Dissection and modelling of abiotic stress tolerance in plants

2 authors:

Francois Tardieu
French National Institute for Agriculture, Food, and Environment (INRAE)
256 PUBLICATIONS   **14,937** CITATIONS

SEE PROFILE

Roberto Tuberosa
University of Bologna
312 PUBLICATIONS   **13,827** CITATIONS
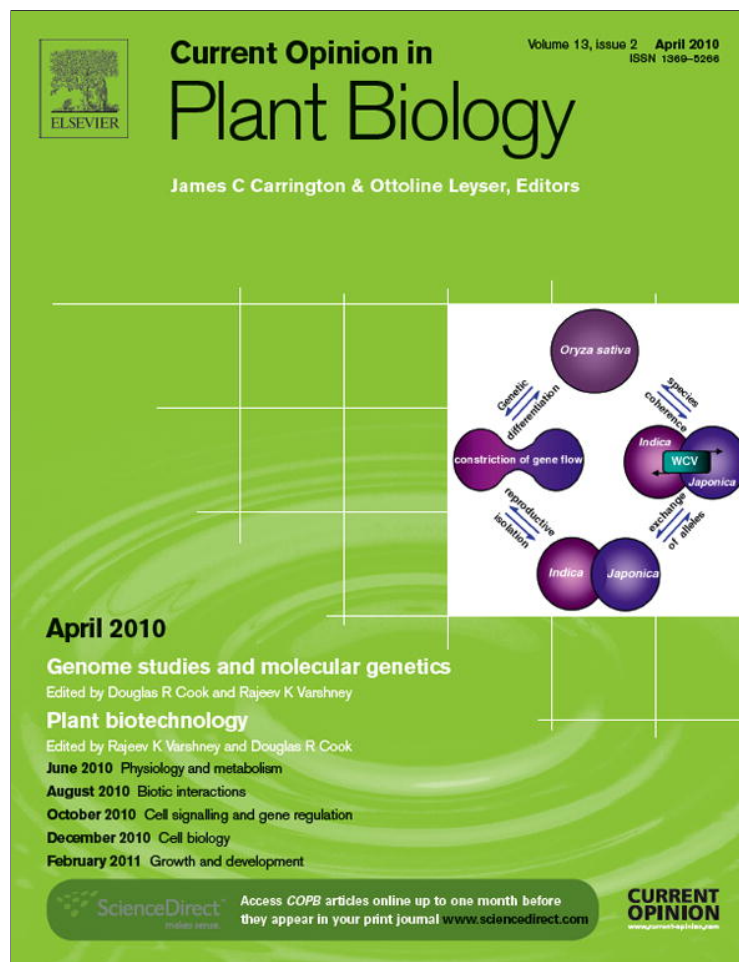
SEE PROFILE

Some of the authors of this publication are also working on these related projects:

Project   Explore the genetic control of leaf, stripe and stem rust resistance in durum wheat View project

Project   Cloning of root QTL View project

Current Opinion in

Plant Biology

Volume 13, issue 2   April 2010
ISSN 1369-5266

James C Carrington & Ottoline Leyser, Editors

April 2010

Genome studies and molecular genetics
Edited by Douglas R Cook and Rajeev K Varshney

Plant biotechnology
Edited by Rajeev K Varshney and Douglas R Cook

June 2010 Physiology and metabolism
August 2010 Biotic interactions
October 2010 Cell signalling and gene regulation
December 2010 Cell biology
February 2011 Growth and development

ScienceDirect

Access *COPB* articles online up to one month before
they appear in your print journal www.sciencedirect.com

CURRENT
OPINION

Current Opinion in Plant Biology

Dissection and modelling of abiotic stress tolerance in plants

François Tardieu[1] and Roberto Tuberosa[2]

Plants have acquired a variety of whole-plant protection mechanisms in response to abiotic stresses, often at the expenses of performance. Hence, a given trait can have positive, negative or no effect depending on the stress scenario. A new approach has emerged that dissects yield and integrative traits that influence stress tolerance into heritable traits (e.g. sensitivity parameters or architectural traits) by using phenotyping platforms with model-assisted methods. The genetic and physiological mechanisms accounting for the variability of these traits and their effects on yield are considered in a second step. Effects of traits on yield are analysed via a combination of modelling and field experiments, which allows identification of the stress scenarios where a given allele has favourable effects.

Addresses
[1] INRA, UMR 759 LEPSE, 2 Place Viala F-34000, Montpellier, France
[2] Department of Agroenvironmental Sciences and Technology, Viale Fanin 44, 40127 Bologna, Italy

Corresponding author: Tardieu, François (tardieu@supagro.inra.fr)

Introduction

Tailoring genotypes with acceptable performance under drought, high temperatures or low nutrient availability is essential for the sustainability of crop production in view of climate change [1–3]. Conventional breeding has been successful [4,5••], but the pace of genetic progress must now increase to meet the projected demand for agricultural products [3]. This is a challenging endeavour because it involves a plethora of loci (mostly quantitative trait loci: QTLs) whose effects differ in the many possible stress scenarios [6••]. In field trials encompassing a broad range of pedoclimatic scenarios, a given QTL has at best shown a significant effect on yield in only half of the tested environments [6••,7••].

The most common strategy has been to identify genes involved in mechanisms of tolerance with a large effect that overrides this complexity. This has led to the isolation and ectopic expression of master genes able to fine-tune the plant reactions to stress via transcription factors, hormonal balance or metabolic protections [8,9]. Although success stories have been reported on the use of such genes to tailor drought-tolerant genotypes [9,10], this approach has not yet led to the release of new cultivars.

Alternative strategies involving the use of natural genetic diversity under diverse environmental conditions require much larger numbers of studied lines and of environmental scenarios. Until recently, it was nearly impossible to perform physiological analyses of such complex situations, but progress in different disciplines opens new avenues: (i) High-throughput phenotyping now allows reproducible measurement of drought-related physiological traits in hundreds of genotypes, in controlled conditions and in the field [11–13]. (ii) Methods are available to describe mathematically traits that vary rapidly with environmental conditions (e.g. growth or gas exchanges), via model-assisted phenotyping [14••,15] and meta-analyses of large datasets [16•,17••]. (iii) The multiplicity of stressing environments, difficult to handle experimentally, can now be addressed owing to the progress of models [6••,18,19••]; if a model adequately describes the effects of the genetic variability in a few climatic scenarios, it can then be extended to a much larger number of scenarios in order to evaluate the comparative advantage of a given allele in different environments [19••]. (iv) Methods for statistical analysis of the genotype × environment × man-management interaction have also enormously progressed, thereby allowing relevant analyses of large networks of field experiments [5••,20•,21].

We review here the implications of this recent progress on the strategy for improving drought tolerance. A two-step strategy is presented in which, first, phenotyping platforms facilitate the genetic dissection of yield into simpler and more heritable traits, associated with QTLs that control their expression. The effects on yield of this genetic variability are then scaled up in a second step, via a combination of modelling and field studies.

Why model? Selection for stress tolerance an optimisation of contradictory processes

Tolerance to abiotic stresses is an ambiguous concept, even after distinguishing different strategies (e.g. escape, avoidance and tolerance) [22]. In this review, we shall not consider traits (e.g. flowering time) that provide an escape mechanism. According to the nature, timing and intensity of the stress episode, tolerance can be defined either by the ability of plants to survive severe stresses and complete their cycle, or to achieve acceptable yield under a milder stress. When the metabolic cost of protection

mechanisms is low, these two definitions can be congruent. For example, the mechanisms that mitigate the negative effects of heat stress (e.g. via the protection of photosystems and of other metabolic processes) may not be very different from those permitting high biomass accumulation at high temperatures [23,24]. Conversely, protection mechanisms against water deficit are most often physiologically associated with a reduction of biomass accumulation, hence yield potential [15,25•]. Biomass accumulation and transpiration are intrinsically linked via their main determinants, that is, stomatal aperture and leaf area [26], so there is a 'built-in' contradiction between biomass accumulation and stress avoidance via transpiration. Breeding can only optimise the terms of this contradiction, for example, by increasing the ratio of accumulated biomass to transpiration (water-use efficiency, WUE) [27–29] or increasing the degree of root or leaf growth maintenance under water deficit [30–32].

Modelling may well provide the most efficient way to find optimums if the effect on yield of a given trait is a trade-off between positive and negative effects, with different optimums depending on the prevailing environmental conditions [6••,19••]. A striking example of such complexity is the genetic improvement of WUE. The introgression into elite material of genomic regions that confer high WUE has led to a clear yield improvement of wheat when subjected to a severe soil water deficit [33••]. Conversely, selection for increased WUE has frequently led to small plants with reduced transpiration, biomass and yield in less severe drought conditions [25•,27]. The genetic variability of root systems is another example. Improving root systems clearly increases yield under water deficit in species with weak root characteristics such as rice [32] but can have more complex and unexpected consequences otherwise. QTL alleles enhancing root architectural features influenced positively maize yield in a particular genetic background [34•] but failed to do so in a different one [35]. Furthermore, breeding programmes aimed at improving maize yield under drought conditions have actually led to a decrease in the weight of the root system [36,37]. A high allocation of biomass to roots can influence positively yield in a soil with water stored in deep layers but not under limited soil water reserve, owing to a poor return in terms of water uptake of the carbon invested in root growth and metabolism. A similar conclusion has been drawn for the relation between root density and nitrogen uptake [38].

## Dissection of complex phenotypes into more simple and heritable traits

The consequence of the studies reviewed above is that any trait involved in stress tolerance can be considered as having positive, negative or no effect on yield depending on the stress scenario. It follows that the genetic variability of those traits should be analysed and dissected *per*

se, independently of its consequences on yield in a given environment [6••,15].

An example of dissection is presented in Figure 1, which synthesises recent studies in maize [13,30,31••,39,40] and rice [16•,41]. The development of leaf area was dissected into that of leaves that grow at different periods of the plant cycle and, consequently, under different environmental conditions. The beginning and the duration of each phase can be modelled as a function of temperature-compensated time for a given genotype [40–43]. Convergent experimental evidence shows that a temporary water deficit essentially affects the growth of leaves which develop during the stress [40] (Figure 1). It is therefore possible to dissect plant leaf area into single leaves, whose individual size will depend on the environmental conditions during their development. Because individual leaf size has usually a low heritability under stress [44], its genetic analysis required further dissection. It was dissected into a duration of development (with a low effect of environment except temperature) and leaf growth rate (highly sensitive to environmental conditions) which can be measured in an automated phenotyping platform [13,41] (Figure 1). While leaf elongation rate varies with time according to environmental conditions, its maximum value observed during the night and its response to evaporative demand or to soil water deficit are common to different experiments for each individual genotype of a mapping population, thereby permitting identification of stable QTLs of sensitivity to environmental variables. A similar approach has been proposed for the dissection of the sensitivity of flowering time to environmental conditions [14••,45].

The dissection approach reviewed above differs from that used in several breeding programmes on the basis of selection for secondary traits correlated to yield [29,46]. Nonetheless, common features of both approaches are the search for higher heritability and for a genetic link to yield. A first major difference is that the traits in a dissection approach are most often 'hidden parameters', not directly measurable, which reproducibly characterise studied lines. They can be, for example, sensitivity parameters detected in a regression analysis [14••,30], architectural features [47] or temperature-compensated leaf appearance rate [40]. A second difference is that the dissection analysis is intimately associated with the model-assisted scale up (see below). Hence, target traits are chosen in such a way that they can be explicitly related to biomass accumulation and yield via equations accounting for environmental conditions [26], which relate biomass accumulation to the amount of light received, the proportion of incident light intercepted by leaves (dependent on leaf area), the efficiency of transformation of intercepted light into biomass (dependent on photosynthesis rate) and the duration of the plant cycle. It is noteworthy that this was the case in the

Figure 1
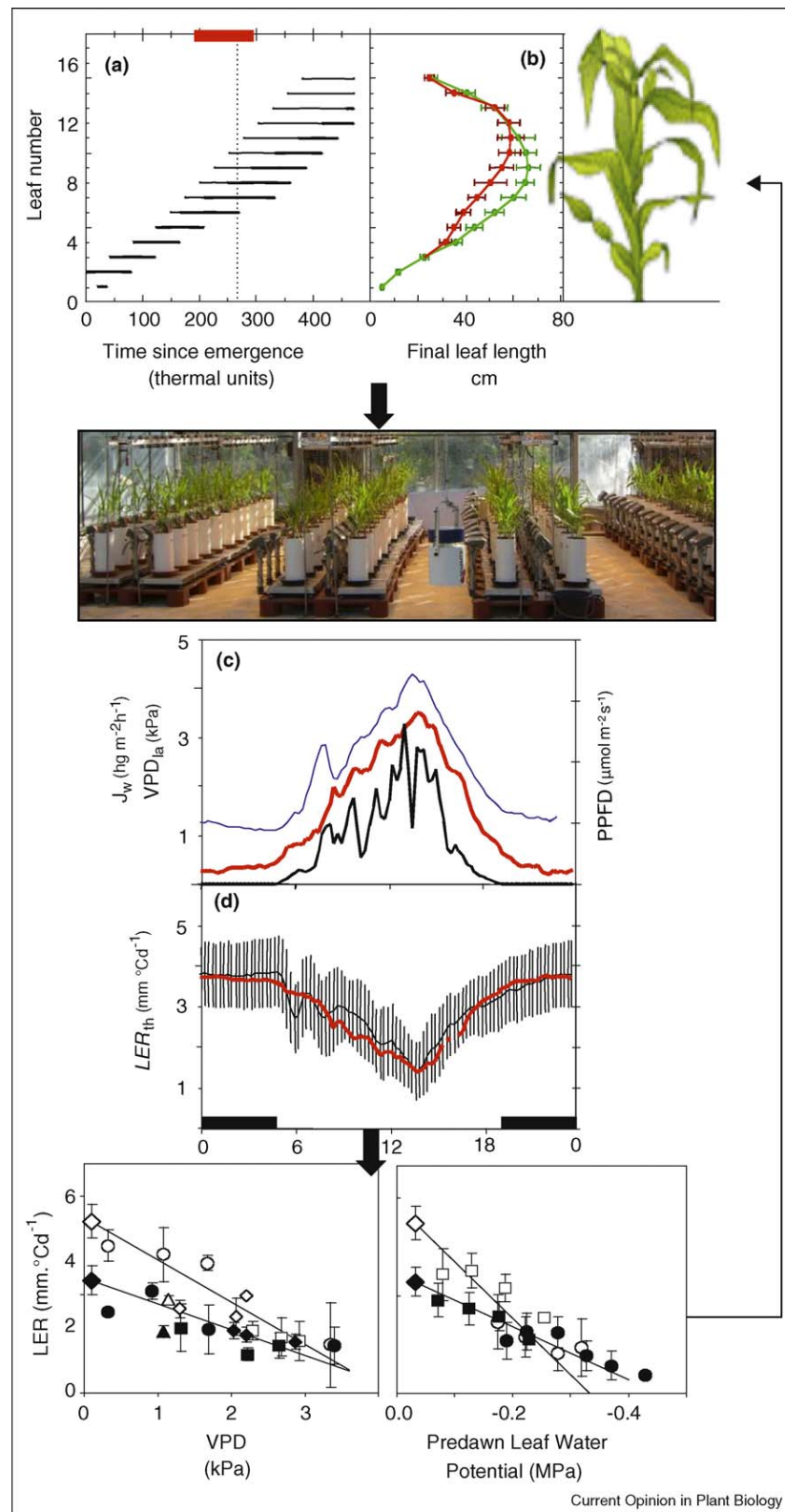
An example of dissection: plant leaf area in maize. **(a)** (Field) Successive leaves develop following a strict programme in terms of thermal time [39]. **(b)** If a stress occurs during a limited period of time (horizontal red bar, in (a)), only leaves which develop during stress are affected in size (green, well watered; red, stressed). The plant leaf area can therefore be modelled as a succession of independent leaves [40]. **(c)** (Phenotyping platform). Leaf

Figure 2
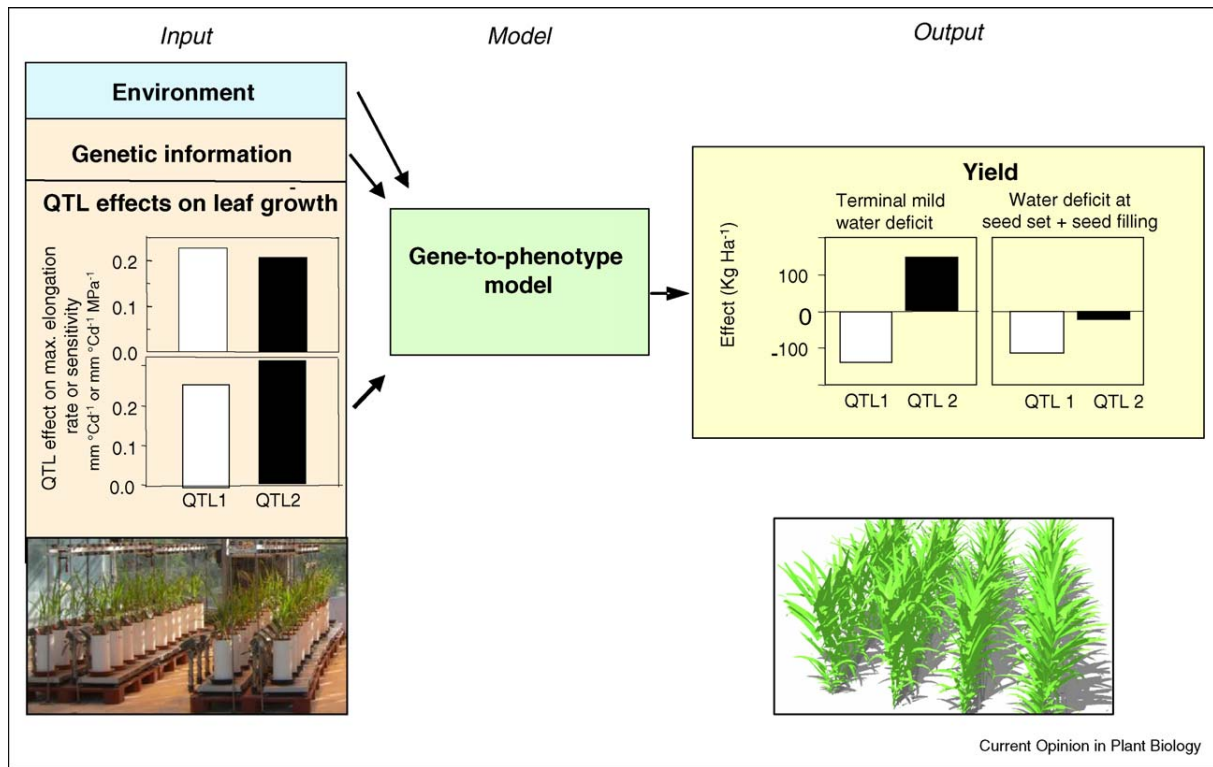
Simulation of the effects on yield of two QTLs involved in leaf elongation rate and its sensitivity to water deficit (modified from [19••]). The simulation is based on climatic data over 45 years of non-irrigated fields and two types of soil. The two QTLs have similar effects on the maximum leaf growth rate (upper panel, *inputs*), but different effects on sensitivities of leaf growth (lower panel) and Anthesis–Silking interval to water deficit. Genotypic data of each recombinant inbred line, QTL effects and environmental data of each year are fed into the model, which then simulates yield in each situation. The effects on yield of alleles at the two studied QTLs are then calculated, and are presented in the right panel in two clusters of pedoclimatic scenarios, either with a favourable soil water status during most of the crop cycle or with a water deficit from flowering time onwards (two additional clusters of situations are not presented here). Note that positive alleles for both elongation rate and sensitivity translate to either positive or negative alleles for yield depending on QTL and environmental conditions. Inputs: allelic effects on maximum leaf growth (upper panel) or on sensitivity of leaf growth to soil water potential (lower panel) a positive effect indicates a greater sensitivity. Virtual field representation in 'outputs', courtesy C. Fournier.

example presented in Figure 1, in which traits measured in a few fields and in a phenotyping platform allowed prediction of leaf area and biomass accumulation in field experiments in Mediterranean and temperate environments in France and Australia [40].

Which levels or type of dissections are relevant to abiotic stress tolerance? The answer largely depends on the heritability observed at each step of the dissection. Heritability is an essential feature for the success of genetic analyses. The high heritability of flowering time [48] has allowed cloning of major QTLs in rice [49] and maize [50], while no QTL of root architecture has been cloned

to date, mainly owing to the usually low heritability of root traits [51]. Unexpectedly, when a rice mapping population was evaluated under managed-stress conditions, yield itself showed the highest heritability compared with secondary traits even in dry conditions [52,53]. This can be partly attributed to the fact that a single, well-controlled water deficit was applied at flowering time in all experiments, thereby resulting in highly reproducible results that apply to one climatic scenario only. Further dissection probably has no major interest in this case. Conversely, the approaches reviewed above, which addressed more diverse climatic scenarios, allowed the genetic dissection of an integrative phenotype with low

(**Figure 1 Legend Continued**) elongation rate of an entire mapping population is measured with a 15-min definition, together with transpiration (Jw, red line) and environmental conditions (light intensity, PPFD, black and leaf-to-air vapour pressure deficit, VPD_la, blue). **(d)** Leaf elongation rate (black line) is at each time related to the reciprocal of transpiration rate (red line). Vertical lines, interval of confidence [62]. **(e, f)**. Multiple experiments in greenhouse and growth chamber allow compilation of response curves which reflect the sensitivity of leaf elongation rate to (e) evaporative demand of well-watered plants during the day and (f) to soil water potential, of drought plants during the night [31••]. Upward arrow: Leaf area in the field can be predicted from the time course of environmental conditions, the model of development in (a) and the sensitivity parameters in (e) and (f) [40].

heritability into a small number of features with higher heritability [14••,30,31••,44].

Finally, it is noteworthy that this dissection step does not require full understanding of the physiological processes that explain the considered traits. In the case of sensitivity of leaf growth to water deficit, the genetic variability might be associated with mechanisms as different as aquaporin activity, abscisic acid effects, cell cycle or cell wall properties, which often show low heritability owing to compensation mechanisms that differ between lines [54–56]. If the selected traits are stable characteristics of a genotype, they can be considered as 'meta-mechanisms' at the whole-plant level [15], managed experimentally for QTL detection and used in modelling.

Scaling up: from QTLs of simple traits to crop performance under stressed conditions

The identification of loci (genes or QTLs) governing variability of traits involved in stress tolerance is of greatest interest if their effects can be scaled up to crop performance in the field under different stress scenarios [57]. Two strategies have been adopted for that.

The co-location of QTLs between simple traits and yield essentially applies to constitutive traits with a large effect on yield. The assumption is that the concurrent effects of each QTL on yield and the target trait are controlled by the same locus and not by tight linkage [34•]. In durum wheat, field testing has revealed two QTLs that consistently influence plant height, kernel weight and yield, across a broad range of soil moisture environments [7••]. Hence, the fine mapping and eventually cloning of these QTLs will be facilitated by measuring plant height rather than yield. Once the cloning of these two QTLs is completed, a better understanding of the mode of action and agronomic value of the allelic series present at these loci will be possible [58].

Another strategy involves the use of simulation modelling, and can be used for adaptive traits whose correlation with yield varies greatly according to the stress scenario. In a pioneering work, Chapman *et al.* [59] have simulated the effect of the genetic variability of four traits on sorghum yield over 100 growing seasons with contrasting climatic scenarios. Afterwards, they calculated the proportion of cases in which a given allele has a positive effect on yield over a long climatic series, under a broad range of simulated cropping systems on the basis of different sowing dates, plant density or fertilizer application, as well as forecasted climate changes. Therefore, one can weigh the agronomic value of an allele in multiple combinations of sites, climatic conditions and cultivation techniques involving thousands of virtual cases, clearly an objective impossible to pursue experimentally. A recent study has extended this approach to the experimental QTLs of leaf growth sensitivity to water deficit originat-

ing from Figure 1 [19••]. Through the model, the QTL allelic effects on the sensitivity of leaf elongation rate to environmental conditions were scaled up into the allelic effects on yield in a large range of environmental scenarios [19••,40] (Figure 2). Notably, Figure 2 shows that a positive allelic effect for leaf growth sensitivity translated into either a positive or a negative effect on yield in a given site, depending on the timing and intensity of the stress.

Conclusion

Fifteen years ago, Passioura argued whether simulation models are science, snake oil, education or engineering [60]. This is a healthy question that still deserves consideration. The dissection-modelling approach reviewed here allows progress in the understanding of the stress effects ('science'), and potentially in the selection process ('engineering'). It has serious limitations in terms of reliability ('snake oil') if it is not appropriately associated with field experiments analysed with suitable statistical methods [5••]. The role of field experiments, in this approach, is to test to what extent simulations can predict yield in a subset of conditions, rather than to explore the whole range of conditions in which the agronomic value of an allele is assessed.

The approach presented herein should be considered as a contribution of Genetics and Ecophysiology to Systems Biology scaled up at the whole-plant level and aimed at bridging the gap between functional polymorphisms and tolerance to abiotic stresses in crops. Its application relies on high-throughput, accurate phenotyping combined with modelling, backed up by multi-environment statistical analyses [5••,21] and high-resolution genetic dissection made possible via genomics approaches [61]. Clearly, the challenge to deploy the deluge of information produced by genomics to predict crop performance under stressed field conditions is in its infancy. Modelling holds promise to streamline and speed up the tortuous gene-to-phenotype journey [6••], thus providing breeders with an additional tool for tailoring cultivars able to better cope with the consequences of global climate change and suitable for a more sustainable agriculture.

References and recommended reading
Papers of particular interest, published within the annual period of review, have been highlighted as:

- • of special interest
- •• of outstanding interest

1. Battisti DS, Naylor RL: **Historical warnings of future food insecurity with unprecedented seasonal heat**. *Science* 2009, **323**:240-244.

2. Lobell DB, Burke MB, Tebaldi C, Mastrandrea MD, Falcon WP, Naylor RL: **Prioritizing climate change adaptation needs for food security in 2030**. *Science* 2008, **319**:607-610.

3. FAO: **2050: Increased investment in agricultural research essential**. *Published online 25 September 2009*, http://www.fao.org/news/story/en/item/35686/icode/2009.

4. Duvick DN: **The contribution of breeding to yield advances in maize (*Zea mays* L.)**. *Advances in Agronomy* 2005, **86**:83-145.

5. Cooper M, van Eeuwijk FA, Hammer GL, Podlich DW, Messina C:
•• **Modeling QTL for complex traits: detection and context for plant breeding**. *Current Opinion in Plant Biology* 2009, **12**:231-240.
This is a thorough presentation of genetic analysis in a genotype × environment × management context, including non additive genetic effects, epistasis and QTL × environment interactions.

6. Hammer G, Cooper M, Tardieu F, Welch S, Walsh B, van Eeuwijk F,
•• Chapman S, Podlich D: **Models for navigating biological complexity in breeding improved crop plants**. *Trends in Plant Science* 2006, **11**:587-593.
Authors review approaches of the gene-to-phenotype approach at different scales of plant organisation, that is, genetic networks, QTL-based modelling, simulation of yield and of breeding programmes.

7. Maccaferri M, Sanguineti MC, Corneti S, Ortega JLA, Ben
•• Salem M, Bort J, DeAmbrogio E, del Moral LFG, Demontis A, El-Ahmed A *et al.*: **Quantitative trait loci for grain yield and adaptation of durum wheat (*Triticum durum* Desf.) across a wide range of water availability**. *Genetics* 2008, **178**:489-511.
The manuscript reports the presence of two major QTLs that affect grain yield of durum wheat in a broad range of environments. Although these findings are an exception to the fact that in multienvironmental studies yield QTLs are mostly detected in specific environments, they suggest that in this genetic background plant height, could be used as a proxy to predict yield across different stress scenarios.

8. Achard P, Cheng H, De Grauwe L, Decat J, Schoutteten H, Moritz T, Van der Straeten D, Peng JR, Harberd NP: **Integration of plant responses to environmentally activated phytohormonal signals**. *Science* 2006, **311**:91-94.

9. Huang XY, Chao DY, Gao JP, Zhu MZ, Shi M, Lin HX: **A previously unknown zinc finger protein, DST, regulates drought and salt tolerance in rice via stomatal aperture control**. *Genes & Development* 2009, **23**:1805-1817.

10. Castiglioni P, Warner D, Bensen RJ, Anstrom DC, Harrison J, Stoecker M, Abad M, Kumar G, Salvador S, D'Ordine R *et al.*: **Bacterial RNA chaperones confer abiotic stress tolerance in plants and improved grain yield in maize under water-limited conditions**. *Plant Physiology* 2008, **147**:446-455.

11. Granier C, Aguirrezabal L, Chenu K, Cookson SJ, Dauzat M, Hamard P, Thioux JJ, Rolland G, Bouchier-Combaud S, Lebaudy A *et al.*: **PHENOPSIS, an automated platform for reproducible phenotyping of plant responses to soil water deficit in *Arabidopsis thaliana* permitted the identification of an accession with low sensitivity to soil water deficit**. *New Phytologist* 2006, **169**:623-635.

12. Montes JM, Melchinger AE, Reif JC: **Novel throughput phenotyping platforms in plant genetic studies**. *Trends in Plant Science* 2007, **12**:433-436.

13. Sadok W, Naudin P, Boussuge B, Muller B, Welcker C, Tardieu F: **Leaf growth rate per unit thermal time follows QTL-dependent daily patterns in hundreds of maize lines under naturally fluctuating conditions**. *Plant Cell and Environment* 2007, **30**:135-146.

14. Yin XY, Struik PC, Tang JJ, Qi CH, Liu TJ: **Model analysis of
•• flowering phenology in recombinant inbred lines of barley**. *Journal of Experimental Botany* 2005, **56**:959-965.
This is, together with [30], one of the first attempt to dissect the phenotype and use hidden parameters for a QTL analysis. Authors check a posteriori that the phenotype can be reconstructed from the parameters.

15. Tardieu F: **Virtual plants: modelling as a tool for the genomics of tolerance to water deficit**. *Trends in Plant Science* 2003, **8**:9-14.

16. Parent B, Turc O, Gibon Y, Stitt M, Tardieu F: **Modelling
• temperature-compensated physiological rates, based on the coordination of responses to temperature of developmental processes**. *Journal of Experimental Botany* 2010, doi:10.1093/jxb/erq003.
Authors derive a common response to temperature of several developmental processes in several species, thereby providing a way to express temperature-compensated rates in phenotyping experiments.

17. Poorter H, Niinemets Ü, Walter A, Fiorani F, Schurr U: **Meta-
•• phenomics: a reference framework for interpreting plant growth responses to a wide range of environmental factors**. *Journal of Experimental Botany*, Advance Access published on January 4, 2010; doi:10.1093/jxb/erp358.
The first example of a very large based meta-analysis of phenotyping experiments in order to derive response laws to environmental conditions in different species, from data originating from the literature.

18. Yin XY, Struik PC, Kropff MJ: **Role of crop physiology in predicting gene-to-phenotype relationships**. *Trends in Plant Science* 2004, **9**:426-432.

19. Chenu K, Chapman SC, Tardieu F, McLean G, Welcker C,
•• Hammer GL: **Simulating the yield impacts of organ-level quantitative trait loci associated with drought response in maize—a 'gene-to-phenotype' modeling approach**. *Genetics* 2009, **183**:1507-1523.
Authors scale up the QTL allelic effects on leaf and silk growth to allelic effects on yield in a large number of pedoclimatic situations. This is the fist attempt with 'real life' QTLs

20. Vargas M, van Eeuwijk FA, Crossa J, Ribaut JM: **Mapping QTLs
• and QTL × environment interaction for CIMMYT maize drought stress program using factorial regression and partial least squares methods**. *Theoretical and Applied Genetics* 2006, **112**:1009-1023.
An example of a new mechanism identified via a statistical analysis of a network of experiments with a QTL × E approach.

21. Malosetti M, Ribaut JM, Vargas M, Crossa J, Boer MP, Eeuwijk FAV: **Multi-trait multi-environment QTL modelling for drought-stress adaptation in maize**. In *Scale and Complexity in Plant Systems Research: Gene-Plant-Crop Relations.* Edited by Spiertz JHJ, Struik PC, van Laar HH. **Wageningen UR Frontis Series**. Springer; 2007:23-34.

22. Levitt J: *Responses of plants to environmental stresses:* New York: Academic Press; 1972.

23. Kotak S, Larkindale J, Lee U, von Koskull-Doring P, Vierling E, Scharf KD: **Complexity of the heat stress response in plants**. *Current Opinion in Plant Biology* 2007, **10**:310-316.

24. Larkindale J, Vierling E: **Core genome responses involved in acclimation to high temperature**. *Plant Physiology* 2008, **146**:748-761.

25. Blum A: **Effective use of water (EUW) and not water-use
• efficiency (WUE) is the target of crop yield improvement under drought stress**. *Field Crops Research* 2009, **112**:119-123.
This manuscript elaborates in a concise and thought-provoking way a number of important issues related to the mechanisms determining yield and water use efficiency in crops exposed to low soil moisture conditions.

26. Monteith JL: **Climate and the efficiency of crop production in Britain**. *Philosophical Transactions of The Royal Society of London B* 1977, **281**:277-294.

27. Condon AG, Richards RA, Rebetzke GJ, Farquhar GD: **Breeding for high water-use efficiency**. *Journal of Experimental Botany* 2004, **55**:2447-2460.

28. Masle J, Gilmore SR, Farquhar GD: **The ERECTA gene regulates plant transpiration efficiency in Arabidopsis**. *Nature* 2005, **436**:866-870.

29. Reynolds M, Tuberosa R: **Translational research impacting on crop productivity in drought-prone environments**. *Current Opinion in Plant Biology* 2008, **11**:171-179.

30. Reymond M, Muller B, Leonardi A, Charcosset A, Tardieu F: **Combining quantitative trait loci analysis and an ecophysiological model to analyze the genetic variability of the responses of maize leaf growth to temperature and water deficit**. *Plant Physiology* 2003, **131**:664-675.

31. Welcker C, Boussuge B, Bencivenni C, Ribaut JM, Tardieu F: **Are
•• source and sink strengths genetically linked in maize plants subjected to water deficit? A QTL study of the responses of leaf growth and of anthesis–silking interval to water deficit**. *Journal of Experimental Botany* 2007, **58**:339-349.
A joint analysis of QTLs in a phenotyping platform and in the field, which reveals co-localisations of QTLs of sensitivity of leaf growth to water deficit and of Anthesis-Silking interval, a secondary trait closely related to yield under drought.

32. Serraj R, Kumar A, McNally KL, Slamet-Loedin I, Bruskiewich R, Mauleon R, Cairns J, Hijmans RJ: **Improvement of drought resistance in rice**. *Advances in Agronomy* 2009, **103**:41-99.

33. Rebetzke GJ, Condon AG, Richards RA, Farquhar GD: **Selection for reduced carbon isotope discrimination increases aerial biomass and grain yield of rainfed bread wheat**. *Crop Science* 2002, **42**:739-745.
•• One of the few examples of successful selection for water use efficiency (WUE) with a positive effect on yield. This was achieved by selecting for high stomatal conductance before selection for WUE.

34. Tuberosa R, Salvi S, Sanguineti MC, Landi P, Maccaferri M, Conti S: **Mapping QTLs regulating morpho-physiological traits and yield: case studies. shortcomings and perspectives in drought-stressed maize**. *Annals of Botany* 2002, **89**:941-963.
• This review summarizes the information on QTLs for drought-adaptive traits in maize. It also dwells with some fundamental aspects of QTL analysis, including aspects related to the genetic causes (i.e. pleiotropy and linkage) of the concurrent action of a QTL on two or more traits.

35. Landi P, Sanguineti M, Liu C, Li Y, Wang T, Giuliani S, Bellotti M, Salvi S, Tuberosa R: ***Root-ABA1* QTL affects root lodging, grain yield, and other agronomic traits in maize grown under well-watered and water-stressed conditions**. *Journal of Experimental Botany* 2007, **58**:319-326.

36. Bruce WB, Edmeades GO, Barker TC: **Molecular and physiological approaches to maize improvement for drought tolerance**. *Journal of Experimental Botany* 2002, **53**:13-25.

37. Campos H, Cooper A, Habben JE, Edmeades GO, Schussler JR: **Improving drought tolerance in maize: a view from industry**. *Field Crops Research* 2004, **90**:19-34.

38. Robinson D: **Resource capture by localized root proliferation: why do plants bother?** *Annals of Botany* 1996, **77**:179-185.

39. Birch CJ, Andrieu B, Fournier C, Kroesen C: **Kinetics of leaf extension in maize: parameterization for two tropically adapted cultivars planted on two dates at Gatton**. *European Journal of Agronomy* 2007, **27**:215-224.

40. Chenu K, Chapman SC, Hammer GL, McLean G, Salah HBH, Tardieu F: **Short-term responses of leaf growth rate to water deficit scale up to whole-plant and crop levels: an integrated modelling approach in maize**. *Plant Cell and Environment* 2008, **31**:378-391.

41. Parent B, Conejero G, Tardieu F: **Spatial and temporal analysis of non-steady elongation of rice leaves**. *Plant Cell and Environment* 2009, **32**:1561-1572.

42. Granier C, Massonnet C, Turc O, Muller B, Chenu K, Tardieu F: **Individual leaf development in *Arabidopsis thaliana*: a stable thermal-time-based programme**. *Annals of Botany* 2002, **89**:595-604.

43. Dosio GAA, Rey H, Lecoeur J, Izquierdo NG, Aguirrezabal LAN, Tardieu F, Turc O: **A whole-plant analysis of the dynamics of expansion of individual leaves of two sunflower hybrids**. *Journal of Experimental Botany* 2003, **54**:2541-2552.

44. Reymond M, Muller B, Tardieu F: **Dealing with the genotype × environment interaction via a modelling approach: a comparison of QTLs of maize leaf length or width with QTLs of model parameters**. *Journal of Experimental Botany* 2004, **55**:2461-2472.

45. Yin XY, Struik PC, van Eeuwijk FA, Stam P, Tang JJ: **QTL analysis and QTL-based prediction of flowering phenology in recombinant inbred lines of barley**. *Journal of Experimental Botany* 2005, **56**:967-976.

46. Betran FJ, Beck D, Banziger M, Edmeades GO: **Secondary traits in parental inbreds and hybrids under stress and non-stress environments in tropical maize**. *Field Crops Research* 2003, **83**:51-65.

47. Manschadi AM, Hammer GL, Christopher JT, deVoil P: **Genotypic variation in seedling root architectural traits and implications for drought adaptation in wheat (*Triticum aestivum* L.)**. *Plant and Soil* 2008, **303**:115-129.

48. Salvi S, Tuberosa R, Chiapparino E, Maccaferri M, Veillet S, van Beuningen L, Isaac P, Edwards K, Phillips RL: **Toward positional cloning of *Vgt1*, a QTL controlling the transition from the vegetative to the reproductive phase in maize**. *Plant Molecular Biology* 2002, **48**:601-613.

49. Yano M, Katayose Y, Ashikari M, Yamanouchi U, Monna L, Fuse T, Baba T, Yamamoto K, Umehara Y, Nagamura Y *et al.*: ***Hd1*, a major photoperiod sensitivity quantitative trait locus in rice, is closely related to the Arabidopsis flowering time gene *CONSTANS***. *Plant Cell* 2000, **12**:2473-2483.

50. Salvi S, Sponza G, Morgante M, Tomes D, Niu X, Fengler KA, Meeley R, Ananiev EV, Svitashev S, Bruggemann E *et al.*: **Conserved noncoding genomic sequences associated with a flowering-time quantitative trait locus m maize**. In *Proceedings of the National Academy of Sciences of the United States of America* 2007, **104**:11376-11381.

51. de Dorlodot S, Forster B, Pages L, Price A, Tuberosa R, Draye X: **Root system architecture: opportunities and constraints for genetic improvement of crops**. *Trends in Plant Science* 2007, **12**:474-481.

52. Venuprasad R, Dalid CO, Del Valle M, Zhao D, Espiritu M, Cruz MTS, Amante M, Kumar A, Atlin GN: **Identification and characterization of large-effect quantitative trait loci for grain yield under lowland drought stress in rice using bulk-segregant analysis**. *Theoretical and Applied Genetics* 2009, **120**:177-190.

53. Kumar R, Venuprasad R, Atlin GN: **Genetic analysis of rainfed lowland rice drought tolerance under naturally-occurring stress in eastern India: heritability and QTL effects**. *Field Crops Research* 2007, **103**:42-52.

54. Muller B, Bourdais G, Reidy B, Bencivenni C, Massonneau A, Condamine P, Rolland G, Conejero G, Rogowsky P, Tardieu F: **Association of specific expansions with growth in maize leaves is maintained under environmental, genetic, and developmental sources of variation**. *Plant Physiology* 2007, **143**:278-290.

55. Parent B, Hachez C, Redondo E, Simonneau T, Chaumont F, Tardieu F: **Drought and abscisic acid effects on aquaporin content translate into changes in hydraulic conductivity and leaf growth rate: A trans-scale approach**. *Plant Physiology* 2009, **149**:2000-2012.

56. Granier C, Tardieu F: **Multi-scale phenotyping of leaf expansion in response to environmental changes: the whole is more than the sum of parts**. *Plant, Cell & Environment* 2009, **22**:1365-1376.

57. Collins NC, Tardieu F, Tuberosa R: **Quantitative trait loci and crop performance under abiotic stress: where do we stand?** *Plant Physiology* 2008, **147**:469-486.

58. Salvi S, Tuberosa R: **Cloning QTLs in plants**. In *Genomics-Assisted Crop Improvement*. Edited by Varshney RK, Tuberosa R. **Genomics Approaches and Platforms**. Springer; 2007:207-226.

59. Chapman S, Cooper M, Podlich D, Hammer G: **Evaluating plant breeding strategies by simulating gene action and dryland environment effects**. *Agronomy Journal* 2003, **95**:99-113.

60. Passioura JB: **Simulation models: science; snake oil, education, or engineering?** *Agronomy Journal* 1996, **88**:690-694.

61. Yano M, Tuberosa R: **Genome studies and molecular genetics-from sequence to crops: genomics comes of age**. *Current Opinion in Plant Biology* 2009, **12**:103-106.

62. Sadok W, Boussuge B, Welckeir C, Tardieu F: **A modelling approach to genotype × environment interaction**. *Scale and Complexity in Plant Systems Research: Gene-Plant-Crop Relations* 2007, **21**:77-91.