growth	**	DNA, imaging thermography[5]	↗ water uptake	Competition for C; ↗ risk of stress at end of cycle	Deep water available	Shallow soil
Root architecture : Deeper roots without change in biomass	?[2]	Rhizotrons	↗ water uptake	↘ nutrient uptake	Deep water available	Low nutrient availability in upper layers
Reduced seed abortion	*	Direct observation seed number	↗ yield	↘ quality	Stress during flowering, relieved afterwards	Terminal severe stress

[1] Not clearly established in non-extreme climatic scenarios, but see (Castiglioni et al., 2008)
[2] Not well documented in the literature to my knowledge
[3] Field thermography, an indirect measurement of water flux and stomatal conductance via temperature (Guilioni et al., 2008)
[4] NDVI normalized difference vegetation index (Aparicio et al., 2000). Proxidetection ;: functional imaging of canopies ((Montes et al., 2007).
[5] DNA technique for rooting depth, see (Mommer et al., 2008). In this case, thermography : reveals differences in access to water via root systems rather than stomatal control.

protected, which is only the case under very severe stresses most often observed in artificial conditions. In naturally occurring water deficits compatible with agriculture, a large range of avoidance mechanisms such as stomatal closure, changes in plant architecture, reduced leaf growth and early leaf senescence avoid cellular stresses by reducing water demand, thereby providing plants with some degree of homeostasy for shoot water status (Tardieu, 1996; Tardieu and Simonneau, 1998). Furthermore, farmers choose cropping systems in order to escape the risk of total water depletion and plant death, by adapting the length and position of the crop cycle in relation to most frequent drought episodes. Hence, tolerance conferred by cell protection mechanisms is probably restricted to extreme drought scenarios, most often not compatible with agriculture except for pasture crops in which it has a role in addition to summer dormancy (Volaire et al., 2005, 2009). However, a cell protection mechanism may have improved maize yield in field conditions in one case at least. RNA binding proteins, acting as chaperones that protect RNAs, have been reported to improve maize growth, photosynthesis, and yield under water deficit in the field (Castiglioni et al., 2008). If confirmed, this would be the first clear case in which cell protection mechanisms induce an increased growth in dry scenarios compatible with agriculture.

In most other cases, tolerance conferred by single genes is linked to avoidance processes, revealed by experimental protocols that consist in comparing the aspect and performance of genotypes some days after withdrawing irrigation. Plants with smallest leaf area or most reduced transpiration rate deplete soil water at the slowest rate, thereby still sensing a wet soil after a few days while plants with larger leaf area or stomatal conductance already experience a dry soil. Stress symptoms therefore appear later, and spectacular pictures lead to the conclusion that a given gene confers drought tolerance (Iuchi et al., 2001; Garg et al., 2002; Rivero et al., 2007).

Biomass accumulation is intrinsically linked to transpiration because stomatal aperture and leaf area determine the rates of both processes (Monteith, 1977). There is, therefore, an inherent conflict between biomass accumulation and stress avoidance *via* reduction of transpiration (Table 1). If dry episodes are long and severe, genotypes with reduced transpiration and leaf growth have an advantage because they save soil water for the later phases of the crop cycle. At a given soil water potential, they also avoid deleteriously low leaf water potentials at high evaporative demands (Tardieu et al., 2010). However these avoidance mechanisms also decrease the potential biomass accumulation during the later phases of the plant cycle if the soil is re-watered. Simulations over a large range of climatic scenarios and irrigation managements show that alleles that confer avoidance traits have a positive effect in the driest situations, but negatively affect yield in most climatic scenarios (Chenu et al., 2009). Hence, avoidance mechanisms such as reduced leaf growth or stomatal conductance have an interest restricted to driest areas with terminal drought (Krishnamurthy et al., 2010; Yadav et al., 2011).

Increased water use efficiency, a positive trait in very dry environments

It may seem straightforward that research programmes on drought should aim at an increased water use efficiency, but this is not necessarily the case (Blum, 2005). Across the scientific community, water-use efficiency can have definitions as different as the ratio of photosynthesis to stomatal conductance over some seconds, the ratio of biomass to transpiration in a plant over some weeks, or the ratio of yield to input water in a field over a crop cycle (Morison et al., 2008). While the latter definition is an obvious target of any research programme linked to drought, it is not closely linked to the first two definitions (Blum, 2009). Breeding for water-use efficiency has frequently led to negative results, resulting in small plants with reduced transpiration, photosynthesis, and yield (Blum, 2005). Because photosynthesis rate is less responsive to environmental conditions than stomatal conductance, the ratio of photosynthesis to stomatal conductance is most often maximised for low values of both variables, resulting in a low biomass accumulation. An interesting result in this domain was obtained in wheat by introgression into elite material of genomic regions that confer high water-use efficiency but maintained photosynthesis (Rebetzke et al., 2002). This was achieved by first selecting lines on stomatal conductance, thereby eliminating those with poor performance, and selecting for water use efficiency in a second step. This has resulted in commercial genotypes with a yield increased by 10% in very dry scenarios. In spite of the protocol aimed at eliminating lines with low performance, the effect of improved water use efficiency may still have acted through avoidance because the yield advantage of improved lines disappeared at rainfalls higher than 400 mm (Rebetzke et al., 2002), a very low rainfall in many wheat-growing regions. It can therefore be concluded that water use efficiency, as it can be measured via isotope discrimination ($\Delta^{13}C$) is a positive trait for yield under very dry conditions but is most often a negative trait in mild water deficits that are common in agricultural conditions (Table 1).

Growth maintenance and high stomatal conductance under water deficit are positive traits in mild to medium deficits and negative traits in severe terminal droughts

Decreased leaf growth, an avoidance mechanism as discussed above, is the first process to occur under water deficit before any reduction in biomass accumulation or stomatal conductance (Saab and Sharp, 1989). Its sensitivity has a large genetic variability, so the degree of avoidance versus maintenance is genetically variable within a species (Reymond et al., 2003; Welcker et al., 2007; Parent et al., 2010). Leaf rolling or epinasty have essentially the same roles as stomatal closure or reduced leaf area, by decreasing the functionally active leaf area.

All these mechanisms confer stress avoidance that is useful under terminal drought, but is usually also associated with a reduced biomass accumulation in milder drought scenarios (Table 1).

The maintenance of leaf growth or of stomatal conductance under water deficit has the opposite advantages and drawbacks compared with stress avoidance, namely a higher growth capacity after the end of water deficit in exchange for a higher risk of deleterious stress in very severe conditions. In addition, growth maintenance has two advantages. (i) Maintaining a high stomatal conductance tends to decrease leaf temperature by up to 8 °C, via the dissipation of incident energy via latent heat. It can therefore avoid heat stress. (ii) The genetic determinism of leaf growth is partly shared with that of processes involved in reproductive growth, such as silk growth and the Anthesis Silking Interval in maize (Welcker *et al.*, 2007). Alleles that help to maintain leaf growth also tend to decrease abortion rate in a given drought scenario. Simulations suggest that alleles that confer a maintained leaf growth or appropriate plant architecture under water deficit are beneficial in most scenarios except severe terminal water deficits (Chenu *et al.*, 2009; Messina *et al.*, 2011). They therefore result in either a positive or a negative effect on yield depending on the drought scenario, including soil type and plant management (Table 1).

Seed abortion, a negative process in mild stress which allows proper seed filling under severe stress

Seed number is a major yield component, mainly determined at flowering and slightly after it. In most species, the number of ovules largely exceeds the number of seeds, and water deficit reduces even more the seed/ovule ratio via abortion (Dosio *et al.*, 2010; Ribaut *et al.*, 2009). This is, again, an adaptive mechanism that allows the remaining seeds to be appropriately filled in spite of reduced photosynthate supply, with a positive or negative effect on yield and yield quality depending on the drought scenario during seed filling.

A large part of the genetic progress of maize yield under water deficit is due to a reduction in abortion rate, via a reduction in the Anthesis Silking Interval (ASI) (Bolanos and Edmeades, 1993; Campos *et al.*, 2004; Messina *et al.*, 2011). This is a clear 'success story' in drought tolerance, in particular with the release of improved cultivars in Africa (Banziger *et al.*, 2006). The reproductive development of maize is particularly sensitive to water deficit, with the involvement of both sugar metabolism (Zinselmeier *et al.*, 1995; McLaughlin and Boyer, 2004) and developmental processes (Carcova and Otegui, 2007). In species that are less prone to abortion and under severe water deficit, a controlled abortion rate can be a positive trait that improves seed filling and quality, for instance, in the case of wheat in Southern Australia (B Parent, personal communication).

Root growth and root system architecture: a positive trait in some cases only

Increasing soil exploration by the root system is widely considered to be a positive feature for improving drought tolerance, so the large genetic variability of root system characteristics would be a source of genetic progress (de Dorlodot *et al.*, 2007). Indeed, genomic regions controlling root system architecture in controlled conditions also affected yield in droughted fields (Tuberosa *et al.*, 2002; Landi *et al.*, 2010). In fields with deep soil and/or the presence of a water table, an increased root length in deep layers improves access to water and plant water status, depending on soil hydraulic properties (Javaux *et al.*, 2008; Shroder *et al.*, 2008).

However, several breeding programmes for drought tolerance have resulted in a decrease in root biomass (Bolanos *et al.*, 1993; Bruce *et al.*, 2002; Campos *et al.*, 2004). In a soil with a limited depth, increasing root length has no consequence on water uptake (Tardieu *et al.*, 1992). Therefore, investing photosynthates in the root system has a poor return in terms of plant water status, so photosynthates would be better invested in other sinks. In deeper soils, it is the root spatial distribution in the soil which defines the ability of a root system to take up water, and not root biomass or total root length (Tardieu *et al.*, 1992; Manschadi *et al.*, 2006, 2008). An 'ideal' root system, with an even distribution of 1 cm root cm^{-3} soil (root length density, RLD) over the rooting depth, is suitable for most field conditions (Tardieu *et al.*, 1992). Higher RLD are appropriate when evaporative demand increases and soil water reserve decreases, but too high RLD values, especially in the upper layers, ultimately result in a waste of photosynthates without an appreciable increase in water uptake. An increase in total root biomass or length can therefore be a beneficial trait if it is accompanied by an increased root density in deep layers. It may be a negative trait otherwise as shown by the results of the above-mentioned breeding programmes.

An alternative way of improving the quality of root systems is to consider the efficiency of root systems in terms of water uptake per unit photosynthate invested in roots, rather than root biomass, as in the work of Manschadi *et al.* (2006, 2008). In this case, the root architecture (angles, gravitropism) is more important that total root length. However, it should be mentioned that increasing the root density in deep layers at the expense of the upper layers may be detrimental for nutrient uptake in the common case in which the highest concentrations of nutrients are located in these layers.

Genotypes with improved yield in most conditions, or genotypes with specific tolerance to water deficit?

Considerable genetic progress has been achieved in the yield of most crops over the last century (Duvick, 2005; Cooper

et al., 2009; Brisson *et al.*, 2010). Interestingly, this genetic progress is observed in both well-watered and stressing conditions. In maize, the yield of genetic material adapted to the US Corn Belt has progressed by more than 60 kg ha^{-1}year^{-1}, at an approximately similar rate in well-watered and dry conditions. This represents considerable progress in dry conditions (200% in 65 years). Breeding for high performance in well-watered conditions has, therefore, tended to increase crop performances under water deficit. This is linked to an overall genetic progress, but possibly also to the selection of traits of drought tolerance linked to the maintenance of stomatal conductance, growth, and seed number in moderately dry conditions (Table 1). This strategy may face a limit in the near future. In a recent study on wheat yields in Europe, it has been shown that yields tend to reach a plateau. A combination of experimental results with modelling suggests that this is due to a sequence of unfavourable years in terms of temperature and water deficit (Brisson *et al.*, 2010). The rate of genetic progress would therefore not be sufficient to counteract the effects of climate change. Furthermore, the traits associated with increased yield regardless of conditions face physical limits such as the ratio of harvested to total biomass (harvest index) or the plant density (Duvick, 2005). Specific breeding programmes combining modelling with experiments are therefore appearing in seed companies and in the public sector (Ribaut *et al.*, 2009; Verulkar *et al.*, 2010; Messina *et al.*, 2011).

Concluding remarks

The above discussion implies that traits are associated with drought tolerance in specific scenarios characterized by drought intensity and timing but also by other environmental conditions such as light intensity and evaporative demand. Table 1, considered as a whole, suggests that it is possible to design a scenario that maximizes the positive effect of any trait. Gene to phenotypes models, such as that of Chenu *et al.* (2009), could even be used as a reverse engineering tool for that. Spectacular results obtained in one drought scenario, therefore, may only have a limited interest for improving food security in other geographical areas with water scarcity.

Hence, the most relevant question on drought tolerance is probably not 'Does a given allele or trait confer drought tolerance' but rather, 'Does a given allele confer a positive effect on yield in an appreciable proportion of years/scenarios in a given area?'; 'In a given site or TPE, what is the trade-off between risk avoidance and maintained performance?'; or 'Will a given allele or trait have an increasingly positive effect with climate change?' In this view, drought tolerance conferred by a given trait would have a stochastic component linked to the year-to-year variability of climatic conditions.

A paradoxical result is that protection and avoidance mechanisms that have been favoured by evolution over millions of years have negative effects on plant performance in most drought scenarios compatible with agriculture. They have indeed been counter selected by breeders, as in the case of root biomass or abortion rate. Conventional breeding has been extremely successful in improving plant performance under water deficit by addressing constitutive traits that are not specific to water deficit, and most often reduce the effect of avoidance mechanisms. Many alleles associated with 'risky' strategies may have been lost in most genotypes during catastrophic climatic events, while plant performance is not essential for evolution. Breeding may, therefore, consist, in good part, of counteracting the conservative strategies chosen by evolution to protect plants again water stress, in favour of more risky but more productive strategies.

Breeding for drought tolerance faces the difficulty that alleles selected each year based on plant performance vary with the climatic scenario of the considered year, even in a TPE. If a single trait and the QTLs that affect it have different effects depending on the year, this leads to oscillations of the allelic composition in the breeding population (Chapman *et al.*, 2003; Hammer *et al.*, 2006). Several strategies have been proposed to face this problem. The first of them consists of breeding in managed drought environments where a nearly stable drought scenario mimics the TPE (Venuprasad *et al.*, 2007; Verulkar *et al.*, 2010). This approach has the merit of simplicity. Nevertheless, it selects positive alleles for the considered drought scenario only, with the risk of being counter-productive in other drought scenarios encountered in the TPE. An alternative approach consists of using a combination of methods, with phenotyping in controlled conditions for identifying the parameters of models, the simulation of trait values in a large range of climatic scenarios by using a model with genotype-specific parameters and, finally, the test of these models in a limited number of field experiments (Chenu *et al.*, 2009; Tardieu and Tuberosa, 2010). This explicitly takes into account the year-to-year variability of drought scenarios, and can be combined with model-assisted breeding programmes (Cooper *et al.*, 2009; Messina *et al.*, 2011) able to deal with TPEs comprising a mixture of drought scenarios. Each of these strategies has its own risks and merits, but clearly abandons the idea that drought tolerance has any sense if not associated with precise scenarios of climate, soil, and management.

Acknowledgements

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