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# The Physiological Basis of Drought Tolerance in Crop Plants: A Scenario-Dependent Probabilistic Approach

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## Keywords

drought, transpiration, yield, modeling, phenomics, genomic prediction

## Abstract

Drought tolerance involves mechanisms operating at different spatial and temporal scales, from rapid stomatal closure to maintenance of crop yield. We review how short-term mechanisms are controlled for stabilizing shoot water potential and how long-term processes have been constrained by evolution or breeding to fit into acclimation strategies for specific drought scenarios. These short- or long-term feedback processes participate in trade-offs between carbon accumulation and the risk of deleterious soil water depletion. Corresponding traits and alleles may therefore have positive or negative effects on crop yield depending on drought scenarios. We propose an approach that analyzes the genetic architecture of traits in phenotyping platforms and of yield in tens of field experiments. A combination of modeling and genomic prediction is then used to estimate the comparative interests of combinations of alleles depending on drought scenarios. Hence, drought tolerance is understood probabilistically by estimating the benefit and risk of each combination of alleles.



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## INTRODUCTION

Drought is a major challenge for agriculture in the context of climate change combined with an increasing need for food (76, 152). The amount of water available for irrigation will decrease or at best be maintained as a result of the depletion of many aquifers and of the increasing competition with other needs such as the maintenance of river flow or the increases in industrial and recreational uses of water. A large effort is therefore required to increase agricultural production, in spite of reduced water availability, via the adaptation of cropping systems and the design of new plant varieties (136). There is no consensus whether drought episodes will be more frequent in future climates (119), but it is clear that they will continue to occur, probably with increasing variability from year to year (57, 123).

The definition of drought in agriculture is paradoxically unclear. It is accepted that the Sahel in Africa is dryer than northern Europe—thereby requiring different agricultural systems—and that a plant that has no access to water will die, but defining indices to characterize drought in an unequivocal way is not straightforward. For instance, one of the indicators used in drought impact assessment is the variance of rainfall rather than the actual rainfall value (66). A stable low rainfall in a dry area has fewer consequences for agriculture than does a dry year in temperate climates, even though the amount of rainfall is one order of magnitude higher in the latter compared with the former (107). Accordingly, drought impacts have been analyzed as a combination of hazard, exposure, and vulnerability (28); where hazard depends on environmental conditions, exposure results from agricultural practices such as the annual position of the crop cycle, and vulnerability depends on the plant varieties and cropping systems in use.

Drought tolerance in plants also requires a context-dependent view. Some drought-tolerant species can grow and survive in very dry conditions via protection mechanisms (148) such as tolerance to desiccation (65), detoxification (94), or repair of xylem embolism (74). Other desert plants lack these mechanisms but have the ability to complete their development cycle in a very short period of time after a rain, thereby producing seeds that will wait for the next rain (111). In an agricultural context, a drought-tolerant plant is one that maintains crop production during gradual and moderate soil water deficits, most often without exhibiting protection mechanisms (127).

This review focuses on the processes associated with drought, whose consequences are considered via a multiscale, context-dependent view, and on the avenues to improve plant production by breeding under drought conditions. We first discuss the definitions of water deficit and plant acclimation at different temporal and spatial scales. We examine the short-term physiological feedback processes that allow plants to buffer changing environmental conditions and consider how short-term responses combine with the plants' intrinsic properties and longer-term feedback processes to result in varying performance under water deficit. We then frame our discussion of avenues for improving production under drought conditions with the understanding that plant traits of interest are context dependent. Finally, we propose a probabilistic approach for handling adaptive traits under uncertain climatic conditions.

## DROUGHT IMPACT ON PLANTS: AN EVOLUTIONARY APPROACH TO INTEGRATE THE SHORT-TERM PHYSIOLOGICAL RESPONSES TO WATER DEFICIT INTO AGRONOMIC OUTCOMES

### Water Deficit: A Physical Definition Involving Supply and Demand

Water deficit in plants results from insufficient soil water availability to meet the demand of a particular plant or canopy at a particular time, resulting in a change in plant water status. This

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**Drought tolerance:** for a crop, the capacity to sustain biomass production or yield despite the occurrence of drought episodes during the crop cycle

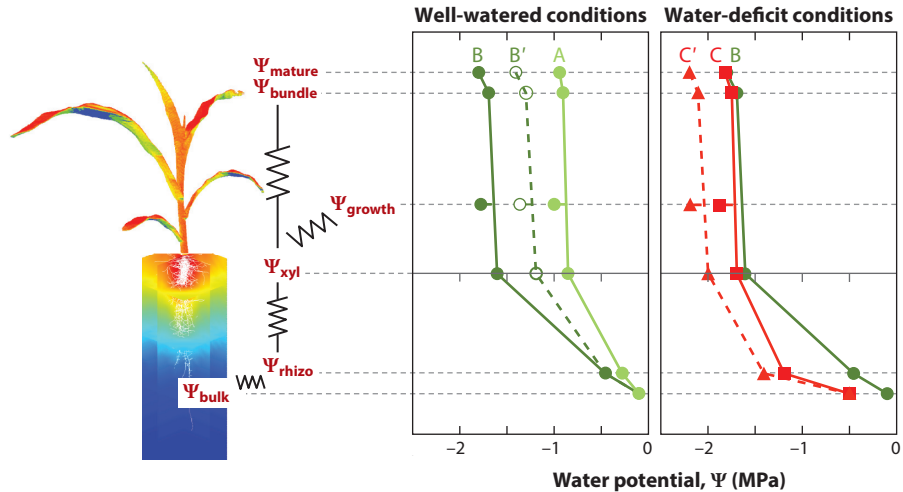
**Development cycle:** the period of time between germination and physiological maturity

**Water deficit:** in soil, the difference between water status at a particular time and that at full retention capacity; often measured via spatial integration of soil water potential

**Adaptive trait:** a phenotypic trait that varies with environmental conditions for a given genotype; can maximize fitness or production in specific environmental scenarios

**Plant water status:** degree of water satisfaction for a plant or canopy, depending on soil water availability and evaporative demand at a particular time; often measured via the water potential of specific organs

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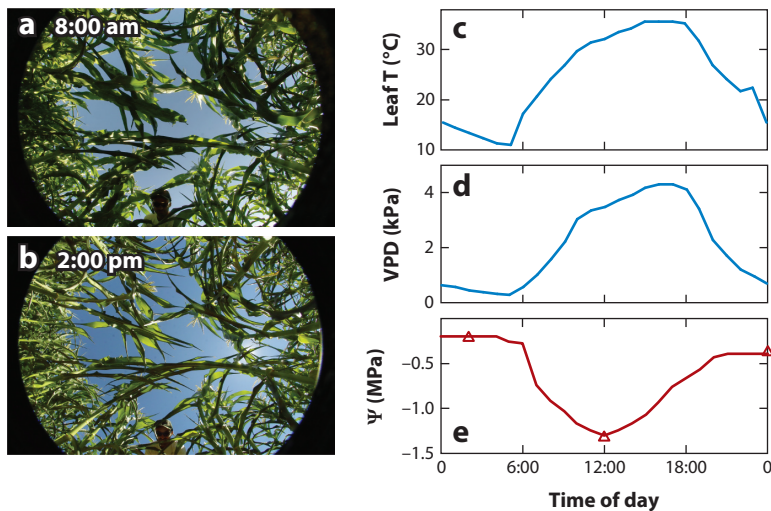


**Figure 1**

Short-term physiological mechanisms affecting plant water potential ( $\Psi$ ) over a 1-h period. As water moves through the plant,  $\Psi$  can be measured at five nodes along the main transpiration route: in bulk soil ( $\Psi_{\text{bulk}}$ ), in the rhizosphere around the roots ( $\Psi_{\text{rhizo}}$ ), in the root and stem xylem (with indistinguishable water potentials at the scale depicted, represented by  $\Psi_{\text{xyl}}$ ), in the leaf bundle sheaths ( $\Psi_{\text{bundle}}$ ), and in the mature cells of the leaves ( $\Psi_{\text{mature}}$ ). The  $\Psi$  of nontranspiring growing organs ( $\Psi_{\text{growth}}$ ) is that of a capacitance in equilibrium with  $\Psi_{\text{xyl}}$ . The graphs depict six cascading scenarios of  $\Psi$  in well-watered plants with low evaporative demand (*A*), well-watered plants with high evaporative demand (*B*), well-watered plants with high evaporative demand and higher conductance from the rhizosphere to the root xylem (with indistinguishable water potentials at the scale depicted, represented by  $\Psi_{\text{xyl}}$ ), plants under water deficit and high evaporative demand with stringent stomatal control (isohydric behavior) (*C*), and plants under water deficit and high evaporative demand with loose stomatal control (extreme anisohydric behavior) (*C'*). Scenario *B* is repeated in the right panel for better comparison. Colors in the soil on the left part of the figure represent the spatial distribution of soil water potential from low (dry soil, *red*) to high (wet soil, *blue*). Intermediate potentials are represented in orange to light blue and roots are represented in white. Colors in the leaves represent local evaporative demands, essentially linked to local illumination, from high (illuminated leaf regions, *red*) to low (shaded leaf regions, *blue*). Graphical data compiled from References 27, 77, and 133, as well as unpublished simulations; leaf colors courtesy of Christian Fournier of LEPSE, Institut National de la Recherche Agronomique.

**Evaporative demand:** transpiration rate of a given plant or canopy at a given time if soil water status was optimum; depends on leaf area, vapor pressure deficit, and wind

dynamic representation involves both the capacity of the root system to supply water to shoots (77) and the plant's transpiration rate, which combines evaporative demand and shoot characteristics (87). In transpiring plants, water moves from the soil to the atmosphere first radially through root cell layers; then axially through a continuum of xylem conduits in roots, stems, and leaves; and then finally through leaf tissues from the xylem to substomatal air spaces (3) (**Figure 1**). Nontranspiring organs (e.g., hidden growing leaves, stem parenchyma, and young reproductive organs) act as deviations off this main route, with a water status that equilibrates to that of the closest xylem vessels. The transfer of water between two points depends on the gradient of water potential multiplied by the hydraulic conductance between those points. For a given transpiration rate, the water potential at any point along the main route depends on the cascade of hydraulic conductance values upstream and downstream (**Figure 1**). The water potential of nontranspiring organs depends on both the hydraulic conductance from these organs to the closest xylem vessels and the hydraulic capacitance of these organs that buffers variation in their water potential (23). This buffering capacity remains very small at the whole-plant level when compared with that in



**Figure 2**

Maize canopies photographed from below in the (a) morning and (b) early afternoon, as well as time courses during the day of (c) leaf temperature (T), (d) leaf-to-air vapor pressure deficit (VPD), and (e) plant water potential ( $\Psi$ ) in the leaves. The change in the appearance of the canopy between panels a and b is due to leaf rolling, a symptom of water stress, and the proportion of visible sky is an indicator of the amount of light that is not intercepted by plants. In panel e, triangles are measured values; lines are model outputs; and a  $\Psi$  of 0 megapascals (MPa) denotes free water, whereas the value of  $-1.5$  MPa is close to lethal for many species. Photographs courtesy of Llorenç Cabrera Bosquet of LEPSE, Institut National de la Recherche Agronomique. Other abbreviation: kPa, kilopascal.

animals: Plants can transpire 50–200% of their water volume during a bright sunny day versus approximately 2% for humans (143). Hence, the water potential in leaves and stems can fluctuate very rapidly—for instance, by one megapascal (MPa) over 1 h during a diurnal cycle (**Figure 2e**).

### Short-Term Responses Versus Long-Term Impact of Water Deficit

Defining water deficit as an imbalance between fluctuating supply and demand generates a massive problem of timescales. For most physiological mechanisms, water deficit is defined over minutes to hours. Evaporative demand dramatically varies between morning and afternoon or during alternations of cloud shade and sunshine (**Figure 2d**). It is determined by the energy balance of the leaf, which affects the leaf-to-air vapor pressure deficit (VPD) via the difference between leaf temperature and dew point temperature in the air (note the difference in definition of air VPD). During a summer day, a plant can register  $11^{\circ}\text{C}$  in the early morning with a VPD close to 0 kilopascals (kPa) and show a favorable water status, but experience  $36^{\circ}\text{C}$  with a VPD of 3.5 kPa and suffer severe symptoms of water stress six hours later (**Figure 2**). Continuous measurements with displacement transducers and gas exchanges reveal that rapid fluctuations in growth and photosynthesis accompany these rapid changes in water status (23, 61, 73) (**Supplemental Figure 1**).

At the other extreme, plant performance and yield are defined over months up to the whole crop cycle. Yield is affected by the amount of light that is intercepted by leaves and converted into biomass via photosynthesis (87). Drought tolerance is the result of integrated processes taking place at different timescales and having long-term impact on leaf growth and transpiration. Two

#### Water potential:

potential energy of water, equal to the algebraic sum of osmotic, turgor, and gravity potentials; water potential gradients drive water fluxes throughout the plant

#### Hydraulic conductance:

a ratio of the water flux between two points to the difference in water potential between those points

#### Hydraulic capacitance:

a ratio of the change in tissue water content to the change in water potential

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**Vapor pressure deficit (VPD):**

difference between partial pressure of water vapor in leaves and atmosphere; driven by temperature, light, and air humidity

**Air VPD:** difference between partial pressure of water vapor in the air and that in water-saturated air at the same temperature; used in many studies

**Absciscic acid (ABA):** a plant hormone with higher rate of biosynthesis under water deficit, which promotes stomatal closure; it affects many other processes, particularly root and shoot hydraulic conductance and root architecture

**Environmental scenario:** a clustered pattern of time courses of soil water status, evaporative demand, light, and temperature in different fields; a given field can belong to different scenarios in different years

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equations are widely used for dissecting yield into major processes. The first, the most useful in our view, is based on light capture by leaves and the transformation of light into photosynthates, with both processes affected by water deficit (87). The second equation is based on cumulated transpiration as affected by water deficit and the ratio of yield to transpiration (103).

## **A Macroscopic Approach, Guided by Evolution, for Addressing the Multiple and Overlapping Mechanisms Involved in Plant Response to Water Deficit**

Water deficit affects a large spectrum of plant functions such as transpiration, photosynthesis, leaf and root growth, and reproductive development (32). It also impacts underlying physiological processes including cell division, hydraulics, cell wall mechanics, primary and secondary metabolism, and the detoxification of reactive oxygen species (18, 140). Several hormones are involved: in particular, the stress hormone abscisic acid (ABA), but also ethylene, cytokinins, strigolactones, and jasmonic acid (62, 128). Finally, a layer of molecular control involves changes in transcription factor expression, in gene silencing by small RNA, and in chromatin status (116). A crucial question is how to sort out the primary events that drive acclimation to water deficit from the secondary, longer-term consequences of these events. Omics offer tools to analyze the succession of molecular events taking place in the plant during the onset of water deficit. However, published information needs to be carefully considered in view of the often drastic protocols used to impose water deficit (7, 19, 121). When moderate and progressive water deficits such as those compatible with crop production are used, the emerging picture is that of subtle changes in transcript abundance (9, 140) or enzyme activities (63). In some cases, such as ovary abortion, massive molecular changes may even be the consequence rather than the cause of developmental events (96). A reductionist approach, consisting of associating plant performance with the time-course of one particular process, runs the risk of confusing effects with those of other processes that could have been detected if the whole system had been taken into account (127, 130).

We have adopted here a different approach, following a seminal review (60) that examined the sequence of events during water deficit as a function of stress intensity and identified growth and transpiration as the primary targets of water deficit. Our starting point is to consider that evolution has selected plants in such a way that the many mechanisms involved in responses to water deficit have been constrained to (a) collectively buffer rapid changes in water potential and in carbon status to different extents depending on environmental scenarios and (b) result, after temporal integration, in long-term controls that allow plants to manage the soil water reserve and produce at least a few viable seeds. These mechanisms, and their genetic variability, are therefore considered to contribute to plants' consistent acclimation strategies in specific environmental scenarios.

## **SHORT-TERM FEEDBACK PROCESSES FOR PARTIAL HOMEOSTASIS OF WATER AND CARBON STATUS**

Many physiological mechanisms triggered in plants by water deficit act as short-term feedback, such that outputs are routed back as inputs in a looping chain of cause and effect (1, 130). For instance, an increase in transpiration rate tends to cause partial stomatal closure (88), thereby stabilizing transpiration. Below we review short-term feedback processes that stabilize plant water and carbon status under progressive and moderate water deficit. We do not review mechanisms involved in tolerance to desiccation (65), in detoxification (94), or in repair of xylem embolism (74) because they are associated with severe stresses that can cause plant failure, an infrequent event because farmers adapt cropping systems to prevailing environmental conditions.



## First Feedback Process: Transpiration Affects Stomatal Control, which Limits Transpiration and the Gradient of Water Potential Between Roots and Other Plant Organs Within Minutes

Stomatal opening facilitates the diffusion of CO<sub>2</sub> toward the carboxylation sites in leaves, but it also increases the gradient of water potential between roots and shoots, potentially leading to critical dehydration of plant tissues (**Figure 1**). Plants have therefore evolved in such a way that increased transpiration causes stomatal closure, which itself decreases transpiration, thereby generating a feedback loop. Stomatal closure results from a turgor loss in guard cells, which involves ion channels (68) and aquaporins (54). It is hydropassive when associated with water loss in bulk leaf tissue and hydroactive when involving other stimuli that trigger ions and water efflux from guard cells (51). Hydropassive stomatal closure probably predominates in the most ancient plant lineages (124). Were the control only hydropassive, erratic bursts of stomatal closure would occur every time leaf water potential was depressed by high evaporative demand. Although responsive stomata are beneficial for water conservation in plant tissues, such reactive, unstable stomatal closure would result in restricted CO<sub>2</sub> diffusion toward photosynthesis sites (73). As a consequence, many plant species subjected to progressive soil drying present dual mechanisms for stomatal control. This allows stomatal conductance to vary with soil water status with neither large changes in leaf water potential nor too unstable stomatal conductance.

The nature of the signal mediating the effects of soil drying on stomata is debated. It has been proposed to be primarily hydraulic in *Arabidopsis thaliana* (i.e., involving the cascade of water potentials in the plant), whereas the associated stomatal control also involves ABA (38). In tomato, the root–shoot signal involves a dialogue between ABA and other compounds, namely, strigolactones (149), the ethylene precursor 1-aminocyclopropane-1-carboxylic acid, or sap pH (44). The signal is probably ABA itself in other species such as maize, sunflower, poplar, and *Nicotiana glauca*, based on experiments with reciprocal grafting (12) or feeding plants with natural or artificial ABA (132). Therefore, signals may differ between species, consistent with the view that multiple systems have been engineered by evolution (20). However, each of these controls may represent a simplification of a more general controlling system with two nonexclusive propositions. The composition of the xylem sap may be considered a signal on its own, based on the equilibrium between ABA, ethylene, nutrients, and sap pH (44). An alternative possibility would be that the main message is hydraulic, with a secondary effector that depends on the species considered (128). A numeric model of stomatal control (133) is based on this second approach: It involves hydraulics as the primary message and ABA as the secondary message, it fits with a large number of experiments in maize, sunflower, and poplar (133), and it may work equally well with compounds other than ABA for other species.

Genetic variation in the control of plant water status by stomata has been observed across and within species. It results in variable efficacy, under conditions of soil drying, to prevent the drop in daytime leaf water potential (132). In particular, a whole-genome association study shows that stomatal conductance and its response to evaporative demand show a large genetic variability in maize (2). Isohydic plants such as maize or poplar exhibit changes in stomatal conductance according to soil water status before they experience any substantial change in leaf water potential (133) (**Figure 1**). Isohydic behavior is associated with a dual contribution of chemical and hydraulic signaling (133). By contrast, anisohydic plants such as sunflower exhibit looser control with a reduced contribution of hydropassive signaling (132) (**Figure 1**). A genetic continuum in isohydic versus anisohydic behaviors exists among genotypes belonging to a common species (41), which may be interpreted as the varying contribution of the plant hydraulic conductance and of ABA to stomatal control. Most of the genes and mechanisms responsible for variation in

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**Aquaporins:** intrinsic membrane proteins that form pores facilitating water transfer through membranes

**Isohydic plants:** plants that keep leaf water potential in a narrow range under water deficit and high evaporative demand through stomatal control

**Anisohydic plants:** plants whose leaf water potential is left to fluctuate in a large range under water deficit and high evaporative demand

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**Plasma membrane intrinsic proteins (PIPs):** a group of aquaporins that facilitate water transfer through the plasma membrane

the accumulation of ABA (92) and sensitivity to this hormone (43) have been identified, opening promising avenues to fine-tune stomatal control. Overall, decreased stomatal conductance upon water deficit and fully isohydric behavior appear to be conservative mechanisms that are favorable under conditions of drought and high evaporative demand but may be unfavorable under milder conditions when compared with anisohydric behavior (**Table 1**). Conversely, lowering stomatal conductance during the night is favorable under a broader range of conditions without obvious trade-off (42).

### **Second Feedback Process: Changes in Tissue Hydraulic Conductance Buffer Rapid Changes in Water Potential and Help Maintain Plant Water Uptake in Dry Soil**

Stabilizing organ water status also involves changes in the conductance to water flow within the plant. The hydraulic conductance of the xylem is very high compared to that of living tissues (81), so the xylem can be considered a connecting organ between roots, stems, nontranspiring organs, and leaves (3) (**Figure 1**). The hydraulic conductance of the whole plant is therefore determined by the water transfer properties of living tissues in roots and leaves (82) rather than those of the xylem, except in cases of embolism. Evaporative demand (39) and transpiration rate (146) tend to increase whole-plant hydraulic conductance, thereby causing stabilization of shoot water potential against fluctuations of evaporative demand. This is another example of short-term feedback (**Figure 1**). In the same way, ABA tends to increase the hydraulic conductance of roots (59, 101, 138) while decreasing that of transpiring leaves (98, 118). This helps organs located between these two plant boundaries—in particular growing leaves and reproductive organs—to keep a water potential closer to that of roots rather than to that of transpiring leaves (**Figure 1**). Plasma membrane intrinsic proteins (PIPs), belonging to the family of aquaporins, are key actors in this control of environmental cues via the accumulation of transcripts or proteins (23, 31) and the phosphorylation of PIPs (82). A large genetic variability exists for plant hydraulic conductance in *A. thaliana* (125) and *Oryza sativa* (rice) (58), but systematic genetic explorations are still needed to estimate whether modulations of plant hydraulic conductivity can be exploited in breeding for improved plant performance under drought conditions.

Root hydraulic conductance and PIP transcript abundance follow a circadian rhythm with maximum conductance in the morning and increasing amplitude when water deficit and evaporative demand have been experienced by the plant in recent days (24). This result is counterintuitive because hydraulic conductance is at its lowest when the plant needs to transfer more water. A simulation study has suggested that this mechanism slows down water depletion within the rhizosphere, thereby avoiding a dramatic decrease in soil hydraulic conductivity near roots that would make the rhizosphere almost irreversibly impermeable (24, 133). The reduction in the hydraulic conductance of the rhizosphere can also be attenuated by the secretion of mucilage (114), by root hairs (27), by hydrotropism (47), and by the hydropatterning of root branching (5).

### **Third Feedback Process: Osmotic Adjustment Buffers Turgor Within Minutes**

Cells show partial homeostasis for turgor due to osmotic adjustment (8, 122). The turgor of roots and shoots, measured directly with cell pressure probes, can show little or no variation even when the water potential of these organs varies by 0.5 MPa (16, 52, 126). This turgor homeostasis is obtained via rapid build-up and/or uptake of solutes that decrease the osmotic water potential of the cell whenever cell water potential decreases. Because organ water potential (negative) is the sum of turgor (positive) and osmotic potential (negative), a decrease in osmotic potential



**Table 1** Diversity of consequences of physiological traits on yield in five typical environmental scenarios, and consequences of these traits on more integrative traits<sup>a</sup>

	Targeted phenotypic traits	Consequences for yield, by soil and climate scenario					Consequences on integrated traits		Efficient phenotyping technique	Reference(s)
		1. Early WD, mild ET, shallow soil	2. Terminal WD, high ET, shallow soil	3. Terminal WD, high ET, deep soil	4. Mild WD, high ET, deep soil	5. Mild WD, high ET, shallow soil	1. Stay-green phenotype	2. Water use efficiency		
Short-term traits	Stringent stomatal control	–	+	=/+	–	–	+	+	CT	85, 107
	Slow/sensitive leaf growth	–	+	=/+	–	+	+	=	Imaging, displacement transducers	37
Intrinsic/ integrated traits	Early flowering	=	++	+	–	+/=	–	+	Recorded in tens of field experiments	80, 86
	Sensitive grain abortion	--	++	+	–	+/=	+/-	–	Recorded in tens of field experiments	101
	High hydraulic conductance	+	–	+	++	–	–	–	HPFM, EFM	110
	Efficient root system (upper layers)	+	–	–	+	+	=	=	Soil water status (diverse), shovelomics	27
	Deep rooting/ efficient root system at depth	–	–	+	+	–	=	–	Water uptake	79
	High transpiration (intrinsic)	=	--	–	++	–	+	–	<sup>18</sup> O discrimination, CT	85
	Long coleoptile (seedling establishment)	+	=	=	=	=	=	=	Imaging	113
	CAM	–	=/+	–	–	–	++	++	Gas exchange, CT	13
	Glauousness	+	=	=	+	+	+	=	CT	113

<sup>a</sup>Efficient phenotyping techniques for evaluating these traits at high throughput and references are mentioned. Note that the evaluation of positive and negative effects is based on simulations and expert diagnosis and therefore can be discussed.

Abbreviations: CAM, crassulacean acid metabolism; CT, canopy temperature; EFM, evaporative flux method; ET, evapotranspiration resulting from evaporative demand; HPFM, high pressure flow meter; T, air temperature (in particular via its effect on ET); WD, soil water deficit.

results in the cell maintaining its turgor even though the water potential decreases (117). Osmotic adjustment is rapid, with a typical halftime of 30 min (52). However, processes such as growth or photosynthesis remain affected by water deficit even when the turgor of leaf cells is maintained via osmotic adjustment (16, 52, 126). This may explain why the genetic variability in the ability of plants to adjust osmotically often does not correlate with the long-term consequences of drought on plant growth and yield (67, 91).

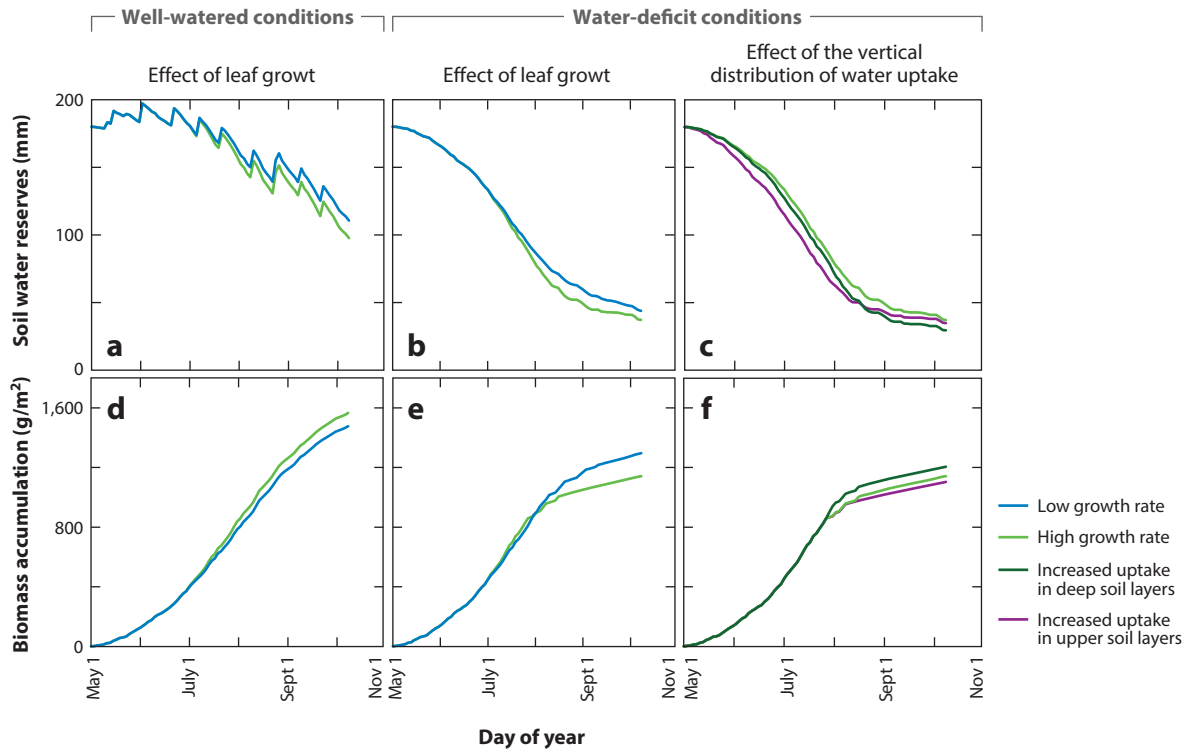
#### **Fourth Feedback Process: Leaf and Root Growth Respond to Drought Within Minutes but Affect Whole-Plant Transpiration and Water Uptake Over Days to Months**

The transpiration rate of plants primarily depends on leaf area, which is strongly affected by water deficit via growth processes. A reduction in leaf expansion cumulated over days may affect transpiration rate as much as or even more than stomatal closure. It saves water for further phases of the plant cycle (**Figure 3**) and reduces the gradient of water potential between roots and leaves (**Figure 1**). It is noteworthy that, unlike stomatal closure that causes leaf heating, reducing leaf area is not associated with a risk of heat stress.

#### **Supplemental Material**

Expansive leaf growth occurs mostly during the night, whereas maximal photosynthesis occurs during late morning and afternoon (131) (**Supplemental Figure 1**), thereby suggesting that it is controlled by water status rather than carbon status. Indeed, leaf growth decreases during the day with increasing evaporative demand (23). Maize silks (modified styles that emerge from ear bracts) follow the same time course in response to evaporative demand (141). The early-morning increase in plants' transpiration rate causes near cessation of leaf expansion within approximately 30 min, whereas irrigation of droughted plants causes the full recovery of leaf growth within 45 min (23). Similar recovery rates have been observed in roots (52). These time constants, together with the close parallelism between aquaporin transcript abundance and leaf elongation rate under constant light (24), and with the rapid effect of manipulations of aquaporin activity upon growth (49), suggest a hydraulic control of growth. However, it is difficult to disentangle experimentally which changes in cell turgor, hydraulic conductivity, and cell wall plasticity contribute to the control of leaf growth. For instance, cell wall stiffening in the growing zones of leaves may be triggered by a root–shoot hydraulic signal within minutes of root polyethylene glycol exposure (33). The rate of leaf expansion is tightly coordinated with the expression of genes coding for expansins (a family of cell wall loosening agents), regardless of the sources of variability—including water deficit (89). This coordination suggests that expansins are downstream, unspecific targets of several converging cues. Soil water status may also affect leaf growth via photosynthesis and carbon partitioning, especially in the early growth of dicotyledon leaves (99). Substantial genetic variability in the sensitivity of leaf growth to water deficit has been observed (139, 151). For instance, some maize genotypes maintain appreciable leaf growth in dry soil at  $-1.5$  MPa, whereas others stop growth at  $-0.8$  MPa (151). Interestingly, the genetic controls of vegetative (leaves) and reproductive (silks) organs are largely common in maize (141).

Root tips (and thus growing zones) are in part disconnected from the plant hydraulic network and do not withstand sudden changes in water potential. As with plant leaves, root tip growth depends on the maintenance of turgor when external water potential drops (117) as well as upon cell wall proteins such as expansins (154). Root growth is less affected by water potential changes than shoot growth; this leads to an increased root-to-shoot ratio under water deficit (104), which is, again, a feedback process that stabilizes leaf water status.



**Figure 3**

Feedback processes over days to weeks. Panels *a* and *d* depict the simulated time courses of soil water reserve and biomass accumulation for plants with high (green) versus low (blue) leaf expansion rate (similar outputs would be observed for high and low stomatal conductance) in an irrigated field (each steep increase in soil water reserve is the consequence of an irrigation). Panels *b* and *e* depict the same simulated time courses in the absence of irrigation (continuous decrease of soil water reserve) as in panels *a* and *d* with the same color codes. Panels *c* and *f* depict the same simulated time courses with three hypotheses of vertical distribution of root water uptake due to differences in root architecture or hydraulic conductance under water deficit. The green lines in panels *c* and *f* represent the same hypothesis as in panels *b* and *e*, the dark green line represents a facilitated water uptake in deep soil layers, and the purple line represents a facilitated water uptake in upper soil layers. Simulations performed with the APSIM (Agricultural Production Systems sIMulator) model (56).

### Fifth Feedback Process: Optimization of Carbon Versus Water Status

When the soil dries, expansive plant growth is affected earlier and more strongly than photosynthesis (90) in part because of the resilience of the photosynthetic apparatus to water deficit (50). As a consequence, crop plants under water deficit often contain excess carbon, and roots and reproductive organs show signs of experiencing sink limitation rather than source limitation (90, 96). Sink limitation can be interpreted as a feedback mechanism to avoid carbon starvation (6). The above statements do not mean that carbon acquisition is never an issue in droughted plants. First, a drought-induced reduction in leaf expansion negatively impacts light interception by the plant as do leaf rolling and leaf wilting, thereby affecting carbon capture. Second, drought often reduces radiation use efficiency (64)—either directly, through the reduction of photosynthesis by stomatal closure at the leaf scale, or indirectly, through changes in the canopy architecture or sink strength (86). Unlike crops, trees exposed to severe and long-lasting drought episodes may

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**Water use efficiency:**

a ratio of carbon capture to water consumption by a plant; may be instantaneous or integrated over the crop cycle

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**Grain abortion:**

termination of the development of ovaries (prefertilization) or young grains (postfertilization), with large consequences on the grain number per unit of soil area

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exhibit a decrease in carbon status or ultimately carbon starvation because they show little or no photosynthesis for several weeks (83).

Crassulacean acid metabolism (CAM) is a powerful strategy to improve water use efficiency in severe water deficit (13) with the usual trade-off of low growth rate, although CAM plants are sometimes capable of the high productivities of  $C_3$  and  $C_4$  plants (93). Interestingly, some CAM plants display an optimization strategy by switching from the  $C_3$  metabolism to CAM upon water deficit (153).

## **Modeling Is Required to Predict the Effects of Feedback Processes 1–5**

The mechanisms presented in this review all contribute to the stabilization of plant water potential and carbon status under conditions of water deficit. Because these mechanisms interact and act as feedback, causes and effects cannot emerge directly from intuitive extrapolations and instead require tools that allow integration over time (1, 130). Dynamic models allow this analysis by calculating state variables (e.g., leaf area or water status) each minute or hour as functions of environmental conditions, which are used by the model at the next time step. Models can therefore simulate feedback and result in predictions of when and where a given change in trait (e.g., growth sensitivity to soil water deficit) may have appreciable consequences on biomass accumulation, crop water use, and yield. The logic that emerges from this approach differs from straightforward cause-and-effect reasoning that would not take system dynamics into account (1, 130).

## **LONG-TERM FEEDBACK AND PLANT INTRINSIC PROPERTIES FOR OPTIMIZING WATER RESOURCES OVER MONTHS**

Intrinsic properties of plant genotypes can also result in causal loops that affect the timing of water use, with large consequences on the availability of resources during the reproductive phase of the plant cycle. In the same way, physiological mechanisms that occur over days or weeks—such as grain abortion or root branching—also have profound long-term consequences for the water and carbon budgets of plants at the whole-cycle scale. These processes can be considered long-term feedback in which low resource consumption during early stages of the plant cycle favors higher consumption at later stages owing to higher water availability (**Figure 3**).

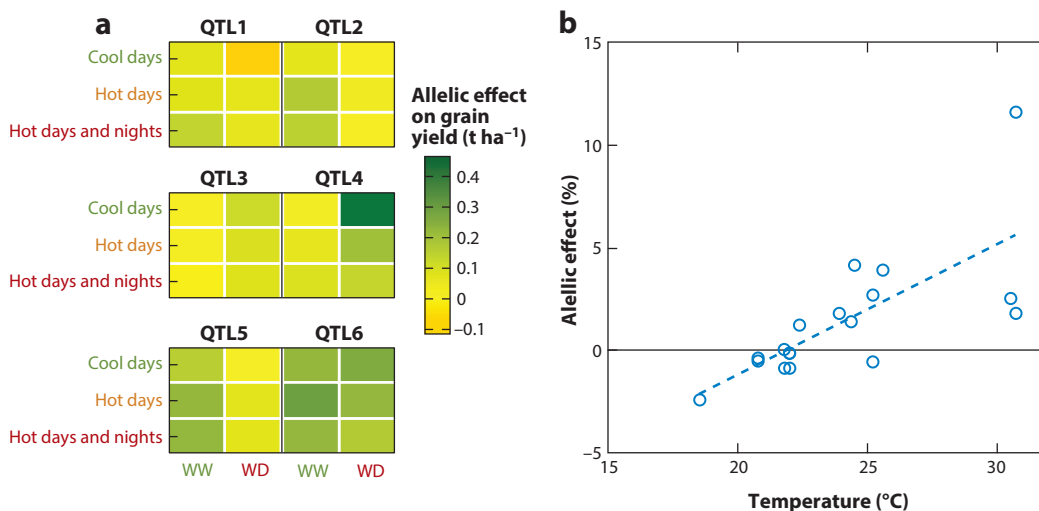
## **Duration of the Crop Cycle and Phenology: A Major Trade-Off Between Water Conservation and Cumulated Light Interception**

Farmers need to manage crops in such a way that the crop development cycle can be completed with sufficient water availability. This requires adjusting the duration of that cycle to the expected amount of water available (where the expected amount equals the sum of the soil water reserve and of expected rainfall). At a given site, crop yield tends to increase with cycle duration because of an increase in cumulated photosynthesis. In the case of a prolonged drought episode, a maximum is observed beyond which increased cycle duration causes soil water depletion during flowering time and grain filling. Short plant cycle is therefore a positive trait under long and terminal drought, but it negatively affects biomass accumulation and yield if water is eventually available because of a rain episode (**Table 1**). In genetic analyses, this translates into the fact that genomic regions associated with yield variations under drought conditions often also control flowering time, with either positive or negative effects on yield depending on environmental conditions (79, 85). Adaptation of the cycle duration applies to plant populations in natural environments, where massive changes in phenology have followed climate change (21). In an agricultural context, farmers and extension service personnel adjust plant cycle duration to water resources in species for which the control of cycle duration is simple and essentially dependent upon temperature. In other species, phenotypic

plasticity for phenology can be a major trait for drought tolerance. For example, the response of sorghum flowering time to photoperiod has been selected in such a way that flowering occurs during the peak of rainy season regardless of sowing date in the dry northern African Sahel (69). Conversely, sorghum genotypes used in wetter southern Sahel are less sensitive to photoperiod, thereby allowing farmers to adjust plant cycle duration to other constraints. Overall, choosing a given cycle duration is a risky bet on the trade-off between water conservation and cumulated light interception when climatic conditions are uncertain (Table 1).

## Grain Abortion Results in Fewer (but Viable) Grains, but Causes Massive Yield Loss

Most crop species show a high sensitivity to water deficit around flowering time, which affects the grain number per plant in maize (46) or wheat (100). Grain abortion can be defined in a broad sense as the proportion of ovaries that develop into grains, as affected by male or female sterility (113) or carbon competition at early stages of grain development (17). Grain abortion causes massive yield loss under water deficit (108), but is essentially an adaptive process allowing plants to produce viable seeds in spite of reduced carbon supply. Even in crop plants, grain abortion can be favorable in very dry climates by securing the full development and filling of a limited number of grains. In a study of 18 wheat field experiments, an allele causing reduced grain number under a combination of high evaporative demand and water deficit had a highly positive effect on yield under high evaporative demand and temperature but a negative effect under milder temperatures (100) (Figure 4). Hence, low abortion rate is a major target for breeding in climatic conditions with mild water deficits only (48) (Table 1).



**Figure 4**

The allelic effects of QTLs upon crop yield depend on environmental conditions. (a) The allelic effects of six QTLs upon maize yield differ between six environmental scenarios originating from a meta-analysis of 19 field experiments in Europe. Scenarios involve three levels of temperature and evaporative demand during flowering time (cool days and nights, hot days/cool nights, and hot days and nights) and two levels of soil water deficit [mild (WW) and severe (WD)]. (b) The allelic effect of one QTL upon wheat yield in 18 field experiments in Australia and Mexico is related to the mean temperature during flowering time. Panel a redrawn from Reference 85; panel b redrawn from Reference 100. This material is copyrighted by the American Society of Plant Biologists and is reprinted with permission. Abbreviations: QTLs, quantitative trait loci; t, ton; WD, water deficit; WW, well watered.

**Stay-green phenotype:** the property of leaf tissues to retain pigments and photosynthetic functions and delay senescence

A common view is that low carbon availability is the main cause of grain abortion under water deficit. It is based on experiments in which sucrose, fed to maize plants at flowering time, caused partial recovery of grain number (17). However, this applied to very severe stresses causing full abortion, in which sucrose feeding allowed the recovery of a few grains. In more realistic water deficits, molecular events associated with drought-induced abortion occur in maize silk rather than in ovaries, and they involve genes associated with expansive growth rather than carbon metabolism (96). The presence of fertilized reproductive organs causes abortion of younger organs in pea (55) and maize (97). In the latter case, abortion occurs in all ovaries whose silks have not emerged two days after pollination of the first emerged silks (97). This is an interesting case in which hydraulics directly translates into the control of reproductive development under dry conditions: The growth of maize silks is directly related to changes in xylem water potential, and the resulting delay of silk emergence causes abortion (141). Consistently, maize breeders have selected lines for a shorter anthesis-silking interval essentially linked to silk growth, resulting in an impressive increase in yield (10).

### **Root Architecture: Optimizing the Time Course of Water Uptake and the Trade-Off Between Water Uptake and Carbon Cost**

Converging results suggest that both domestication and breeding have led to reduced root system size compared with either wild-type ancestors or landraces (35, 150). This is probably due to the metabolic cost of root growth and maintenance [root respiration can be as high as 50% of daily photosynthesis (71)]. Also, the selection of elite material with an optimized ratio of grain weight to whole biomass (harvest index) has likely promoted parsimonious genotypes in terms of biomass allocation to root systems (25). Low-cost root systems can be designed via the presence of cortical aerenchyma, or low density of lateral roots, resulting in deep and cheap root systems (78).

The recurrent selection of drought tolerance in maize has led to the development of genetic lines with limited root systems, possibly because breeding schemes were run in shallow soils (11). Consistently, several Poaceae species tend to decrease the root system size under water deficit by partial or total suppression of the roots initiated from belowground basal nodes of the shoot (115). An appreciable genetic variability exists for this trait in maize, suggesting that it may have been differentially selected in wet and dry regions (115). Indeed, the positive effect of deep and/or vigorous rooting depends on the climatic scenario. In situations where water is present at sowing and no more rain or irrigation occurs during the cropping season, it might be desirable to reduce water consumption in the early stages to secure water availability at later (e.g., grain filling) stages (145) (**Figure 3**). A breeding program in Australia has successfully selected wheat lines with reduced axial hydraulic conductance resulting from smaller xylem vessel diameters to limit water uptake in the early stages of growth and secure water availability at the later stages (109) (**Table 1**). The same strategy has been applied to the vertical distribution of roots because a dense root system in upper layers can result in early water depletion and low yield (26). Conversely, genetic improvement of the size of root systems can have positive effects on deep soils for durum wheat (72) and can generate spectacular yield increase in rice, which has a naturally weak root system (142). Hence, as other plant traits, root system architecture has a context-dependent effect on yield under water deficit (**Table 1**).

### **The Stay-Green Phenotype and Water Use Efficiency as the Results of Managing Water and Nutrient Resources**

The stay-green phenotype (i.e., delayed senescence) maintains an efficient photosynthesis for a longer period, thereby promoting biomass accumulation (137). For example, stay-green sorghum



genotypes continue to fill grain for longer time, resulting in higher yield but also higher soil water depletion (14). Delayed senescence under water deficit can be engineered via the metabolism of cytokinins (110), but in field conditions it often appears as a consequence of early events in the plant cycle (**Table 1**). In sorghum, the stay-green phenotype is probably the consequence of low water consumption during the vegetative phase in plants presenting reduced tillering and lower leaf size (53). Low water consumption increases water availability during late stages of the plant cycle, thereby causing the stay-green phenotype (53) (**Table 1**). This phenotype can also result from increased root growth and soil exploration in deep soils, as suggested by a common genetic control for the stay-green phenotype and root architecture (15) (**Table 1**).

Water use efficiency can be regarded as the result of partially independent processes related to plant transpiration on the one hand and plant growth on the other hand. Using  $^{13}\text{C}$  discrimination in plant tissues as proxy for water use efficiency, researchers confirmed that part of the variation in water use efficiency across species and varieties is under genetic control, but this trait has a low heritability and is largely dependent on the environment (34). Selection for  $^{13}\text{C}$  discrimination has resulted in a 15% increase in yield in very dry scenarios (106), but this effect decreased with rainfall and was nullified with rainfall of 400 mm (40) (**Table 1**). This was interpreted as a conservative behavior with reduced stomatal conductance (40). In the same way, isohydry tends to limit both photosynthesis and transpiration, thereby increasing water use efficiency because of the nonlinear relationship between these variables, whereas anisohydry favors photosynthesis and transpiration at the cost of lower water use efficiency and at the risk of severe water deficit (**Table 1**).

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**Genomic selection:**

the phenotypic values of individuals are predicted based on the knowledge of values at thousands of markers; requires a training panel in which phenotypes are measured

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### **A Partial Conclusion: Most Constitutive and Adaptive Traits Show Contrasting Responses Under Mild Versus Severe Water Deficit**

Most traits, either constitutive or resulting from adaptive processes, show different effects on growth and yield depending on environmental scenarios. This is synthesized in **Table 1** with a limited set of traits and scenarios involving the temporal patterns of rainfall and evaporative demand, together with soil depth and soil water content at sowing. In these examples, all traits could have positive or negative effects on yield depending on the scenario. Because these effects might be still more complex and sometimes less expected than in **Table 1**, the table should be considered an object of discussion between physiologists, modelers, and breeders rather than a conclusive statement on the value of each individual trait.

### **AVENUES FOR PROGRESS: TOWARD A PROBABILISTIC APPROACH TO DROUGHT TOLERANCE?**

Breeders have been successful in increasing yield in dry conditions. For instance, the genetic progress over generations has been 19 and 80 kg ha<sup>-1</sup> year<sup>-1</sup> in wheat (112) and maize (48), respectively, in water-deficit conditions. Interestingly, this progress was essentially based on selection for yield, often in well-watered conditions. The contribution of selection based on physiological traits for drought adaptation has been small (112), and genetic engineering has at best contributed to incremental progress rather than causing a shift in tendencies. Drought-tolerant transgenic plants released in the last 10 years are not numerous, and have caused yield increases of 2–4%, i.e., within the same range as novel varieties obtained by conventional breeding (29, 95). To our knowledge, none of the spectacular improvements of drought tolerance in engineered plants tested in controlled conditions has resulted in improved varieties (7). Novel breeding techniques such as genomic selection may well reinforce the power of yield-based selection, perhaps at the expense of physiology-based breeding (135). Furthermore, it has been proposed that breeding

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**Scalability:** the translatability of a process or mechanism from a smaller scale (e.g., photosynthesis rate) to a larger scale (e.g., yield)

**Phenotypic distance:** the temporal, spatial, and organization scales to be crossed between two phenotypic traits; can be measured via the number of equations, parameters, and input variables necessary to derive one trait from the other

**Allelic effect:** the difference between mean phenotypic values of plants carrying two different alleles at a given genomic position

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strategies based on traits or genes for tolerance should only complement direct selection for yield, which would continue as the benchmark for all other strategies (112). In this context, physiologists need to carefully consider their potential contribution to the domain of breeding for drought tolerance.

## How Can Plant Physiology Contribute to Breeding for Drought Tolerance? Scalability, Phenotypic Distance, and Context Dependency

The modest success of selection based on physiological traits has been interpreted in terms of loss of gain when scaling up between levels of plant organization (scalability) (108, 112). For example, biochemical pathways affecting photosynthesis have decreasing impact when one incorporates physiological processes from the single leaf to the whole plant and canopy (120). In this view, a physiological trait is considered scalable if it remains agronomically relevant at higher level and eventually affects yield (112). Reported scalable traits of drought tolerance are most often constitutive, such as the presence of awns or long coleoptiles, or glaucousness (112). As previously mentioned, a physiological trait, carbon isotope discrimination, has also proved scalable because breeding on its basis has allowed impressive improvement of wheat yield under severe water deficit (40). In this view, the interest of a trait for breeding would therefore depend on the correlation of the trait with yield (4). Most adaptive traits described in the first part of this review may therefore be considered irrelevant because they show no stable correlation with yield. This raises two remarks. First, we are not aware of any trait, even considered positive and scalable in a given environment, whose effect would not be negative in other environments (**Table 1**). Scalability is therefore context dependent, thereby restricting the interest of this concept. Second, an approach based on the correlation between a given trait and yield under drought conditions favors traits with small phenotypic distances from yield (ironically, one could state that the best yield predictor is yield itself). Physiological traits necessarily present less-straightforward statistical relations with yield because of their larger phenotypic distance with it. They can nevertheless be related to yield via sets of equations that involve other traits and environmental conditions (134).

This situation might change if physiologists proposed methods for taking advantage of adaptive physiological traits in breeding programs. Physiologists may have no competitive advantage for identifying combinations of alleles that increase average yield in dry regions, compared with genomic selection. Their contribution to breeding may involve two novel questions: (*a*) Where and when does each genotype or allele have comparative advantages? (*b*) Can one predict the effect of combinations of alleles controlling adaptive traits as a function of environmental conditions? In particular, what would be the consequences on yield of the variation of an adaptive trait or a combination of those traits in a set of specific environmental scenarios?

## Where and When: Context Dependency Is a Major Feature of the Impact of Alleles on Yield Under Water Deficit

In meta-analyses of field experiments, a given allele has a positive effect in at most half of the fields, and usually for much smaller proportions (79, 112, 147). This poses a major problem in the breeding for drought tolerance (108). However, allelic effects at quantitative trait loci (QTLs) are not random, and these can be analyzed as a function of measurable environmental conditions (85, 100, 147). In a meta-analysis of the result of 29 maize field experiments across Europe, nearly all QTLs had conditional effects upon yield that were positive, negative, or null depending on environmental conditions at flowering time (**Figure 4**) (85). A limited number of environmental scenarios were defined as sets of experiments that shared common temporal patterns for light,

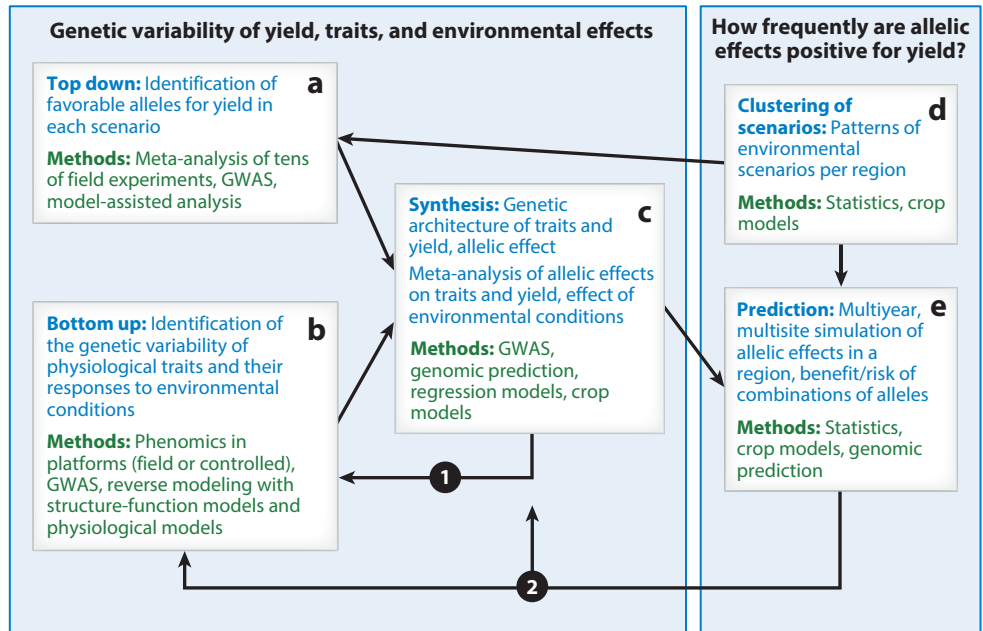
air temperature, evaporative demand, and soil water status. As discussed above, alleles at QTLs related to late flowering time had a positive effect under mild conditions and a negative effect under water deficit. This was also the case with other QTLs, for example, for an allele associated with the increased biosynthesis of ABA, which was favorable in fields subjected to both water deficit and high evaporative demand but was detrimental in well-watered fields (85). In another study of wheat, the allelic effect at one QTL, analyzed in 18 fields in Australia and Mexico, was linearly related to temperature (interpreted here as an effect of evaporative demand) around flowering time (**Figure 4**) (100). Finally, in a meta-analysis of field experiments in Mexico (147), a QTL affecting silk emergence in maize had a temperature-dependent effect on yield. In these three studies, experiments were clustered into environmental scenarios on the basis of measured environmental conditions rather than geographic locations because geography alone failed to provide any insight into the conditional effects of QTLs. Indeed, fields located at a short distance apart—or even the same field during two different years—were often classified under different scenarios because of the spatial and temporal variability of rainfall (85).

A novel view of the QTL  $\times$  environment interaction emerges from the examples presented above. First, context dependency can be considered the rule rather than the exception for QTLs associated with yield in drought scenarios. Second, the QTL  $\times$  environment interaction can be analyzed as a nonrandom consequence of measurable environmental conditions, rather than as a complication that blurs the scalability of the traits and alleles involved. Third, a trait often considered to be nonscalable, such as ABA biosynthesis, shows a consistent effect on yield provided that environmental scenarios, and not regional patterns, are considered.

### Predicting the Effect of Combinations of Alleles Controlling Adaptive Traits in Different Environments

Beyond addressing where and when each genotype or allele has comparative advantages, physiologists may contribute to the prediction of yield of plants presenting different combinations of alleles that control physiological traits. The context dependency presented above suggests that this prediction involves not only the genetic analysis of traits but also the genetic variability of their responses to local environmental conditions in the considered field and the way they contribute to the feedback processes presented in this review. For an adaptive trait or allele to relate to drought tolerance, it needs to have a genetic variability available in public collections of accessions, a high heritability, and an effect on different genetic backgrounds. It also needs to have a positive effect on yield in drought scenarios with at least some reasonable frequency. We propose hereafter an approach that deals with these points by taking into account recent progress of phenomics and modeling (129, 134, 144) (**Figure 5**). The first and second steps characterize the genetic variability of both yield and traits and how they respond to drought scenarios in various environmental conditions in the field and in automated phenotyping platforms. The third step jointly analyzes these data sets to predict traits and yield of any genotype genetically related to the considered panel of genotypes in multiple drought scenarios. The fourth and fifth steps simulate yields of these genotypes over long time series in multiple fields to identify the frequency at which combinations of alleles have positive effects on yield in a region of interest.

1. A top-down approach analyzes the genetic variability of yield in tens of field experiments (**Figure 5a**), resulting in the identification of QTLs of yield, and in the elucidation of the relationship between allelic effects and environmental conditions (as in **Figure 4**). This approach requires detailed (but cheap) characterization of environmental conditions in each experiment and basic field phenotyping, already carried out by breeders (yield and its



**Figure 5**

Overall approach for predicting the yield of hundreds of genotypes in thousands of dry fields by analyzing the genetic variability of yield and traits in various environmental scenarios (panels *a–c*) and estimating the consequence on yield of traits and alleles in various environmental scenarios (panels *d* and *e*). (*a*) Tens of field experiments are carried out in a region (e.g., Europe) with measurement of environmental conditions and of yield of hundreds of genotypes. This results in a genome-wide association study (GWAS) of yield depending on environmental scenarios. (*b*) In parallel, physiological traits of the same genotypes (e.g., stomatal conductance, radiation use efficiency, sensitivity of leaf growth to water deficit) are derived from images and sensor outputs in phenotyping platforms in field or controlled conditions via the inversion of structure-function and physiological models (2, 129). This results in GWAS of traits, including the dependency of allelic effect on measured environmental conditions. (*c*) The results of the steps in panels *a* and *b* are analyzed jointly, resulting in a meta-analysis of allelic effects on both traits and yield as a function of environmental conditions. The step depicted in this panel involves genomic prediction of traits and of their responses to measured environmental conditions, statistical modeling, and crop modeling. Arrow ① denotes that the steps in panels *a–c* are evaluated via their ability to result in a consistent theory across diverse scenarios. This evaluation may result in changes in methods of phenomics and modeling. (*d*) Environmental scenarios are identified by clustering the time courses of environmental conditions as sensed by the plants during specific phenological stages, in hundreds of fields of the considered region over tens of years. This involves both statistical and crop models, helps the meta-analysis of field experiments in panel *a*, and allows multiyear, multisite modeling. (*e*) The effects of combinations of alleles are simulated in the same sites and years as in panel *d* on the basis of statistical or crop models whose parameters are predicted in panel *c*. The outcome is the proportion of cases in which a combination of alleles is favorable for yield in a region, thereby estimating the value of new genotypes. Arrow ② denotes that the whole approach is evaluated for its ability to reproduce yields measured in the field and, eventually, to result in improved varieties, resulting in the fine-tuning of methods at previous steps (panels *a–c*).

components). This phenotyping may be extended to new traits based on the progress of imaging in the field (129).

2. A parallel bottom-up approach analyzes the genetic variability of physiological traits in phenotyping platforms either in the field or under controlled conditions (129) (Figure 5*b*). These traits, for example, leaf growth (70), light interception (22), stomatal conductance

(2), root architecture (45), or pattern of water extraction (105), usually show high genetic variability and heritability but also high QTL  $\times$  environment interaction, often as high as that of yield. To the difference of field, this interaction can be disentangled at this step on the basis of detailed environmental control, resulting in sets of equations that model the QTL  $\times$  environment interaction (70). Furthermore, complex traits encapsulating trait responses to specific environmental variables (e.g., trait sensitivity to water potential or to evaporative demand) (151) and possible interactions with CO<sub>2</sub> concentration can be identified, analyzed genetically (105), and used in plant models (70).

3. A joint analysis of the genetic architecture of yield components and traits can be carried out based on the previous two steps (**Figure 5c**), potentially resulting in the genomic prediction of the genotype-dependent parameters of regression models or of crop models that simulate traits and yield as a function of local environmental conditions. Whether the previous steps have been successful can be evaluated via the presence or absence of a plausible theory and a model that link traits, alleles, and yield in environmental conditions of interest. This may result in changing the definition and measurement of traits and environmental conditions for further analyses.
4. The comparative advantage of a trait or of a combination of allelic values can then be addressed via a combination of simulation and of field experiments (**Figure 5e**). It is based on environmentally defined drought scenarios built by clustering environmental conditions in multiple sites (37, 56) (**Figure 5d**). These scenarios help the interpretation of field experiments in order to detect specific traits or alleles of interests for each scenario (85). Simulations using a crop model can then be run for a large number of years at many sites in a region of interest to ascertain the impacts of traits or alleles on yield, based on the frequency with which a given combination of alleles has a positive impact on yield across years and sites. The success of the whole approach depends on the consistency of simulated and observed impacts and, ultimately, on the development of improved varieties.

This general approach is still at the proof-of-concept stage, but elements of it have been successfully used to test the effects of traits such as stomatal response to high evaporative demand (84), root architecture (80), transpiration efficiency (144), and sensitivity of leaf growth to water deficit (36). It requires up-to-date phenomic tools and models and a detailed environmental characterization of each site that is increasingly available by combining sensor networks and public environmental databases (129). Overall, it has interesting properties. (a) It can be extended to test the effect of specific traits or alleles in scenarios of climate change (57). (b) It can address the importance of traits and alleles for specific climatic variables such as high evaporative demand (75). (c) It can be used for numerous traits, regardless of scale of organization, provided that these traits can be explicitly placed in a causal chain and inserted in a specific model (102), thereby solving the problem of scalability.

## CONCLUDING REMARKS

The main aim of this review is to facilitate the dialogue between physiologists, geneticists, and breeders by proposing a new definition of and approach to drought tolerance in plants, in terms hopefully as clear and perhaps as provocative as those in other recent and thoughtful reviews (108, 112). Twenty years of day-to-day interactions with breeders in national and European projects suggests to us that a probabilistic approach is familiar to them, but that methods are needed in order to fully exploit adaptive processes in the selection of plants able to cope with water deficit and high evaporative demand. Because the feedback processes presented here have contrasting effects on plant performance over different years, the corresponding alleles can hardly be selected

via classical breeding approaches (30). A combination of phenomics and modeling may help to analyze the genetic variability of these adaptive processes, and then modeling may help predict where and when a combination of alleles is favorable in a region with frequent water deficit. Multiyear, multisite simulations help evaluate the potential benefit and associated risk or resulting virtual genotypes within each region.

### SUMMARY POINTS

1. Evolution has constrained the mechanisms involved in drought acclimation to act as feedback strategies that correspond to specific environmental scenarios.
2. Short-term mechanisms (e.g., stomatal conductance or leaf and root growth) stabilize the water potential of shoots in spite of varying evaporative demand and soil water status, involving trade-offs with carbon capture.
3. Short- plus long-term responses of traits (e.g., root architecture, grain abortion, and senescence) and constitutive traits (e.g., plant cycle length) are controlled or selected to manage soil water in such a way that plants can produce at least a few viable seeds.
4. All these feedback processes have trade-offs in terms of carbon cost and the risk of water depletion; strategies favorable to plant performance in dry conditions optimize the carbon/water balance in a given drought scenario on a multiannual basis.
5. A given trait can therefore be related to yield with positive or negative correlations depending on drought scenarios, which are defined by the clustering of time courses of environmental conditions.
6. The genetic variability of adaptive processes can be analyzed by using phenotyping platforms (under controlled or field conditions) with hundreds of genotypes. It is analyzed jointly with alleles for yield observed in meta-analyses of field experiments under contrasting environmental scenarios.
7. Combinations of alleles and traits that optimize yield can be simulated over years under current or future regional climatic conditions, and the outputs of these simulations can be compared with the results of field experiments.
8. This probabilistic approach, based on the genetic variability of adaptive traits and on the context-dependence of their effect, may ultimately help breeders improve plant drought tolerance of major crops and contribute to food security.

### DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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27. Examines how root hairs and mucigels can affect the hydraulic conductance at the soil root interface by using original phenotyping and a physical approach.

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30. Serves as the first clear demonstration that context dependency of traits largely affects breeding programs based on yield.

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85. Estimates allelic effects at quantitative trait loci of yield in tens of fields as a function of environmental scenarios.

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**100. Disentangles the effects of environmental conditions upon yield in tens of field experiments and estimates allelic effects at one quantitative trait locus of yield as a function of temperature.**

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144. Analyzes via simulation studies in different environmental scenarios the comparative advantages of genotypes bred in two locations in India, with marked differences in duration of two phenological stages.

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145. Estimates the costs and benefits of large root systems under water deficit and introduces a novel efficiency term of water gained per unit cost of carbon invested in roots.

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