



**HAL**  
open science

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

Francois Tardieu

### ► To cite this version:

Francois Tardieu. Different avenues for progress apply to drought tolerance, water use efficiency and yield in dry areas. *Current Opinion in Biotechnology*, 2022, 73, pp.128-134. 10.1016/j.copbio.2021.07.019 . hal-03342431

**HAL Id: hal-03342431**

**<https://hal.inrae.fr/hal-03342431>**

Submitted on 22 Aug 2023

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NonCommercial 4.0 International License

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

**Francois Tardieu**

*LEPSE, Univ Montpellier, INRAE, Institut Agro, Montpellier, France*

### **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 constitutive 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 require identification of scenario-dependent combinations of alleles, involving phenomics, modelling and genomic prediction.

## 1 **Introduction**

2 Agriculture needs to ensure food security in spite of the negative effects of climate change and  
3 limited water resource for irrigation. This requires increased yield under dry conditions, often  
4 considered as equivalent to increased "crop per drop" (water use efficiency, WUE) or increased  
5 drought tolerance. However, these three concepts get less and less similar as one considers, over  
6 time, the involved individual processes and their consequences (Fig. 1). For example, plants with high  
7 WUE are obtained by decreasing transpiration via stomatal density and stomatal conductance [1].  
8 Nevertheless, keeping high transpiration is considered as a key trait for high yield under water deficit,  
9 as shown by the correlation between yield and canopy temperature (a proxy of transpiration rate)  
10 [2]. Very different processes have been considered to improve plant responses to water deficit, e.g.  
11 the manipulation of hormonal balance [3], of the adaptive response of root systems [4, 5], of sugar  
12 metabolism [6] or of genes involved in plant development [7]. Such a diversity of processes and  
13 methods to reach a common goal is puzzling, thereby suggesting that involved groups used common  
14 words with different meanings.

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

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

30 Evaporative demand is the second component of water deficit, if the latter is defined as an  
31 insufficient ability of the soil water captured by the root system to meet the transpiration demand of  
32 a particular plant or canopy at a particular time [8]. It essentially depends on incident light and air  
33 vapour pressure deficit. Hence, transpiration (and therefore water stress) varies over minutes to

34 hours depending on fluctuations of light and temperature. Rapid fluctuations also apply to the water  
35 status of leaves and of reproductive organs, which result from a continuous water flow through roots  
36 , xylem, leaf tissues and atmosphere. Typically, leaf water status fluctuates from -0.1 MPa at dawn to  
37 -2 MPa at noon time, with more rapid fluctuations when transient shading occurs. This translates in  
38 rapid variations of leaf elongation rate or stomatal conductance, with half times of about 20 minutes  
39 [11].

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

#### 44 **Strategies selected by evolution for coordinating physiological adaptive processes in specific** 45 **environments: a conceptual base for analysing drought responses**

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

#### 60 **Genetic improvement of plant survival and recovery: conservative strategies with no theoretical** 61 **limitations**

62 Resurrection plants show impressive abilities to survive extreme water deficits and to rapidly recover  
63 to ensure reproduction when conditions become milder. This involves cessation of growth, near-  
64 complete cessation of transpiration via morphological changes and metabolic protections during dry  
65 phases, and repair mechanisms during recovery [14] (Fig. 1). Another case of extreme conservative  
66 strategy is the CAM metabolism which disconnects photosynthesis from transpiration, thereby

67 making plants almost insensitive to evaporative demand. To the difference with other strategies in  
68 Fig. 1, improving plant survival and recovery does not involve major trade-offs nor optimization of  
69 contradictory processes, so they might be improved by genetic engineering without foreseen  
70 theoretical limitations.

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

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

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

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

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

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

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

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

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

122 Hence, improving yield in dry conditions involves considering local environmental conditions during  
123 the considered year because alleles and traits for yield differ between environmental scenarios.  
124 Genomic prediction is still possible by considering the responses to light, water status and  
125 temperature as genotype-specific traits. Indeed, the slopes of the regression lines of grain number  
126 with environmental variables are heritable, and can be predicted from genomic information (Fig. 5)  
127 [12]. Hence, it is feasible to design a combination of alleles, at whole-genome scale, for each  
128 environmental scenario. The problem remains that climatic conditions are not predictable at the  
129 time of sowing. Indeed, a given field can be subjected to quite different environmental scenarios  
130 over years [29]. The only information at sowing is the probability for different scenarios to occur in  
131 the considered field. Taking into account adaptive traits or alleles with conditional effects on yield

132 therefore needs to consider, firstly, the best combination of alleles corresponding to a given  
133 environmental scenario and, secondly, the probability that this scenario occurs in the considered  
134 field [8]. This complexity explains why adaptive alleles, with specific effects under water deficit, have  
135 not been selected until now with current breeding methods. However, current progress in  
136 environmental characterization and trait evaluation (sensor networks, environmental grids, remote  
137 sensing) [29,30] and in genomic prediction [12] may allow this approach to be considered in  
138 breeding, but also in plant engineering.

## 139 **Conclusion**

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

## 150 **Acknowledgements**

151 This work was supported by the EU project H2020- 731013 (EPPN<sup>2020</sup>), the Agence Nationale de la  
152 Recherche projects ANR-10-BTBR-01 (Amaizing) and ANR-11-INBS-0012 (Phenome\_Emphasis).

153

154

## 155 **References**

- 156 1. Dunn J, Hunt L, Afsharinafar M, Al Meselmani M, Mitchell A, Howells R, Wallington E, Fleming AJ,  
157 Gray JE: **Reduced stomatal density in bread wheat leads to increased water-use efficiency.**  
158 *Journal of Experimental Botany* 2019, **70**:4737-4747.
- 159 2. Langridge P, Reynolds M: **Breeding for drought and heat tolerance in wheat.** *Theoretical and*  
160 *Applied Genetics* 2021.
- 161 3. Gupta A, Rico-Medina A, Cano-Delgado AI: **The physiology of plant responses to drought.** *Science*  
162 2020, **368**:266-269.
- 163 4. Klein SP, Schneider HM, Perkins AC, Brown KM, Lynch JP: **Multiple integrated root phenotypes are**  
164 **associated with improved drought tolerance.** *Plant Physiology* 2020, **183**:1011-1025.

- 165 5. Orman-Ligeza B, Morris EC, Parizot B, Lavigne T, Babe A, Ligeza A, Klein S, Sturrock C, Xuan W,  
166 Novak O, et al.: **The Xerobranching response represses lateral root formation when roots**  
167 **are not in contact with water.** *Current Biology* 2018, **28**:3165-+
- 168 \* 6. Nuccio ML, Wu J, Mowers R, Zhou HP, Meghji M, Primavesi LF, Paul MJ, Chen X, Gao Y, Haque E,  
169 et al.: **Expression of trehalose-6-phosphate phosphatase in maize ears improves yield in**  
170 **well-watered and drought conditions.** *Nature Biotechnology* 2015, **33**:862-+.  
171 *Genetic engineering of carbon metabolism resulting in increased yield under drought, but also in well*  
172 *watered conditions: an example of the interest of a constitutive trait.*
- 173 7. Wu JR, Lawit SJ, Weers B, Sun JD, Mongar N, Van Hemert J, Melo R, Meng X, Rupe M, Clapp J, et  
174 al.: **Overexpression of zmm28 increases maize grain yield in the field.** *Proceedings of the*  
175 *National Academy of Sciences of the United States of America* 2019, **116**:23850-23858.
- 176 \* 8. Tardieu F, Simonneau T, Muller B: **The Physiological Basis of Drought Tolerance in Crop Plants:**  
177 **A Scenario-Dependent Probabilistic Approach.** . *Annual Review of Plant Biology* 2018,  
178 **69**:733-759.  
179 *Many concepts and mechanisms presented here are considered with more space in this paper*
- 180 9. Iuchi S, Kobayashi M, Taji T, Naramoto M, Seki M, Kato T, Tabata S, Kakubari Y, Yamaguchi-  
181 Shinozaki K, Shinozaki K: **Regulation of drought tolerance by gene manipulation of 9-cis-**  
182 **epoxycarotenoid dioxygenase, a key enzyme in abscisic acid biosynthesis in Arabidopsis.**  
183 *The Plant Journal* 2001, **27**:325-333.
- 184 \*\* 10. Messina CD, Sinclair TR, Hammer GL, Curan D, Thompson J, Oler Z, Gho C, Cooper M: **Limited-**  
185 **transpiration trait may increase maize drought tolerance in the US Corn Belt.** *Agronomy*  
186 *Journal* 2015, **107**:1978-1986.  
187 *The relation between water use efficiency and yield depends on environmental scenarios, with maps*  
188 *in the USA*
- 189 11. Caldeira CF, Bosio M, Parent B, Jeanguenin L, Chaumont F, Tardieu F: **A Hydraulic model is**  
190 **compatible with rapid changes in leaf elongation under fluctuating evaporative demand**  
191 **and soil water status.** *Plant Physiology* 2014, **164**:1718-1730.
- 192 \* 12. Millet EJ, Kruijer W, Coupel-Ledru A, Prado SA, Cabrera-Bosquet L, Lacube S, Charcosset A,  
193 Welcker C, van Eeuwijk F, Tardieu F: **Genomic prediction of maize yield across European**  
194 **environmental conditions.** *Nature Genetics* 2019, **51**:952-+.  
195 *A genomic prediction of yield that explicitly takes into account local environmental conditions and*  
196 *genotypic sensitivity to drought, temperature and light, based on phenomics and modelling.*
- 197 13. Tardieu F, Granato ISC, Van Oosterom EJ, Parent B, Hammer GL: **Are crop and detailed**  
198 **physiological models equally ‘mechanistic’ for predicting the genetic variability of whole-**  
199 **plant behaviour? The nexus between mechanisms and adaptive strategies.** *in silico Plants*  
200 **2020, 2.**
- 201 \*\* 14. Oliver MJ, Farrant JM, Hilhorst HWM, Mundree S, Williams B, Bewley JD: **Desiccation**  
202 **Tolerance: Avoiding cellular damage during drying and rehydration.** In *Annual Review of*  
203 *Plant Biology, Vol 71, 2020.* Edited by Merchant SS; 2020:435-460. *Annual Review of Plant*  
204 *Biology, vol 71.]*  
205 *A thorough review of conservative strategies for extreme drought conditions*
- 206 \* 15. Keep T, Sampoux JP, Barre P, Blanco-Pastor JL, Dehmer KJ, Durand JL, Hegarty M, Ledauphin T,  
207 Muylle H, Roldan-Ruiz I, et al.: **To grow or survive: Which are the strategies of a perennial**  
208 **grass to face severe seasonal stress?** *Functional Ecology* 2021, **35**:1145-1158.  
209 *Ecological consequences of conservative strategies*
- 210 16. Chen J, Chang SX, Anyia AO: **Gene discovery in cereals through quantitative trait loci and**  
211 **expression analysis in water-use efficiency measured by carbon isotope discrimination.**  
212 *Plant Cell and Environment* 2011, **34**:2009-2023.
- 213 17. Blum A: **Effective use of water (EUW) and not water-use efficiency (WUE) is the target of crop**  
214 **yield improvement under drought stress.** *Field Crops Research* 2009, **112**:119-123.
- 215 18. Condon AG, Richards RA, Rebetzke GJ, Farquhar GD: **Breeding for high water-use efficiency.**  
216 *Journal of Experimental Botany* 2004, **55**:2447-2460.



- 217 19. Furbank RT: **Walking the C-4 pathway: past, present, and future.** *Journal of Experimental Botany*  
218 2016, **67**:4057-4066.
- 219 20. Sedelnikova OV, Hughes TE, Langdale JA: **Understanding the genetic basis of C-4 Kranz anatomy**  
220 **with a view to engineering C-3 crops.** In *Annual Review of Genetics, Vol 52*. Edited by Bonini  
221 NM; 2018:249-270. *Annual Review of Genetics*, vol 52.]
- 222 \*\*21. Coupel-Ledru A, Lebon E, Christophe A, Gallo A, Gago P, Pantin F, Doligez A, Simonneau T:  
223 **Reduced nighttime transpiration is a relevant breeding target for high water-use efficiency**  
224 **in grapevine.** *Proceedings of the National Academy of Sciences of the United States of*  
225 *America* 2016, **113**:8963-8968.
- 226 *WUE can be improved in vine without drought penalties by combinations of alleles reducing night*  
227 *transpiration.*
- 228 \*\*22. Cooper M, Gho C, Leafgren R, Tang T, Messina C: **Breeding drought-tolerant maize hybrids for**  
229 **the US corn-belt: discovery to product.** *Journal of Experimental Botany* 2014, **65**:6191-6204.
- 230 *Genetic progress in maize, with parallel progress regardless of environmental conditions, even for*  
231 *drought tolerant plants*
- 232
- 233 \*\* 23. Brisson N, Gate P, Gouache D, Charmet G, Oury F, Huard F: **Why are wheat yields stagnating**  
234 **in Europe ? A comprehensive data analysis for France.** *Field Crops Research* 2010, **119**:201-  
235 212.
- 236 *The plateauing of wheat yield results from continuous genetic progress but increasingly unfavourable*  
237 *environmental conditions.*
- 238 24. Boehm JD, Abdel-Haleem H, Schapaugh WT, Rainey K, Pantalone VR, Shannon G, Klein J, Carter  
239 TE, Cardinal AJ, Shipe ER, et al.: **Genetic Improvement of US Soybean in Maturity Groups V,**  
240 **VI, and VII.** *Crop Science* 2019, **59**:1838-1852.
- 241 \*\*25. Sadras VO, Richards RA: **Improvement of crop yield in dry environments: benchmarks, levels**  
242 **of organisation and the role of nitrogen.** *Journal of Experimental Botany* 2014, **65**:1981-  
243 1995.
- 244 *A healthy and interesting view of breeders for genetic improvement under drought, essentially based*  
245 *on selection for yield.*
- 246 26. Technow F, Messina CD, Totir LR, Cooper M: **Integrating crop growth models with whole**  
247 **genome prediction through approximate Bayesian computation.** *PLoS ONE* 2015,  
248 **10**:e0130855.
- 249 27. Millet EJ, Welcker C, Kruijer W, Negro S, Coupel-Ledru A, Nicolas SD, Laborde J, Bauland C, Praud  
250 S, Ranc N, et al.: **Genome-wide analysis of yield in Europe: allelic effects vary with drought**  
251 **and heat scenarios.** *Plant Physiology* 2016, **172**:749-764.
- 252 28. Sadeh Y, Zhu X, Dunkerley D, Walker JP, Zhang YX, Rozenstein O, Manivasagam VS, Chenu K:  
253 **Fusion of Sentinel-2 and PlanetScope time-series data into daily 3 m surface reflectance**  
254 **and wheat LAI monitoring.** *International Journal of Applied Earth Observation and*  
255 *Geoinformation* 2021, **96**.
- 256 29. Casadebaig P, Mestries E, Debaeke P: **A model-based approach to assist variety evaluation in**  
257 **sunflower crop.** *European Journal of Agronomy* 2016, **81**:92-105
- 258 30. Babet A, Vu PVH, Jacquemoud S, Viallefont-Robinet F, Fabre S, Briottet X, Sadeghi M, Whiting  
259 ML, Baret F, Tian J: **MARMIT: A multilayer radiative transfer model of soil reflectance to**  
260 **estimate surface soil moisture content in the solar domain (400-2500 nm).** *Remote Sensing*  
261 *of Environment* 2018, **217**:1-17.
- 262 31. Bethenod O, Tardieu F, Katerji N: **Relationship between net photosynthetic rate and stomatal**  
263 **conductance in leaves of field-grown maize subjected to soil compaction or soil drying.**  
264 *Photosynthetica* 1996, **32**:367-379

265 **Figure captions**

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

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

274 **Fig. 3. Optimizing Water use efficiency (WUE).** WUE, defined as the ratio of CO<sub>2</sub> uptake to  
275 transpiration (a; b) or of biomass accumulation to transpiration (c, d) decreases with stomatal  
276 conductance and photosynthesis (A), thereby favouring small plants, but a genetic reduction of night  
277 transpiration can increase both WUE and biomass accumulation. In (c) and (d), each symbol  
278 represents allelic values at the VRZAG83 marker on LG 4. Redrawn from [20]. In (a), the relation  
279 between stomatal conductance and photosynthesis as in [30]. WUE is calculated as the ratio of A to  
280 transpiration on the same data, for a VPD of 4 kPa.

281 **Fig. 4. Allelic values at QTLs of yield differ between environmental scenarios of temperature and**  
282 **soil water status.** For example, the B73 allele at QTL3, involved in the synthesis of the stress  
283 hormone abscisic acid, had a positive effect in water deficit (WD) and a negative or neutral effect in  
284 mild conditions (mild). Note that the sign of allelic effects differ for each QTL. Result of a genetic  
285 analysis of 244 maize hybrids over 29 field experiments over Europe. Cool, daily mean temperature  
286 at flowering time lower than 20°C night and 33°C day. Warm (middle line), mean T >33°C in days and  
287 <20°C in nights; HotDN, mean T >33°C in days and >20°C in nights. Mild, mean soil water potential at  
288 30 and 60 cm depth never decreased below -0.1 MPa at flowering time. WD, soil water potential at  
289 the same depths decreased below -0.1 MPa. Redrawn from [27]

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

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

302

303

304

305

306

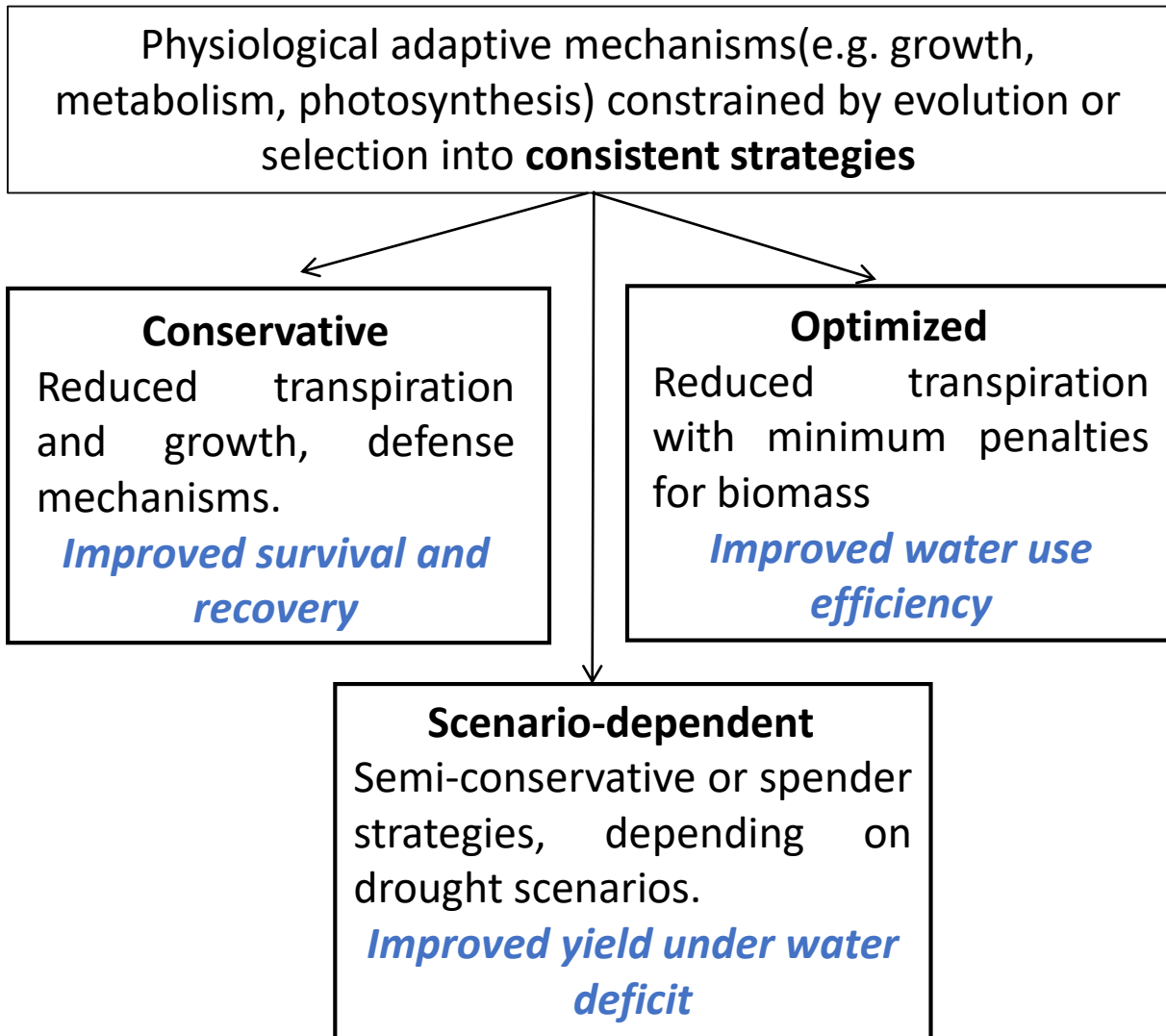





Fig. 1 **Summary of strategies and traits involved in the response to water deficit:** The numerous physiological mechanisms involved in the response to water deficit are constrained by evolution or breeding into consistent strategies for different environmental scenarios. This translates in conservative,, 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 <sup>2</sup> Minutes / days	Cell- Organ Minute/days	Plant or Canopy Minute to weeks	Canopies in a range of environments Weeks to months
Genetic complexity	<i>Single genes, combined</i>			<i>Genome wide allelic composition</i>
Typical heritability	Stomatal Conductance: 0.44	Leaf growth: 0.60	WUE: 0.47	Grain number: 0.57
Typical mechanisms	Transcripts Ion channels Biophysics	Hydraulics Metabolism hormones	Coordination, Hormones, nutrients	Feedbacks, time- dependent water balance
Relevance indiv. mechanisms				
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]

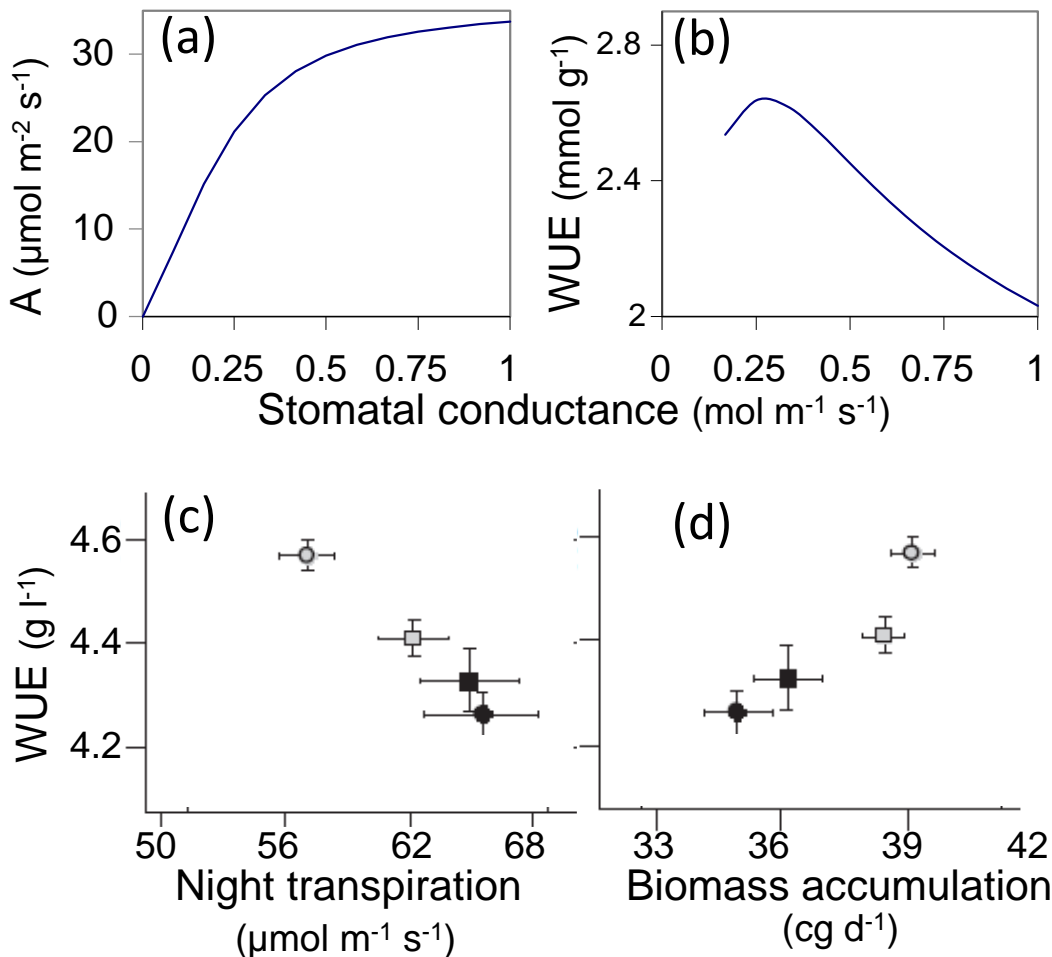
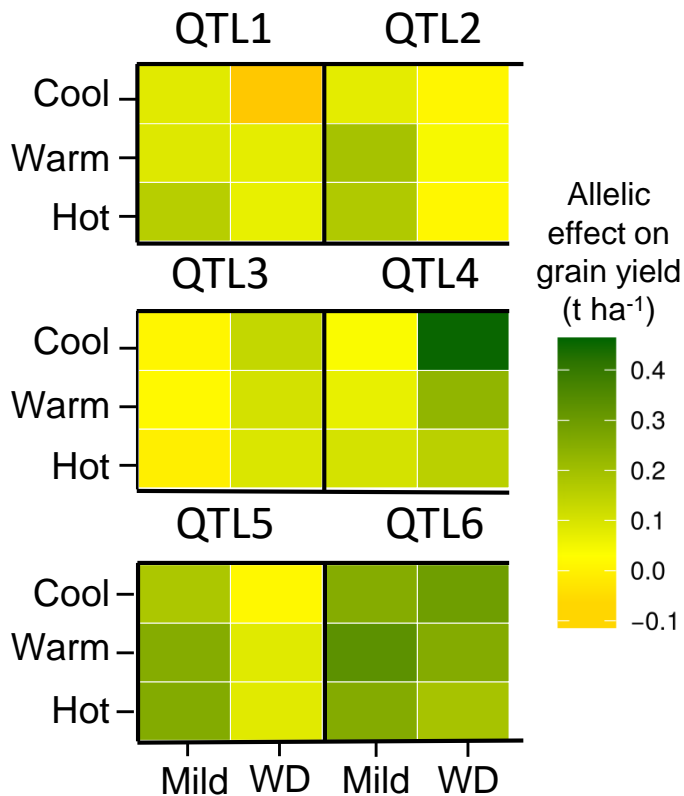
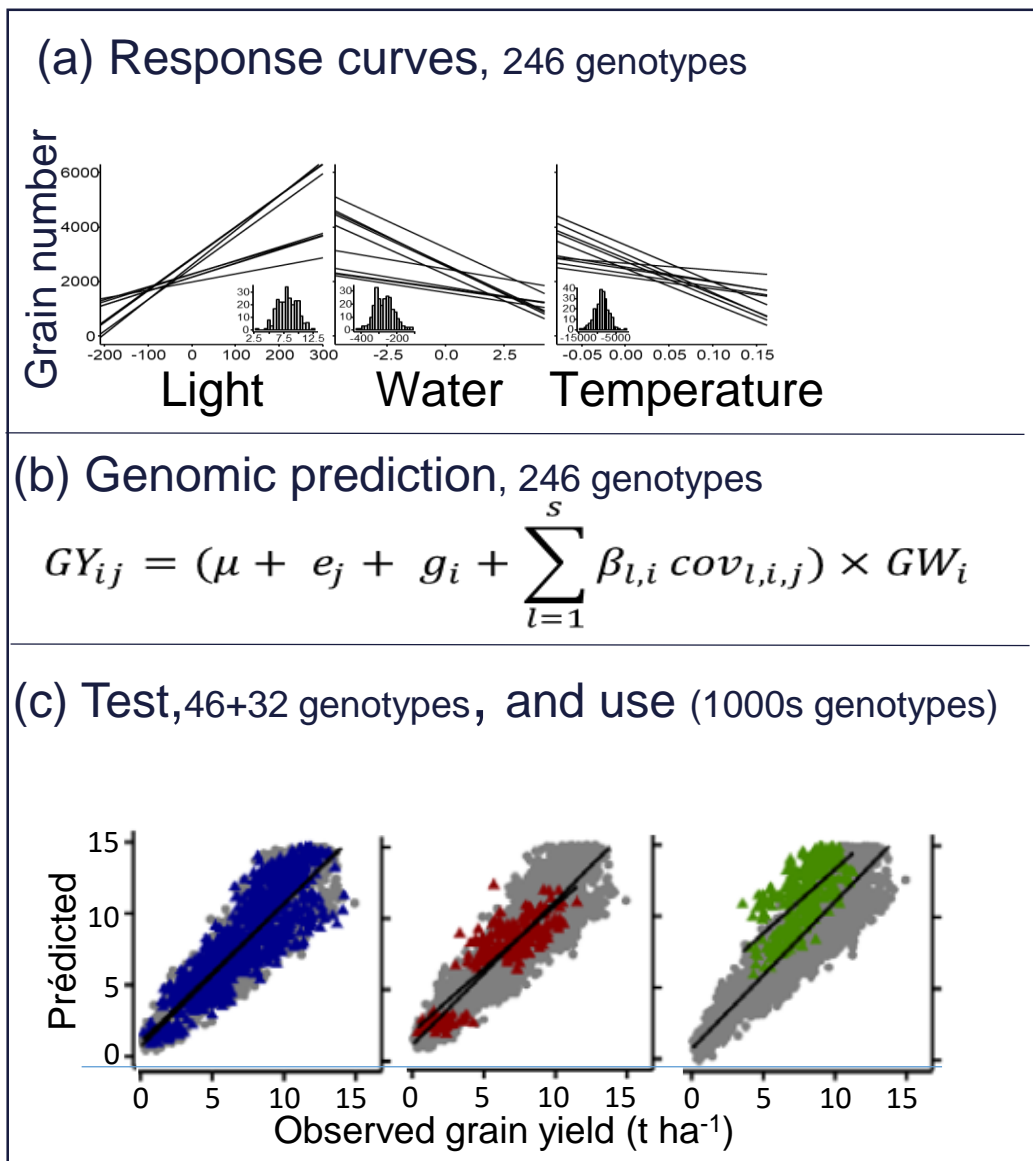


Fig. 3. Water use efficiency, defined as the ratio of  $\text{CO}_2$  uptake to transpiration (a; b) or of biomass accumulation to transpiration (c, d) decreases with stomatal conductance and photosynthesis ( $A$ ), thereby favouring small plants, but a genetic reduction of night transpiration can increase both WUE and biomass accumulation. In (c) and (d), each symbol represents allelic values at the VRZAG83 marker on LG 4 of grapevine. Redrawn from [21]. In (a), the relation between stomatal conductance and photosynthesis as in [31]. 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, in maize, 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 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 genotypic 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

