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# Different avenues for progress apply to drought tolerance, water use efficiency and yield in dry areas

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## Abstract

Drought tolerance, water use efficiency (WUE) and yield in dry areas are often considered as synonyms. However, they correspond to markedly different suites of physiological mechanisms, based on combinations of alleles constrained by evolution into consistent strategies. Improving (i) drought tolerance, sensu stricto, involves extreme conservative strategy with protection and repair mechanisms; (ii) WUE most often results in small plants but avenues exist with lower penalties for growth, i.e. by reducing night transpiration; (iii) yield for drought prone areas involves both constititutive traits (e.g. phenology or plant architecture), favourable for most environmental scenarios, and adaptive physiological traits whose effects suited to a given scenario. Genetic improvement of the latter would requires identification of scenario-dependent combinations of alleles, involving phenomics, modelling and genomic prediction.

## Introduction

Agriculture needs to ensure food security in spite of the negative effects of climate change and limited water resource for irrigation. This requires increased yield under dry conditions, often considered as equivalent to increased "crop per drop" (water use efficiency, WUE) or increased drought tolerance. However, these three concepts get less and less similar as one considers, over time, the involved individual processes and their consequences (Fig. 1). For example, plants with high WUE are obtained by decreasing transpiration via stomatal density and stomatal conductance [1]. Nevertheless, keeping high transpiration is considered as a key trait for high yield under water deficit, as shown by the correlation between yield and canopy temperature (a proxy of transpiration rate) [2]. Very different processes have been considered to improve plant responses to water deficit, e.g. the manipulation of hormonal balance [3], of the adaptive response of root systems [4, 5], of sugar metabolism [6] or of genes involved in plant development [7]. Such a diversity of processes and methods to reach a common goal is puzzling, thereby suggesting that involved groups used common words with different meanings.

## Drought, a dynamic status resulting from offer, demand and plant traits

Water availability to plants is defined by the amount of soil water at the vicinity of plant roots [8]. It decreases over time as soil water is depleted by transpiration, more rapidly for shallow than for deep soils/root systems. Soil water is also depleted more rapidly by plants with highest transpiration rate associated with, for instance, large leaf area, high stomatal conductance or low biosynthesis of the stress hormone abscisic acid (ABA) [8]. Hence, the genetic variability of traits affects the depletion rate of soil water, resulting in most favourable water status in plants with lowest transpiration. Early studies describing drought tolerant plants were often based on this principle, with transgenic plants smaller or with lower transpiration than wild types [9]. However, canopy photosynthesis increases with leaf area and stomatal conductance, in such a way that plant performance under mild water deficits and conservative strategies are usually not compatible. They can nevertheless be combined over time. Because yield is most sensitive to water deficit at some stages of the crop cycle, strategies were developed by breeders to reduce transpiration at early plant stages or in periods with highest evaporative demand, in order to maintain soil water status at sufficiently high values during flowering time and grain filling [10].

Evaporative demand is the second component of water deficit, if the latter is defined as an insufficient ability of the soil water captured by the root system to meet the transpiration demand of a particular plant or canopy at a particular time [8]. It essentially depends on incident light and air vapour pressure deficit. Hence, transpiration (and therefore water stress) varies over minutes to hours depending on fluctuations of light and temperature. Rapid fluctuations also apply to the water status of leaves and of reproductive organs, which result from a continuous water flow through roots , xylem, leaf tissues and atmosphere. Typically, leaf water status fluctuates from -0.1 MPa at dawn to -2 MPa at noon time, with more rapid fluctuations when transient shading occurs. This translates in rapid variations of leaf elongation rate or stomatal conductance, with half times of about 20 minutes [11].

From a physiological point of view, water stress of plant organs is therefore a highly dynamic process. Transient conditions are the rule in natural conditions whereas the steady water fluxes and water status experienced by plants in growth chambers is the exception. "Water stress" is most often used in a loose way, without reference to explicit environmental conditions over time.

## Strategies selected by evolution for coordinating physiological adaptive processes in specific environments: a conceptual base for analysing drought responses

A system where tens of processes vary over minutes with different half times, and where individual processes have partly contradictory effects on plant metabolism and growth, would lead to a near infinite number of combinations and, probably, to an unpredictable plant behaviour. This is not what is observed: plant behaviour in terms of growth or yield is repeatable in a range of conditions, is predictable as long as environmental conditions are properly characterized and it can even be inferred from genomic and environmental information [12]. To solve this paradox, we recently proposed that evolution constrained short-term adaptive mechanisms into coordinated strategies: the complexity of plant system would be similar at all scales from cell to canopy in a "fractal" way, because of potent simplifying rules at integrated levels that make the system predictable (Fig. 2) [13]. Mechanisms at one scale would differ in nature from those at more integrated scales, thereby explaining why integrated traits (e.g. grain yield) and upstream traits (e.g. stomatal conductance) have similar heritabilities (Fig. 2). Integrated strategies are at the base of following paragraphs: I argue that improving drought tolerance, water use efficiency or grain yield under drought correspond to different strategies (Fig. 1).

## Genetic improvement of plant survival and recovery: conservative strategies with no theoretical limitations

Resurrection plants show impressing abilities to survive extreme water deficits and to rapidly recover to ensure reproduction when conditions become milder. This involves cessation of growth, near-complete cessation of transpiration via morphological changes and metabolic protections during dry phases, and repair mechanisms during recovery [14] (Fig. 1). Another case of extreme conservative strategy is the CAM metabolism which disconnects photosynthesis from transpiration, thereby making plants almost insensitive to evaporative demand. To the difference with other strategies in Fig. 1, improving plant survival and recovery does not involve major trade-offs nor optimization of contradictory processes, so they might be improved by genetic engineering without foreseen theoretical limitations.

Extreme conservative strategies have agronomical and ecological interests for specific cases, for instance in perennial pastures undergoing severe summer droughts or for plants avoiding erosion in dry areas [15]. However, they involve mechanisms that are in opposition with high performance under the milder conditions compatible with agriculture. To my knowledge, engineering plants with genes of desert plants has never led to commercialized crop varieties for agricultural contexts.

**Improving water use efficiency: optimizing opposite constraints with avenues for progress.**

Water use efficiency, if defined as the ratio of biomass accumulation to transpiration, is constrained by the tight coupling between both traits (Fig. 3ab). Genetic analyses using $^{13}C$ discrimination in plant tissues as a proxy, revealed that part of the variation in WUE is under genetic control in several species but with a low heritability [16]. Indeed, WUE fluctuates with evaporative demand, which affects transpiration more than photosynthesis: it is higher during days with low than with high evaporative demand, and even oscillates between morning and afternoon. Crops growing during early spring, with low evaporative demand, show a higher WUE than those growing in summer.

WUE is to a large extent in opposition with growth unless special precautions are taken. This is due to the non-linear relation between stomatal conductance and photosynthetic rate (Fig. 3ab). Plants with small size or low stomatal conductance have a higher WUE than plants with higher transpiration rate. Breeding plants for high WUE most often led to non-interesting plants from an agronomical point of view because of their slow growth rate [17]. An interesting breeding programme consisted in breeding for both growth and WUE. This resulted in a 15% increase in yield in very dry scenarios, but this effect still decreased with rainfall and nullified with rainfall of 400 mm [18], still a dry situation in many regions. This can be interpreted as a semi-conservative strategy with reduced stomatal conductance. Several avenues exist for improving WUE while minimizing penalties in terms of growth.

- Improving photosynthesis, in particular by inserting a C4 metabolism in C3 plants. In addition to increasing the photosynthesis term of the ratio, this also decreases the transpiration term because of lower stomatal conductance. Engineered C4 rice plants with higher yield and increased WUE were described from 1989 onwards, but face difficulties [19,20]. Because more than 60 C3-C4 transition events occurred in evolution, this strategy may still be reachable.

- Decreasing night transpiration. Stomata close in the dark but a residual diffusion through stomata still causes night transpiration [21], which can be as high as 30% of 24-h transpiration with an appreciable genetic variation in several species. Because no photosynthesis occurs during the night, a reduction in night transpiration can limit water use without altering growth. Indeed, the genetic architecture of night transpiration largely overlaps with that of WUE in vine, and genotypes with favourable alleles exhibit reduced night transpiration without altered growth (Fig. 3cd).

### Increasing yield in drought-prone areas: a probabilistic, scenario dependent approach

Breeders have been successful in increasing yields in dry conditions, essentially based on selection for yield [22-24]. The contribution of trait-based selection has been smaller [25], whereas genomic selection may well re-inforce the power of yield-based selection [26]. The genetic progress in the last decades is essentially parallel in dry and favourable conditions, suggesting that selected plants have acquired traits for better yields in all conditions, without specific adaptations to drought. Most successful engineered plants for dry conditions are also based on constitutive traits, e.g. sugar metabolism or development [5,6]), with a positive advantage for yield observed in both dry and favourable conditions.

Nevertheless, most quantitative trait loci (QTLs) for yield have positive, negative or neutral effects depending on the considered environmental scenario [8]. In a multi-site experiment in 29 fields across Europe, nearly all QTLs of yield had allelic effects depending on environmental scenarios based on soil water status and evaporative demand at flowering time (Fig 4) [27]. For example an allele that increases the biosynthesis of ABA was favourable in dry and hot fields, but detrimental in well-watered fields. The QTL x environment interaction can be analysed as a non-random consequence of measured environmental conditions, rather than as a complication that blurs the scalability of involved traits and alleles.

Hence, improving yield in dry conditions involves considering local environmental conditions during the considered year because alleles and traits for yield differ between environmental scenarios. Genomic prediction is still possible by considering the responses to light, water status and temperature as genotype-specific traits. Indeed, the slopes of the regression lines of grain number with environmental variables are heritable, and can be predicted from genomic information (Fig. 5) [12]. Hence, it is feasible to design a combination of alleles, at whole-genome scale, for each environmental scenario. The problem remains that climatic conditions are not predictable at the time of sowing. Indeed, a given field can be subjected to quite different environmental scenarios over years [29]. The only information at sowing is the probability for different scenarios to occur in the considered field. Taking into account adaptive traits or alleles with conditional effects on yield therefore needs to consider, firstly, the best combination of alleles corresponding to a given environmental scenario and, secondly, the probability that this scenario occurs in the considered field [8]. This complexity explains why adaptive alleles, with specific effects under water deficit, have not been selected until now with current breeding methods. However, current progress in environmental characterization and trait evaluation (sensor networks, environmental grids, remote sensing) [29,30] and in genomic prediction [12] may allow this approach to be considered in breeding, but also in plant engineering.

## Conclusion

Drought tolerance, water use efficiency and yield in drought-prone areas depend on markedly different combinations of alleles and traits so they probably cannot be combined in a given plant. Drought tolerance, sensu stricto, corresponds to an extreme conservative strategy that can be improved by fine tuning protection and repair mechanisms. WUE involves optimization of biomass accumulation and transpiration, which can be improved via profound changes in the system, e.g. a C4 metabolism or reduced night transpiration. Progress in yield for drought prone areas was obtained by breeders by selecting for yield, but is parallel in dry and favourable conditions. Specific breeding or genetic engineering for drought adaptation needs to select combinations of adaptive alleles/traits for specific environmental scenarios, thereby representing a change in approaches in breeding and plant engineering, involving phenomics, modelling and genomic prediction [8].

## Acknowledgements

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*Many concepts and mechanisms presented here are considered with more space in this paper*

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## Figure captions

**Fig. 1 Graphical summary**: The numerous physiological mechanisms involved in the response to water deficit are constrained by evolution or breeding in consistent strategies for different environmental scenarios. This translates in conservative, optimized or scenario-dependent strategies that sustain imprroved drought tolerance (survival and recovery), water use efficiency or yield under water deficit.

**Fig. 2. Relevance of individual physiological mechanisms vs coordinated strategies at different scales of organization and time-scales**. The complexity, appreciated here via heritability, is similar at all scales because of potent simplifying rules selected by evolution or breeding. Modified from [12]

**Fig. 3. Optimizing Water use efficiency (WUE)**. WUE, defined as the ratio of $CO_2$ uptake to transpiration (a; b) or of biomass accumulation to transpiration (c, d) decreases with stomatal conductance and phtotsynthesis (A), thereby favouring small plants, but a genetic reduction of night transpiration can increase both WUE and biomass accumulation. In (c) and (d), each symbol represents allelic values at the VRZAG83 marker on LG 4. Redrawn from [20]. In (a), the relation between stomatal conductance and photosynthesis as in [30]. WUE is calculated as the ratio of A to transpiration on the same data, for a VPD of 4 kPa.

**Fig. 4. Allelic values at QTLs of yield differ between environmental scenarios of temperature and soil water status.** For example, the B73 allele at QTL3, involved in the synthesis of the stress hormone abscisic acid, had a positive effect in water deficit (WD) and a negative or neutral effect in mild conditions (mild). Note that the sign of allelic effects differ for each QTL. Result of a genetic analysis of 244 maize hybrids over 29 field experiments over Europe. Cool, daily mean temperature at flowering time lower than 20°C night and 33°C day. Warm (middle line), mean T >33°C in days and <20°C in nights; HotDN, mean T >33°C in days and >20°C in nights. Mild, mean soil water potential at 30 and 60 cm depth never decreased below -0.1 MPa at flowering time. WD, soil water potential at the same depths decreased below -0.1 MPa. Redrawn from [27]

**Fig. 5. Which combinations of alleles are suited to which environments for maximizing yield?** An approach of genomic prediction taking adaptive strategies into account. (a) the response curves of grain number to intercepted light, soil water potential and meristem tempsrature are established over the multi-site field experiment (xx experiments), for phenological phases calculated from data in a phenotyping platform and local environmental conditions. (b) genomic prediction of yield (GY) with environmental and genotypiic main effects, plus effect of measured covariables in each field associated with the slopes established in (a). Individual grain weight was considered through a genotypic main effect. (c) test of the quality of prediction either in the same set of genotypes with

cross validation for 46 new genotypes in tested environments (left), 46 new genotypes in 5 new environments (center), or tested with 32 external genotypes (right). Grey symbols, training set. This allows identification of which combinations of alleles are best suited to which environments, for a large number of virtual genotypes and fields. Redrawn from [11]

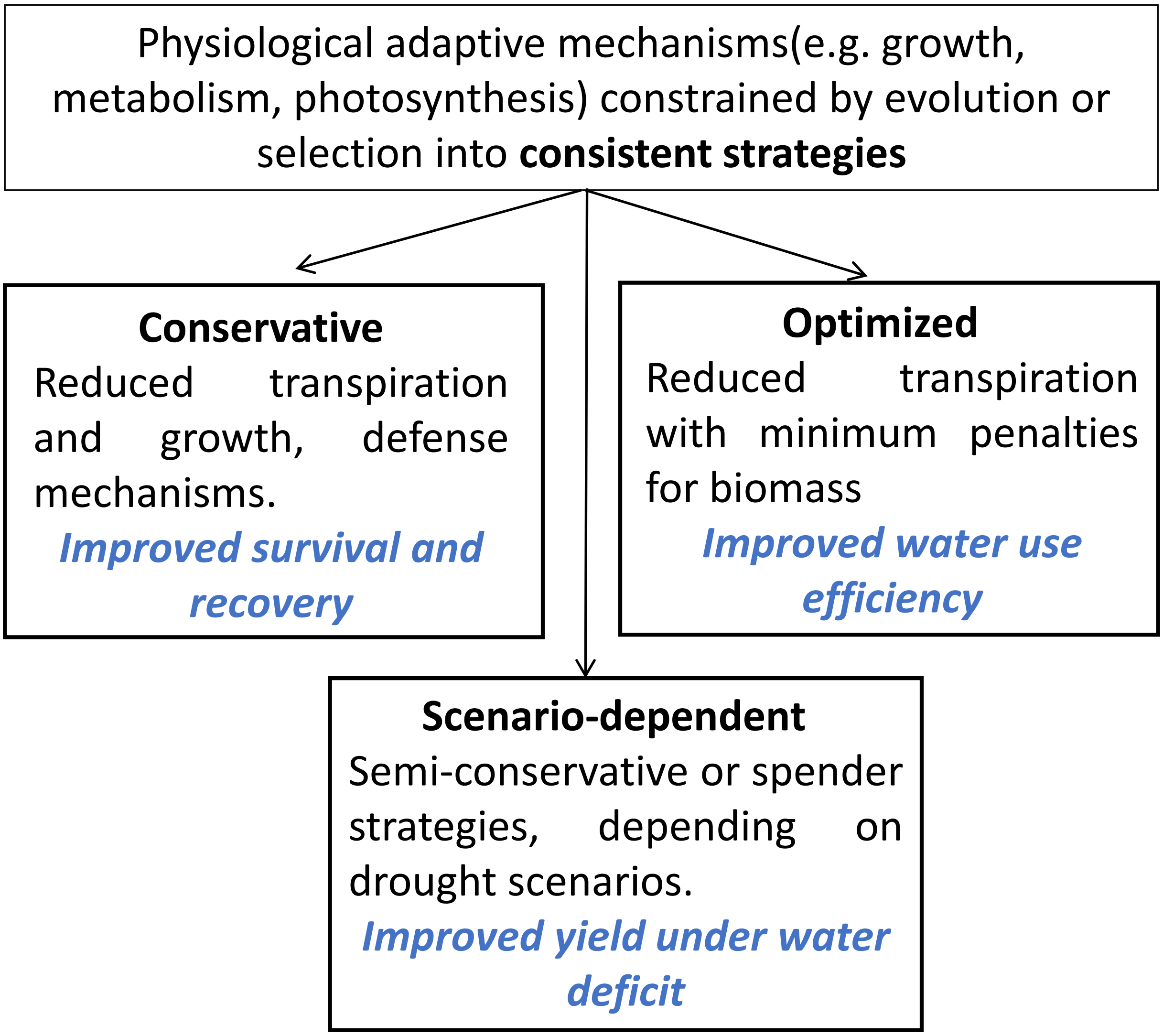
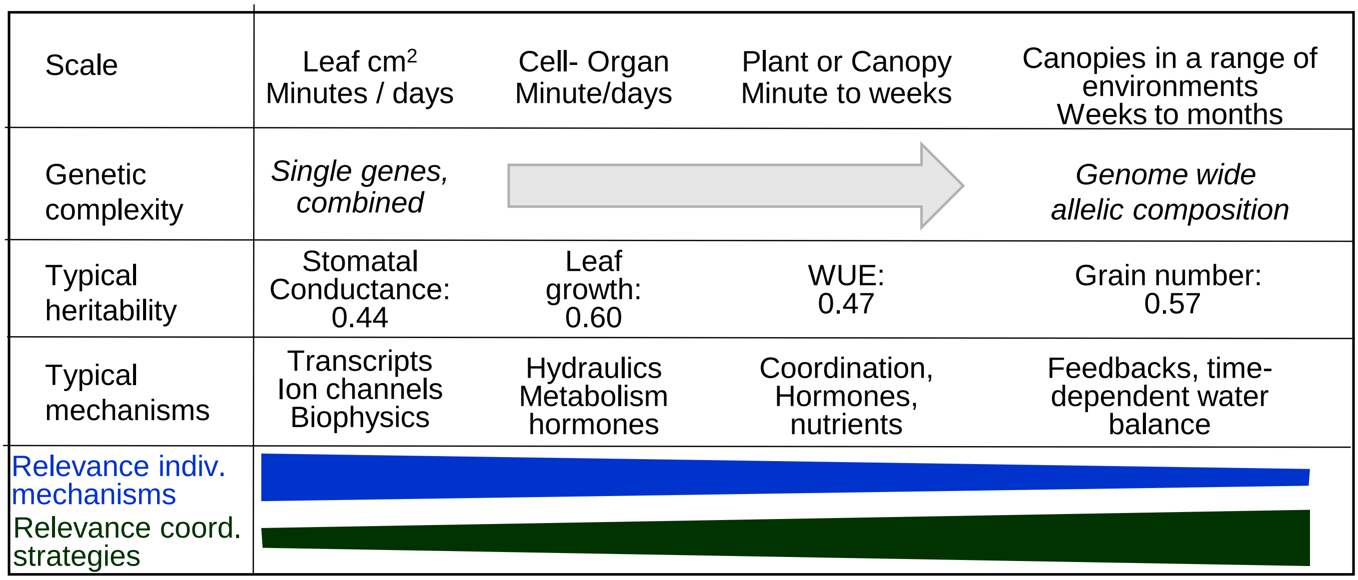
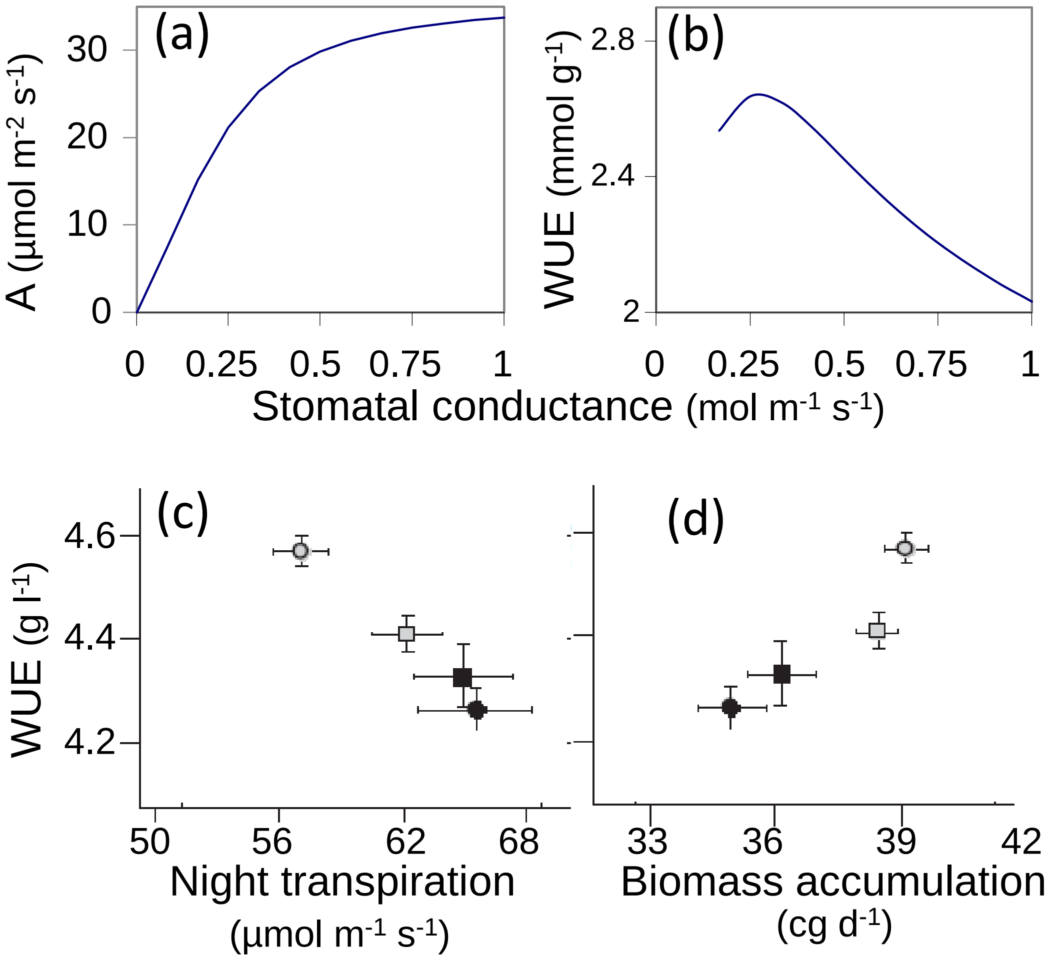


Fig. 1 **Summary of strategies and traits involved in the response to water deficit**: The numerous physiological mechanisms involved in the response to water deficit are constrained by evolution or breeding into consistent strategies for different environmental scenarios. This translates in conservative,, optimized or scenario-dependent strategies that sustain either improved drought tolerance (survival and recovery), water use efficiency or yield under water deficit.



| Scale | Leaf cm$^2$ Minutes / days | Cell- Organ Minute/days | Plant or Canopy Minute to weeks | Canopies in a range of environments Weeks to months |
|---|---|---|---|---|
| Genetic complexity | *Single genes, combined* | | | *Genome wide allelic composition* |
| Typical heritability | Stomatal Conductance: 0.44 | Leaf growth: 0.60 | WUE: 0.47 | Grain number: 0.57 |
| Typical mechanisms | Transcripts<br>Ion channels<br>Biophysics | Hydraulics<br>Metabolism<br>hormones | Coordination,<br>Hormones,<br>nutrients | Feedbacks, time-dependent water balance |
| Relevance indiv. mechanisms<br>Relevance coord. strategies | | | | |

Fig. 2.. **Relevance of individual physiological mechanisms vs coordinated strategies at different scales of organization and time-scales**. The complexity, appreciated here via heritability, is similar at all scales because of potent simplifying rules selected by evolution or breeding. Redrawn from [12]



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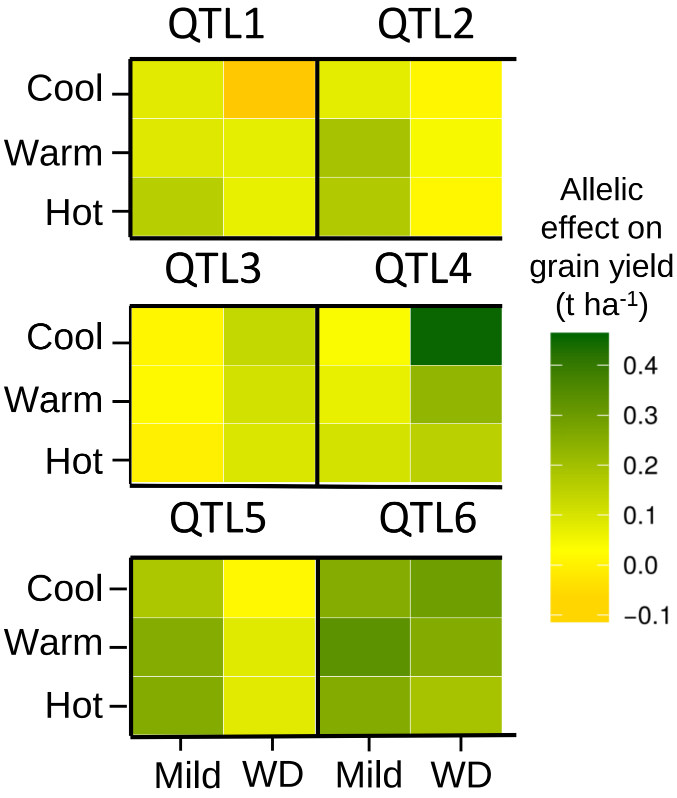

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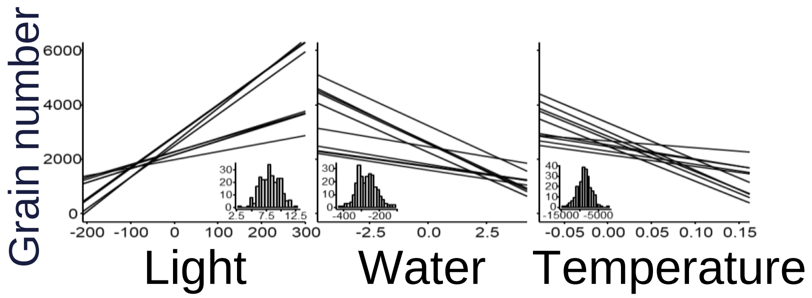
(a) Response curves, 246 genotypes



(b) Genomic prediction, 246 genotypes

$$GY_{ij} = (\mu + e_j + g_i + \sum_{l=1}^{s} \beta_{l,i}\, cov_{l,i,j}) \times GW_i$$

(c) Test, 46+32 genotypes, and use (1000s genotypes)

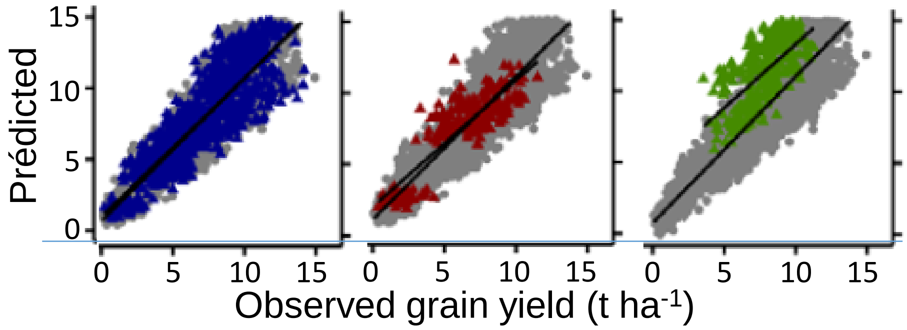
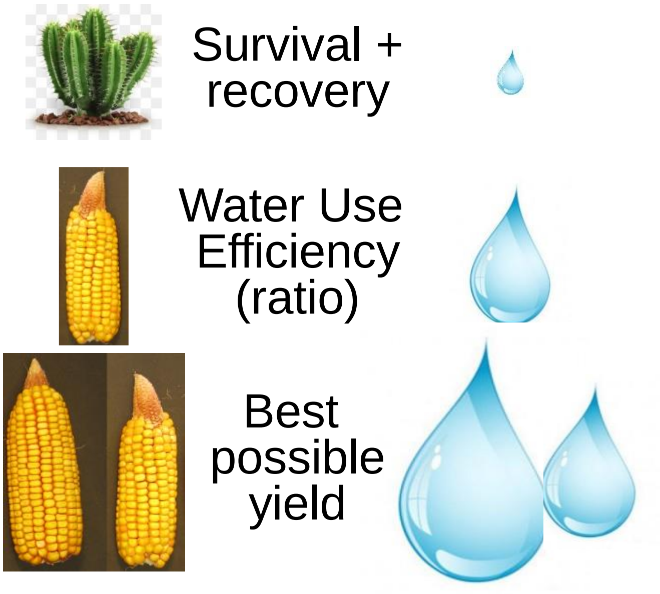


**Fig. 5. Which combinations of alleles are suited to which environments for maximizing yield?** An approach of genomic prediction in maize taking adaptive strategies into account. (a) the response curves of grain number to intercepted light, soil water potential and meristem temperature are established over the multi-site field experiment (25 experiments), for phenological phases calculated from data in a phenotyping platform and local environmental conditions. (b) genomic prediction of yield (GY) with environmental and genotypiic main effects, plus effect of measured covariables in each field associated with the slopes established in (a). Individual grain weight was considered through a genotypic main effect. (c) test of the quality of prediction either in the same set of genotypes with cross validation for 46 new genotypes in tested environments (left), 46 new genotypes in 5 new environments (center), or tested with 32 external genotypes (right). Grey symbols, training set. This allows identification of which combinations of alleles are best suited to which environments, for a large number of virtual genotypes and fields. Redrawn from [11]



Survival +
recovery

Water Use
Efficiency
(ratio)

Best
possible
yield