Are crop and detailed physiological models equally 'mechanistic' for predicting the genetic variability of whole-plant behaviour? The nexus between mechanisms and adaptive strategies

Francois Tardieu, I.S.C. Granato, E. J. van Oosterom, Boris Parent, G. L. Hammer

To cite this version:

Francois Tardieu, I.S.C. Granato, E. J. van Oosterom, Boris Parent, G. L. Hammer. Are crop and detailed physiological models equally 'mechanistic' for predicting the genetic variability of whole-plant behaviour? The nexus between mechanisms and adaptive strategies. in silico Plants, 2020, 2 (1), pp.diaa011. 10.1093/insilicoplants/diaa011 . hal-03246970

HAL Id: hal-03246970
https://hal.inrae.fr/hal-03246970v1

Submitted on 2 Jun 2021

in silico Plants Vol. 2, No. 1, pp. 1–12
doi:10.1093/insilicoplants/diaa011
Advance Access publication 01 December 2020
Special Issue: Linking Crop/Plant Models and Genetics
Review

in silico Plants
OXFORD

Are crop and detailed physiological models equally 'mechanistic' for predicting the genetic variability of whole-plant behaviour? The nexus between mechanisms and adaptive strategies

F. Tardieu[1*], I. S. C. Granato[1], E. J. Van Oosterom[2], B. Parent[1] and G. L. Hammer[2*]

[1]INRAE LEPSE, Université de Montpellier, 2 place Viala, 34000 Montpellier, France
[2]QAAFI, University of Queensland, Brisbane, QLD 4072, Australia
*Corresponding authors' e-mail addresses: francois.tardieu@inrae.fr; g.hammer@uq.edu.au

Handling Editor: Vincent Vadez

Citation: Tardieu F, Granato ISC, Van Oosterom EJ, Parent B, Hammer GL. 2021. Are crop and detailed physiological models equally 'mechanistic' for predicting the genetic variability of whole-plant behaviour? The nexus between mechanisms and adaptive strategies. *In Silico Plants* **2021**: diaa011; doi: 10.1093/insilicoplants/diaa011

ABSTRACT

Tailoring genotypes for the variety of environmental scenarios associated with climate change requires modelling of the genetic variability of adaptation mechanisms to environmental cues. A large number of physiological mechanisms have been described and modelled, e.g. at transcript, metabolic or hormonal levels, but they remain to be assembled into whole-plant and canopy models. A 'bottom-up' approach combining physiological mechanisms leads to a near-infinite number of combinations and to an unmanageable number of parameters, so more parsimonious approaches are required. We propose that natural selection has constrained the large diversity of mechanisms into consistent strategies, in such a way that not all combinations of mechanisms are possible. These constraints, and resulting feedbacks, result in integrative 'meta-mechanisms', e.g. response curves of traits to environmental conditions, measurable via high-throughput phenotyping, and resulting in robust and stable equations with heritable genotype-dependent parameters. Examples are provided for the responses of developmental traits to temperature, for the response of growth and yield to water deficit and evaporative demand, and for the response of tillering to light and temperature. In these examples, it was inoperative to combine upstream mechanisms into whole-plant mechanisms, whereas the evolutionary constraints on the combinations of physiological mechanisms render possible the use of genotype-specific response curves at plant or canopy levels. These can be used for a new generation of crop models capable of simulating the behaviour of thousands of genotypes. This has significant consequences for plant modelling and its use in genetics and breeding.

KEYWORDS: abiotic stress; genetics; mechanisms; model; selection.

1. INTRODUCTION

Optimal use of genetic resources is required for food security in a changing climate (Tester and Langridge 2010; IPCC 2014). Appropriate methods are therefore required to predict how a given genotype would behave in the variability of climates that characterizes climate change, including the increased frequency of extreme events. Process-based crop models are potentially relevant for that (Harrison *et al.* 2014; Hammer *et al.* 2020). Combined with models describing the changes in allelic composition in breeding populations as a result of selection pressure, they have even been used to predict the result of breeding programs on yield in a range of environmental scenarios (Chapman *et al.* 2003; Messina *et al.* 2011). Nevertheless, the current use of crop models for simulating the genetic variability of yield is limited to either experimentally tested effects of a limited number of genes, such as those affecting flowering time (Bogard *et al.* 2011; Zheng *et al.* 2013) or canopy development (Chenu *et al.* 2009), or to approaches that incorporate crop models in whole-genome prediction algorithms (Messina *et al.* 2018).

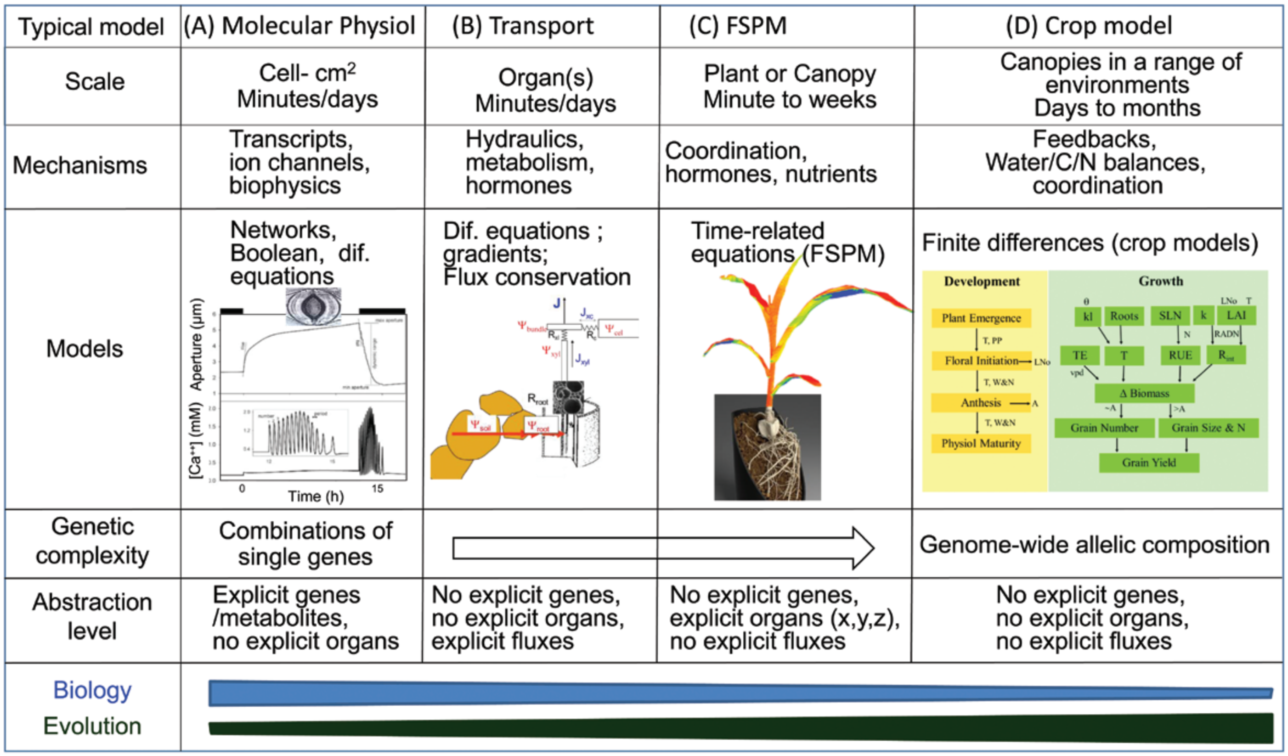
The main difficulty for the use of process-based crop models in genetics and breeding is the representation of genetic effects. In contrast to regressive models, which can statistically link yield to allelic values at genome markers and to environmental indicators (Millet *et al.* 2019; van Eeuwijk *et al.* 2019), two steps are needed in process-based models: (i) link allelic values to genotype-specific parameters of functional equations and (ii) compute yield by integration of these equations, using genotype-specific parameters together with environmental variables. However, it is not currently feasible to build mechanistic models of action of every gene on traits in different environmental conditions, together with their integrative effect on yield (Hammer *et al.* 2019b). This contradiction is the basis of controversies, in particular among the communities of plant biology, genetics and modelling. We believe that these controversies are healthy and that it is essential that crop modellers question their own models for being 'science, snake oil, education or engineering' (Passioura 1996). In particular, we address here the question of why crop models, based on simplistic concepts, allow prediction of yield in diverse conditions in spite of the enormous complexity of the combinations of physiological mechanisms that underpin adaptive traits.

2. WHICH MODELS, AT WHICH SCALES, TO REPRESENT ALLELIC EFFECTS ON PLANT TRAITS IN FLUCTUATING ENVIRONMENTAL CONDITIONS?

We do not review here regressive models, based on a statistical relationship between a final, integrative variable (e.g. yield, final biomass or accumulated transpiration) and allelic values at genome markers (van Eeuwijk *et al.* 2019). They are discussed, in comparison to process-based models, at the end of this paper.

All process-based dynamic models begin at a certain time at which initial environmental conditions are provided to the model (e.g. soil water reserve), together with the initial status of plant traits (e.g. physiological status of the apex or organ size). From this first time point onwards, the new status of traits is computed at the end of each time step (lasting typically seconds for some process models to 1 day for most crop models). This computation is based on environmental conditions during step i and the status of plant traits and cumulative environmental conditions at the end of step $i - 1$. The latter variables are computed and updated for step i and fed to the model for step $i + 1$. This process is repeated until the end of the simulation. While this general principle is common to process models at all scales, the nature of objects handled in the model, the time steps and the involved equations greatly change between four categories of models presented in Fig. 1.

- Models used in molecular physiology (Fig. 1A) take individual genes into account, each with a few allelic variants. These models have in common short time scales, typically minutes, and explicit objects, genes and metabolites (i.e. names can be given to each considered leaf, root, gene or metabolite). In the resulting equations, each term and parameter is in principle measurable but, in practice, parameters are often optimized, i.e. inferred to minimize the error on the output variable (e.g. yield, leaf number or organ shape). Except in the case of developmental models, the plant is not considered as changing in size, shape or physiological status over time. Some of these models simulate the translation and transduction phases from alleles to proteins, often as networks of genes (Bertheloot *et al.* 2020). In other models, genotypes carrying each allele are considered as qualitative variants, based on mutant analyses, for which the plant behaviour is simulated. For example, a model that relates alleles (expressed as mutations) to the oscillations of Ca^+ concentration in the symplast has been used to infer stomatal aperture (Vialet-Chabrand *et al.* 2017). Another model considers the interplay of gene action, tissue growth and mechanical processes to predict the shape of sepals or leaves (Hervieux *et al.* 2016). A development model involving several genes (FLC, FRI, FT) considers the effects of several proteins on several promoters of other genes, but results in a relatively simple behaviour (perennial, vernalizer or rapidly cycling plants) depending on the respective timings of the expression of the FLC gene and of cold episodes (Whittaker and Dean 2017).
- Transport models (Fig. 1B) consider the fluxes between the soil, several compartments in the plant and the atmosphere. Their time step is also seconds to minutes. They use differential equations that predict the fluxes based on differences in potential (water, chemical or heat potentials) and on the conservation of mass and energy (Caldeira *et al.* 2014; Meunier *et al.* 2017). The studied objects are discretized for such simulations, either by finite element methods or by considering explicit regions of organs or soil. Here, the allelic differences are represented via their effect on parameters of conductance or capacitance, established via measurements or optimization for mutants or accessions. As in the former case organs most often do not change in size, shape or physiological status with time. Whole-plant hormonal or hydraulic effects on fluxes are considered with this category of model, for instance with coupled transport of solutes, hormones and water as a function of the conditions at the system boundaries (e.g. transpiration demand, water status or temperature).
- Functional–structural plant models (FSPMs; Fig. 1C) consider whole-plant developmental changes, with explicit individual organs appearing, growing and senescing as a function of time and, usually, environmental conditions (Prusinkiewicz and Runions 2012). Their time step is often 1 day. Organs have positions in the 3-dimensional space and interact, for example causing self-shading for light or local depletions of water or nutrients in the soil (de Dorlodot *et al.* 2007; Perez *et al.* 2019). Three-dimensional representations are coupled with models of diffusion of light, water or nutrients, but frequently with less detail than in the former case. Genetic variants are considered qualitatively with accessions or mutants described *per se*, in particular they consider hormonal or solute effects via qualitative genotypic effects.
- Finally, crop models are more abstract than the above three categories (Fig. 1D). Here, organs are not explicit but represented by virtual objects such as whole-plant leaf area, root biomass or rooting depth, or by cohorts of organs such as leaves (Lacube *et al.* 2020) or ovaries (Messina *et al.* 2019). These objects change in size and physiological status over time (e.g. thermal time-driven leaf growth and senescence, or root



Typical model	(A) Molecular Physiol	(B) Transport	(C) FSPM	(D) Crop model
Scale	Cell- cm^2 Minutes/days	Organ(s) Minutes/days	Plant or Canopy Minute to weeks	Canopies in a range of environments Days to months
Mechanisms	Transcripts, ion channels, biophysics	Hydraulics, metabolism, hormones	Coordination, hormones, nutrients	Feedbacks, Water/C/N balances, coordination
Models	Networks, Boolean, dif. equations	Dif. equations ; gradients; Flux conservation	Time-related equations (FSPM)	Finite differences (crop models)
Genetic complexity	Combinations of single genes			Genome-wide allelic composition
Abstraction level	Explicit genes /metabolites, no explicit organs	No explicit genes, no explicit organs, explicit fluxes	No explicit genes, explicit organs (x,y,z), no explicit fluxes	No explicit genes, no explicit organs, no explicit fluxes
Biology Evolution				

Figure 1. Examples of models at different levels of organization. Each column displays typical models. (A) Models used in molecular physiology; (B) models of water, heat or nutrient transport; (C) functional–structural plant models (FSPMs); (D) crop models. 'Scale' denotes the objects the model applies to, the time step and the duration over which the model is run. 'Mechanisms' denote examples of principles on which equations are based. The first lines in 'models' show typical equations in each category of model, illustrated by examples. 'Genetic complexity' denotes the number of genes taken into account, from combinations of single genes in (A) to allelic composition in (D). 'Abstraction level' presents what is explicit and what is used as proxies in considered models. The last two lines illustrate the respective importance of individual mechanisms versus constrained meta-mechanisms derived from evolutionary processes. Displayed example: (A) Vialet-Chabrand *et al.* (2017), (B) Tardieu *et al.* (2015), (C) a composition of Perez *et al.* (2019) for shoots and Mairhofer *et al.* (2012) for roots, (D) Hammer *et al.* (2019a).

system characteristics). Genetic differences are represented by vectors of parameters, most often not explicitly linked to allelic values at markers (Hammer *et al.* 2010). Equations involve (i) the progress of developmental stages with thermal time, in some cases corrected for other effects such as light, water status or photothermal coefficients that consider the ratio between available light and temperature (Kim *et al.* 2010), (ii) conservation of mass, for instance with water, carbon or nitrogen balances at each time step, (iii) response curves of key processes, such as leaf growth or the progression of development stages to environmental conditions such as water, carbon or nitrogen availabilities.

3. WHICH OF THOSE MODELS ARE 'MECHANISTIC'?

Each category of model is preferred by a given scientific community (although more categories, and also intermediate categories may be identified). The biological community often considers the first category as the only one qualified as mechanistic, because it involves gene action and control mechanisms at molecular level. Communities involved in water or nutrient transfer consider that only the second category has the necessary properties for mechanistic calculations of fluxes at canopy level, whereas the FSPM community considers that characterization of 3D objects is essential for a rigorous model. Crop models are widely used by the agronomic community but often considered as empirical by other communities. However, these views are challenged by several facts:

- The four categories of models are each based on simplifications, but of different natures, and often involve parameters that are optimized. For example, the rate of RNA synthesis and degradation is often fitted and constrained based on limited measurements. Parameters are therefore associated with a similar degree of empiricism as integrative parameters fitted in a crop model. Furthermore, the first two categories of model are usually tested over short time periods, in such a way that the change in shape and physiological status of organs is not considered. While this is valid when the model is run over short time periods, it is tempting to extend conclusions to longer periods, thereby involving strong scaling assumptions.

- The number of parameters does not greatly differ in the four categories of models. It ranges from 50 to 100 in the stomatal model of Vialet-Chabrand *et al.* 2017 or in the developmental model of Hervieux *et al.* 2016, which is a similar number of parameters as in most crop models (Hammer *et al.* 2010) and FSPM (de Dorlodot *et al.* 2007; Perez *et al.* 2019). In practice, many of these parameters are fixed, so the number of parameters for representing the genetic variability is of a few tens, in all categories of models.
- The phenotypic distribution, the narrow-sense heritability and the number of quantitative trait loci (QTLs) for explaining 30 % of the genetic variance were similar for traits at different levels of integration in the diversity panel analysed in Millet *et al.* 2019 and Alvarez Prado *et al.* 2018 (Fig. 2). This was the case for a physiological trait like maximum stomatal conductance, for whole-plant leaf growth rate in optimum conditions, for a still more integrated trait such as radiation interception efficiency and for field-measured grain number (Fig. 2). Even the amount of transcripts in the same panel had similar patterns, with a normal-like distribution and a heritability similar to those in Fig. 2. This is counter-intuitive, because a reduced number of controlling genes could be expected to result in non-normal (e.g. bimodal) distributions, in a higher heritability and a lower number of stronger QTLs.

We raise the possibility that potent simplifying rules, linked to evolutionary constraints, operate at the integrated levels of whole plant and canopy, potentially rendering these levels simpler and more reproducible than the combination of underlying mechanisms captured by detailed models. In the following, we illustrate this view with three cases: (i) the response of developmental processes to temperature (Parent *et al.* 2012), (ii) the response of plant growth and grain number to water deficit (Tardieu *et al.* 2018) and (iii) the control of tillering according to carbon availability (Alam *et al.* 2014a).

3.1 First example: from diverse individual responses to temperature to a coordinated response at plant level, unique for a range of genotypes

Temperature affects processes as different as C or N metabolisms (Xu and Zhou 2006; Usadel *et al.* 2008), tissue expansion rate (Ong 1983), cell division rate (Granier *et al.* 2000), organ appearance rate (Yin and Kropff 1996), duration of phenological phases (Ravi Kumar *et al.* 2009) or flowering time (Tirfessa *et al.* 2020). Each process involves different temperature-dependent signalling pathways, enzymes activities and gene actions. The temperature response of protein abundance largely depends on the considered protein, and on whether the temperature at sampling differs from growth temperature (Fig. 3A) (Campbell *et al.* 2007). Similarly, the activities of 10 enzymes had markedly different responses to temperature in three species (Fig. 3B) (Parent *et al.* 2010). The response of transcript abundance to temperature largely varies between considered genes (Fig. 3C) (Penfield 2008). Hence, the response to temperature is extremely complex at a molecular level, with each transcript, protein or activity displaying different responses, either positive or negative, depending on the timing of temperature changes for protein abundances.

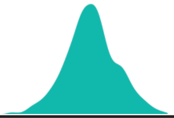
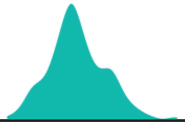
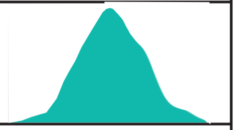
Scale	Leaf cm^2 Minutes / days	Cell- Organ Minute/days	Plant or Canopy Minute to weeks	Canopies in a range of environments Days to months
Trait	*Maximum stomatal conductance*	*Leaf growth rate*	*Radiation interception efficiency*	*Grain number*
Phenotypic distribution				
Narrow sense heritability *(proportion of variance accounted for by markers)*	0.44	0.63	0.73	0.57
QTL # for explaining 30% of gen. variance	6	5	5	6

Figure 2. Genetic characteristics of traits at four levels of integration, in a panel of 240 maize hybrids analysed in an in-door phenotyping platform and in a multisite field experiment. The distribution of trait values is shown for each trait, together with the narrow-sense heritability, i.e. the proportion of variance accounted for by 758 863 SNP markers on the genome, and with the number of QTLs that were necessary to take into account for explaining 30 % of the phenotypic variance. Maximum stomatal conductance was calculated at canopy level by inversion of the Penman Monteith equation for near-saturation light intensity (Alvarez Prado *et al.* 2018), leaf growth rate was calculated from whole-plant leaf area over time, the value displayed is that at the inflexion point (Cabrera Bosquet *et al.* 2016; Alvarez Prado *et al.* 2018), radiation interception efficiency is the ratio between incident and intercepted light, calculated with a functional structural plant model (Perez *et al.* 2019); grain number is the genotypic mean value calculated with a mixed model by Millet *et al.* (2019).

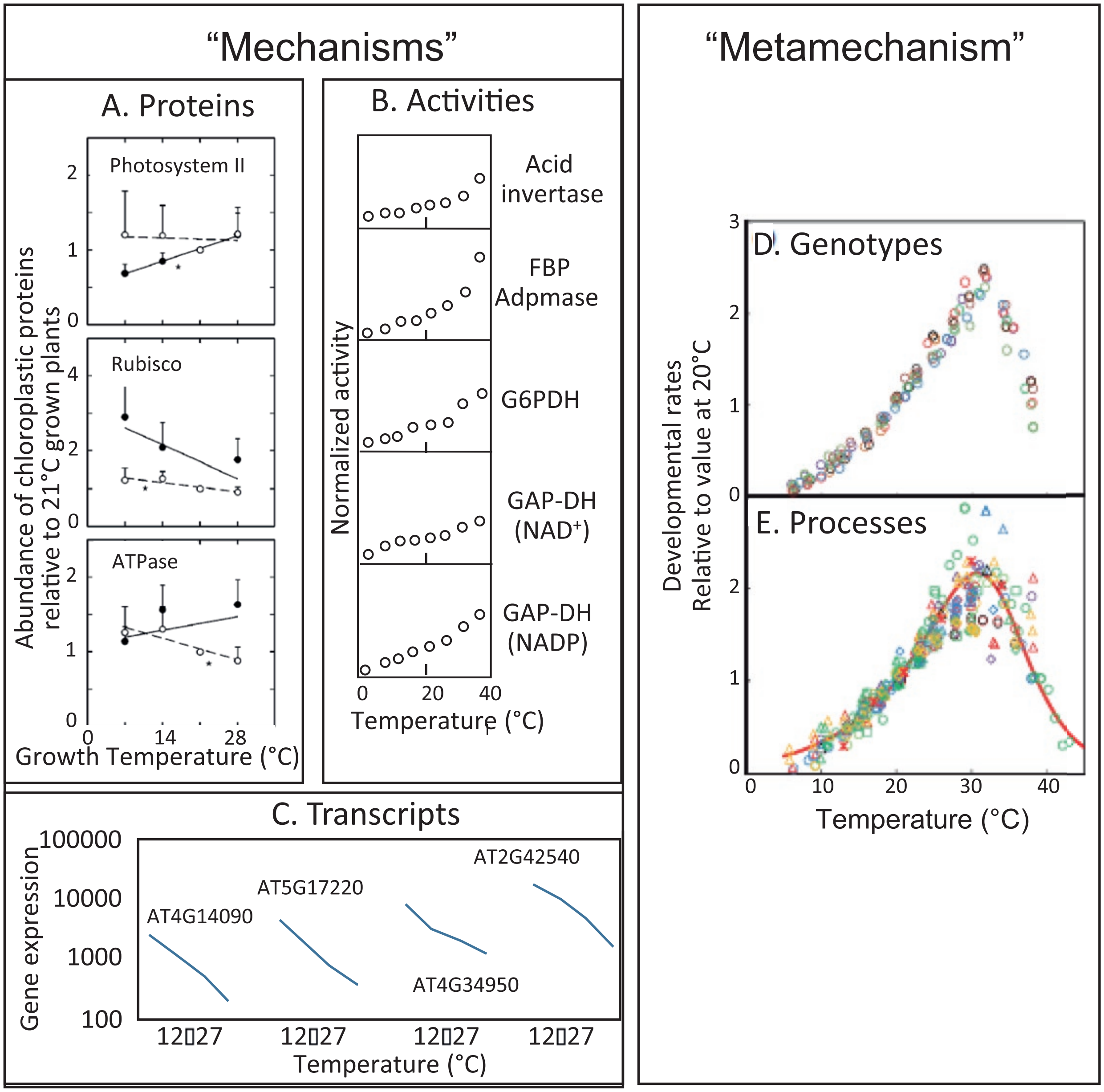


Figure 3. Complexity of temperature responses of transcripts or protein amounts, and enzyme activities (A), (B), (C), compared with the commonality of responses between genotypes (D) and between 17 developmental processes in different studies (E). (A) Amount of three proteins involved in light signalling, photosynthesis or respiration, relative to the amounts at 21 °C (Campbell *et al.* 2007), as a function of the temperature during plant growth. Black and white symbols refer to experiments in which the temperature at sampling was the same, or different, compared to the growth temperature. (B) Activities of five enzymes involved in carbon metabolism, plotted against temperature during the reaction (Parent *et al.* 2010). (C) Amount of cold-inducible gene transcripts as a function of temperature during plant growth (Penfield *et al.* 2008). (D) Response to temperature of leaf elongation rate in nine maize hybrids, with either temperate or tropical origins (Parent *et al.* 2012). (E) Response to temperature of 17 developmental rates, namely of cell division, tissue expansion, reciprocal of time to flowering or of time to germination, resulting from a meta analysis of 72 published studies (Parent *et al.* 2012). In (D) and (E), see the latter reference for the meaning of individual symbols.

The situation is simpler at an integrated level. Indeed, the temperature response of several developmental processes (e.g. cell division, tissue expansion, reciprocal of time to flowering or of time to germination; Fig. 3E) is remarkably similar, within each species, in 72 literature references if normalized by the value at a given temperature (Warrington and Kanemasu 1983; Parent and Tardieu 2012). Counter-intuitively, the integrated response is therefore simpler and more stable than underlying mechanisms. A possible explanation of this paradox is that if each process followed its own response, a plant which experiences fluctuating temperatures would display severe disorders due to a lack of coordination of the growth and development of different organs. Furthermore, plants of a given genotype growing under different temperature scenarios would differ in architecture and organ shape. This is observed in the extreme case of chilling temperatures, which results in appreciable changes in cell size, protein content, leaf thickness and the root/shoot ratio (Atkin *et al.* 2006). It is not observed in nonstressing ranges of temperature, so architectural variables and timing of development have a high heritability (reproducible values for each genotype, with large genotypic differences) in different experiments with contrasting temperature scenarios (Alvarez Prado *et al.* 2018; Millet *et al.* 2019; Lacube *et al.* 2020). This suggests that the commonality of integrated temperature responses is the result of natural selection rather than of a gene-driven coordination between temperature responses. Interestingly, the temperature responses did not differ among genotypes of either maize, rice or wheat, whereas they did differ among 17 species. It was argued (Parent *et al.* 2016) that this might also be due to selection pressure. If plant viability requires that the temperature response of several developmental processes remains coordinated, this considerably reduces the rate of evolution. In the domain of modelling, this commonality of temperature response of developmental processes is the base for the use of thermal time, considered as common to all processes and stages of development (Porter and Gawith 1999; Sánchez *et al.* 2014). This would be impossible if each process followed its own temperature response. An *argumentum ad absurdum* suggests that the wide use of thermal time would not have been possible if temperature responses clearly differed among processes.

3.2 Second example, the response to water deficit and evaporative demand, a robust and heritable meta-mechanism

Integrated plant responses to water deficit are the result of a large range of mechanisms including cell division, hydraulics, cell wall mechanics, primary and secondary metabolism and reactive oxygen species detoxification (Bray 1997; Todaka *et al.* 2017). Several hormones are involved, in particular the stress hormone ABA, but also ethylene, cytokinins, strigolactones or jasmonic acid (Huang *et al.* 2008; Tardieu 2016). A layer of molecular control involves changes in transcription factor expression and small RNA or chromatin status (Seki *et al.* 2007). Responses at transcript level involve under- or overexpressed genes, with an expression that rapidly changes with time of the day, together with light and evaporative demand. Furthermore, transcriptional changes are striking when a plant undergoes a rapid change in evaporative demand or soil water potential, whereas they are less straightforward under stable conditions (Baerenfaller *et al.* 2012). Phenotypic responses are also changing over minutes, for instance leaf elongation rate can vary from a near-zero value to its maximum genotypic value over 2 h (Caldeira *et al.* 2014). Based on these observations and as in the former paragraph, one could expect that the integrated response to water deficit is nearly unpredictable.

However, the response to water deficit becomes predictable if considered as the quantitative relationship between soil water potential, as sensed by plants, and integrative traits such as leaf growth or grain number. The responses of leaf elongation rate to soil water potential or evaporative demand are common between different experiments carried out in the field, in a greenhouse or a growth chamber, and markedly differ among genotypes (Fig. 4B) (Reymond *et al.* 2003). At the whole-plant level, the response of leaf area to soil water potential was heritable in a panel of 240 maize hybrids (Fig. 4C). At a still more integrated level, the response of grain number to soil water potential, considered in a multisite field experiment, is heritable and predictable, provided that the effects of light interception and temperature are also considered in the analysis (Fig. 4C) (Millet *et al.* 2019). In the latter study, the regressive model between allelic values and response curves also applied to genotypes that were not considered in the initial parameterization. As above, the simplicity of the integrated behaviour, compared with the complexity of individual mechanisms, could be linked to natural selection. Plant fitness and survival requires that the rapid changes in water potential and carbon status associated with diurnal and day-to-day variations of light and evaporative demand are buffered to avoid deleterious water and carbon status during hours with most severe conditions. Plants therefore need that the diversity of mechanisms of response to water deficit is constrained into consistent strategies avoiding such deleterious events. We can therefore propose that the simplicity of integrated responses in Fig. 4B is due to the fact that plants which did not constrain individual mechanisms into strategies were eliminated by natural selection during periods with severe stresses and produced no offspring.

3.3 Third example: the meta-mechanism controlling tillering in sorghum links to hormonal and plant sugar status drivers

The extent of tillering affects crop adaptation in cereals. Outgrowth and survival of tillers regulates the canopy leaf area (Klepper *et al.* 1982; Kirby *et al.* 1985; Lafarge *et al.* 2002) so that the temporal dynamics of light interception and use of available water through the life cycle are affected. Reduced tillering and canopy size are advantageous in water-limited conditions, but disadvantageous in more favourable seasons (Fig. 5; van Oosterom *et al.* 2011; Hammer *et al.* 2019a). Hence, for enhanced fitness in an evolutionary context, an ability for the plant to react to the environmental context and tune its adaptive strategy for tillering is advantageous.

Bud outgrowth is regulated by a complex gene network involving interplay among the hormones auxin, cytokinin, and strigolactone (Barbier *et al.* 2019; Bertheloot *et al.* 2020). Auxin originating from the apical bud indirectly inhibits the outgrowth of axillary buds of the same stem via cytokinins and strigolactones. Auxin represses cytokinins, which stimulate bud outgrowth, and stimulates strigolactones, which repress bud outgrowth. The behaviour of this network is also influenced by sugar signalling. Mason *et al.* (2014) showed that sugar demand of the growing apex, not auxin, is the initial regulator of apical dominance through its influence on plant sugar status in axillary buds. Further, Wang *et al.* (2020) found that the circadian clock integrates sugar signalling and regulates expression of strigolactone pathway genes to control tillering in rice. While this gene network is becoming

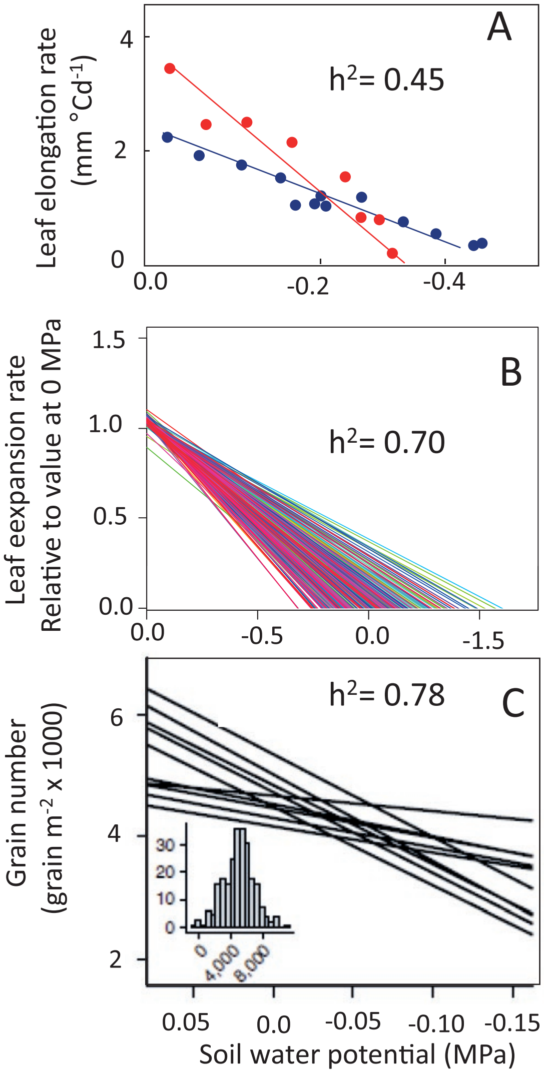


Figure 4. Response of integrated traits to soil water potential. (A) Leaf elongation rate plotted against predawn leaf water potential, a proxy of soil water status, for two genotypes (red and blue) in different experiments (Reymond *et al.* 2003), (B) whole-plant leaf expansion rate plotted against soil water potential for 240 maize hybrids, values of leaf expansion rate are normalized by their value at 0 MPa, (C) grain number plotted against soil water potential in the same panel of maize hybrids, values of soil water potential are normalized by mean values, and averaged during flowering time (Millet *et al.* 2019).

better understood qualitatively, its ability to predict tillering as a function of environmental conditions is limited, and will probably remain so in view of the amount of parameters required to model all above-mentioned interactions.

In contrast, predicting tillering at whole-plant level for diverse sets of genotypes across diverse environments has been achieved successfully using quantitative relationships between integrative traits via an index of plant sugar status and a background propensity to tiller (Alam *et al.* 2014a, 2017; Fig. 5). The expression of tillering propensity, which is under strong genetic control, was assessed by growing entries at low plant density to ensure minimal plant–plant competition and high plant sugar status. The index of plant sugar status, which responds to both genetic and environmental factors, was derived by considering assimilate supply and the extent of internal plant competition for assimilate (Kim *et al.* 2010; Alam *et al.* 2014a). Assimilate supply was related to incident radiation and plant leaf area, while demand was related to the potential rate of growth of the main shoot (Lafarge and Hammer 2002). That demand was associated with organ size and the temperature-driven rates of leaf appearance and expansion. A high assimilate supply relative to demand during a critical period favoured tillering.

Quantitative trait locus analysis from experiments with multiple sorghum populations across a range of environments (Alam *et al.* 2014b) identified 34 QTLs for tillering with half of those co-locating with QTL for component traits underlying plant sugar status (i.e. phyllochron, leaf length, leaf width) or the derived estimate of propensity to tiller (Fig. 5). Quantitative trait locus co-locating with factors affecting plant sugar status is consistent with the hypothesis that availability of assimilate beyond the requirement of existing culms regulates tillering (Bos and Neuteboom 1998; Lafarge and Hammer 2002; Kim *et al.* 2010). Quantitative trait locus for propensity to tiller co-located with genes involved with hormonal control of tiller bud outgrowth, such as the biosynthesis of strigolactones (Beveridge and Kyozuka 2010).

The simplicity of the integrated behaviour, compared with the complexity of the underlying gene networks, could again be linked to natural selection. Plant fitness and survival require that tillering best matches the environmental context to reduce the uncertainty associated with successful seed set for an annual plant. For example, there must be sufficient water available towards the end of the life cycle in dry seasons to support viable seed production. But the opportunity must be captured to be prolific in seasons when water is plentiful. Genetic control of propensity to tiller provides a background scaffold for selection to operate, but moderating this to the environmental context, via plant sugar status, provides a means to constrain this mechanism into an adaptive strategy with superior fitness. The integrated responses in Fig. 5 capture the adaptive strategy in a manner that is akin to 'modelling hormone action without modelling the hormones' (de Wit and Penning de Vries 1983).

4. FROM INDIVIDUAL MECHANISMS TO 'META-MECHANISMS' CONSTRAINED BY EVOLUTION: SIMILAR COMPLEXITIES AT DIFFERENT SCALES OF ORGANIZATION

The three cases presented above show marked similarities in spite of their different natures. Controlling mechanisms considered for simulating a canopy over months were reproducible, rigorous and heritable, as much as those controlling simpler objects such as a group of stomata or of cells over hours (Fig. 2). A first possible cause might be the limited ability of our brain to handle complex systems, thereby resulting in

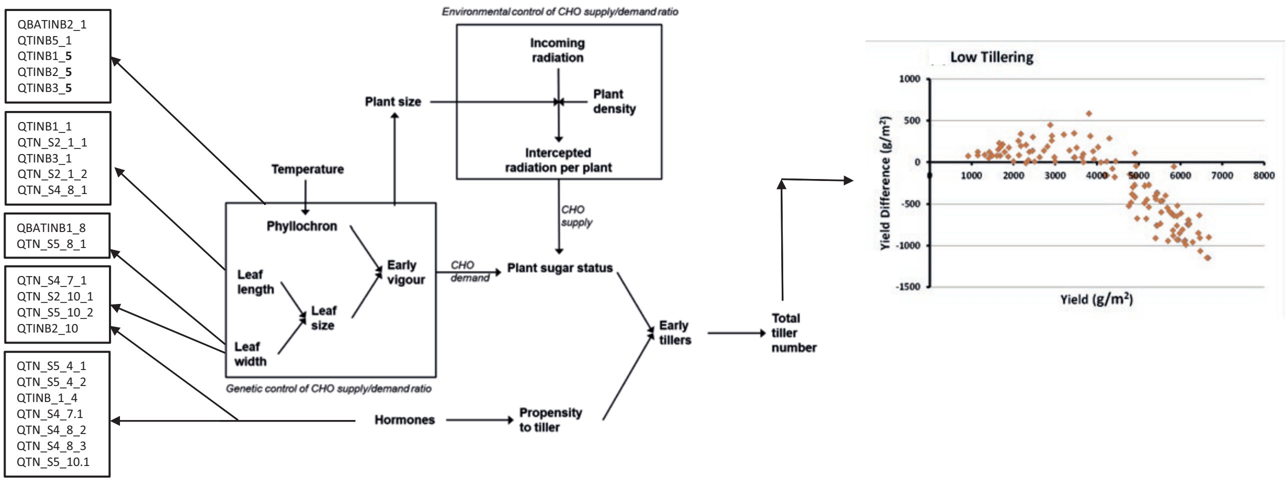


Figure 5. The interplay of environmental and genetic regulation of tillering in sorghum via internal plant competition for sugars and hormonal regulation of propensity to tiller (Alam *et al.* 2014a, 2017), the simulated consequences of reduced tillering on yield difference relative to standard tillering (Hammer *et al.* 2019a), and the association of component traits with QTL for tillering (Alam *et al.* 2014b).

a similar number of considered mechanisms and equations regardless of the real complexity of the system. However, this explanation does not easily explain the similarity in genetic architecture of either simple or integrative traits, nor the reproducibility of integrated mechanisms. We consider as more likely the possibility that, in the three cases, feedback loops and evolutionary constraints were the main cause of simplification at integrated scales.

Changes in environmental conditions affect plant growth and development at various levels of biological organization, for example from cell division to whole-plant biomass accumulation. However, natural or breeding selections operate at the organism level of organization, based on emergent phenotypes, essentially yield for agronomic species and fitness for wild species. Those traits derive from the integrated expression of genes and gene networks, of the translation into proteins, and of metabolic chains affected by protein activities, with environmental or developmental controls at each of these steps. We suggest that, whereas the interaction between individual molecular mechanisms may result in a near-infinite number of situations, integrated adaptive traits are constrained into strategies by evolution, and are largely driven by feedback loops at high levels of integration, resulting in the simpler 'meta-mechanisms' presented in the above examples (Figs 3–5). These meta-mechanisms are unique and reproducible across a range of situations and their parameters have a heritability as high as those of equations describing detailed physiological mechanisms.

The view of simpler behaviour at an integrated level was also proposed for other complex adaptive biological systems (Gell-Mann and Lloyd 1996), which use contextual information to control responses at the integrated level. In particular, Flack (2019) suggested that complexity and the multiscale structure of biological systems are the predictable outcome of evolutionary dynamics driven by the minimization of uncertainties in the face of a wide range of possible events. She argues that hierarchical organization facilitates information extraction and enables biological systems to tune their strategies at the aggregate level. While such 'meta-mechanisms' can be linked directly to phenotypic consequences for the organism, they are also linked to the underlying mechanisms and genetic architecture (Barghi *et al.* 2020).

The 'meta-mechanisms' ultimately depend on dynamic interactions and feedbacks operating among mechanisms at cell/molecular level (Tardieu and Parent 2017). They characterize the interdependence across scales of biological organization and provide the avenue for mechanistic modelling at all levels. This overcomes the complexities of working via a linear dependence across scales of biological organization from transcription, to metabolism, to cellular responses, to effects at organ scale. Tardieu *et al.* (2018) have reviewed the interdependencies of short-term mechanisms and long-term acclimation strategies resulting in varying performance under specific water-limitation scenarios. They found that avenues for improving production under drought conditions varied with the situation, as the utility of plant traits of interest was context-dependent. It was necessary to move beyond the reductionist approach of associating plant performance with the time course of one particular process. They argued that breeding for drought tolerance would benefit from an approach that optimizes the conflict between minimization of risk, similar to the general case suggested by Flack (2019), and expectation of maximum performance.

5. IN THIS CONTEXT, SHOULD ONE USE PROCESS-BASED OR REGRESSIVE MODELS?

The above paragraphs suggest that one might want to go one step further in abstraction and consider the use of regressive models, unashamedly simplistic, rather than process-based models for predicting the genetic variability of yield in a range of environmental conditions. Indeed, regressive models have shown successful predictions of genome effects on yield, based on synthetic indicators of environmental conditions and on allelic values at thousands of markers (Navarro *et al.* 2017; van Eeuwijk *et al.* 2019). For instance, Millet *et al.* (2019) proposed a model based on measured environmental conditions and on the genomic prediction of the sensitivity of plants to three environmental indicators, namely the amount of light intercepted during the vegetative phase and the mean temperature and soil water potential during flowering time. This model allowed prediction of yield for experiments and genotypes that were not taken into account for parameterizing the model.

However, regressive models also show limitations, in particular in the context of climate change. First, their validity is limited to those environmental scenarios in which they were established, whereas scenarios of climate change may present combinations of events that are not represented in current scenarios (e.g. higher concentration of CO_2 combined with higher evaporative demand and limited access to soil nitrogen). Secondly, short extreme events of high temperature and drought, which are expected to increase in frequency, cannot be easily represented by environmental indicators calculated over key phenological periods of the crop cycle. Using a crop model potentially avoids the difficult step of clustering environmental conditions over a series of sites and years in the considered target population of environments. Another potential advantage of crop models, compared with statistical models, is the possibility of exploring the multiscale phenotypic space resulting from the combination of traits (Chenu *et al.* 2009), itself resulting from allelic values. This is hardly possible in a regressive model because of the limited number of trait combinations in experimental data sets, whereas it is with a process-based crop model that considers the effect of many trait combinations via model parameters (Hammer *et al.* 2005; Messina *et al.* 2011). Indeed, it is now possible to measure genotype-dependent traits for hundreds of genotypes, from which model parameters such as transpiration efficiency, radiation use efficiency or sensitivity of growth to environmental conditions can be calculated and their genetic correlations taken into account (Tardieu *et al.* 2017; Alvarez Prado *et al.* 2018).

6. CONCLUDING REMARKS, IMPLICATIONS FOR MODELLING AND CROP IMPROVEMENT

We propose here an approach with a 'fractal' complexity, in which the mechanisms at plant or canopy level are as reproducible, rigorous and heritable as those at organ or cell level. Hence, the categories of models presented in Fig. 1 may be considered as equally mechanistic and rigorous, but differing in the degree of simplification associated with the scale of plant organization. This view implies that potent feedback loops operate at high level of integration, so natural selection or breeders have selected plants in such a way that the many mechanisms involved in the short-term responses to environmental cues underpin successful 'meta-mechanisms'. Most upstream physiological mechanisms tend to buffer rapid changes in water, nutrient and carbon status, to different extents depending on environmental scenarios, and scale up into reproducible long-term controls by which plants manage the soil water and nutrient reserves, so they can produce viable seeds. These upstream physiological mechanisms are therefore considered as jointly contributing to consistent acclimation strategies to specific environmental scenarios. The genetic architecture of parameters describing these strategies may be relevant to crop adaptation and to modelling, with the same legitimacy as mechanisms at cell or organ level, which can also be considered as simplifications in relation to still more detailed levels of organization.

Representing adaptive strategies via sets of equations at plant or canopy levels is considerably simpler than representing them by a combination of equations representing each physiological mechanism and how these mechanisms are coordinated. We propose here that this approach is also more robust, and is now made possible by the progress of high-throughput phenotyping. Indeed, each genotype can be represented by a vector of parameters calculated from direct measurements in field or in-door phenotyping platforms. Plant or crop models constructed in this way provide an avenue (i) for predicting consequences at phenotypic scale of manipulating adaptive traits and their underlying physiological mechanisms, (ii) for unravelling the complexity of genetic control of adaptive traits and linking it with that of individual mechanisms and, ultimately, (iii) for supporting advanced breeding strategies that improve breeders' abilities to handle complex trait–environment interactions.

SOURCE OF FUNDING

G.L.H. contribution was supported by Australian Research Council Centre of Excellence for Plant Success in Nature and Agriculture (CE200100015). F.T., I.S.C.G. and B.P. were supported by the EU projects FP7-244374 (DROPS) and H2020-731013 (EPPN^{2020}), the Agence Nationale de la Recherche projects ANR-10-BTBR-01 (Amaizing) and ANR-11-INBS-0012 (Phenome).

CONTRIBUTIONS BY THE AUTHORS

G.F.T. and G.L.H. wrote the paper, I.S.C.G., E.J.V.O. and B.P. provided elements and discussed the contents

ACKNOWLEDGEMENTS

The authors acknowledge John Wiley and Sons, OUP, ASPB and Springer Nature for permissions to reuse figures.

LITERATURE CITED

Alam MM, Hammer GL, van Oosterom EJ, Cruickshank AW, Hunt CH, Jordan DR. 2014a. A physiological framework to explain genetic and environmental regulation of tillering in sorghum. *The New Phytologist* **203**:155–167.

Alam MM, Mace ES, van Oosterom EJ, Cruickshank A, Hunt CH, Hammer GL, Jordan DR. 2014b. QTL analysis in multiple sorghum populations facilitates the dissection of the genetic and physiological control of tillering. *Theoretical and Applied Genetics* **127**:2253–2266.

Alam MM, van Oosterom EJ, Cruickshank A, Jordan DR, Hammer GL. 2017. Predicting tillering of diverse sorghum germplasm across environments. *Crop Science* **57**:78–87.

Alvarez Prado S, Cabrera-Bosquet L, Grau A, Coupel-Ledru A, Millet EJ, Welcker C, Tardieu F. 2018. Phenomics allows identification of genomic regions affecting maize stomatal conductance with conditional effects of water deficit and evaporative demand. *Plant, Cell & Environment* **41**:314–326.

Atkin OK, Loveys BR, Atkinson LJ, Pons TL. 2006. Phenotypic plasticity and growth temperature: understanding interspecific variability. *Journal of Experimental Botany* **57**:267–281.

Baerenfaller K, Massonnet C, Walsh S, Baginsky S, Bühlmann P, Hennig L, Hirsch-Hoffmann M, Howell KA, Kahlau S, Radziejwoski A, Russenberger D, Rutishauser D, Small I, Stekhoven D, Sulpice R, Svozil J, Wuyts N, Stitt M, Hilson P, Granier C, Gruissem W. 2012. Systems-based analysis of *Arabidopsis* leaf growth reveals adaptation to water deficit. *Molecular Systems Biology* **8**:606.

Barbier FF, Dun EA, Kerr SC, Chabikwa TG, Beveridge CA. 2019. An update on the signals controlling shoot branching. *Trends in Plant Science* **24**: 220–236.

Barghi N, Hermisson J, Schlötterer C. 2020. Polygenic adaptation: a unifying framework to understand positive selection. *Nature Reviews Genetics* **21**:769–781.

Bertheloot J, Barbier F, Boudon F, Perez-Garcia MD, Péron T, Citerne S, Dun E, Beveridge C, Godin C, Sakr S. 2020. Sugar availability suppresses the auxin-induced strigolactone pathway to promote bud outgrowth. *The New Phytologist* **225**:866–879.

Beveridge CA, Kyozuka J. 2010. New genes in the strigolactone related shoot branching pathway. *Current Opinion Plant Biology* **13**:34–39.

Bogard M, Jourdan M, Allard V, Martre P, Perretant MR, Ravel C, Heumez E, Orford S, Snape J, Griffiths S, Gaju O, Foulkes J, Le Gouis J. 2011. Anthesis date mainly explained correlations between post-anthesis leaf senescence, grain yield, and grain protein concentration in a winter wheat population segregating for flowering time QTLs. *Journal of Experimental Botany* **62**:3621–3636.

Bos HJ, Neuteboom JH. 1998. Morphological analysis of leaf and tiller number dynamics of wheat (*Triticum aestivum* L.): responses to temperature and light intensity. *Annals of Botany* **81**:131–139.

Bray EA. 1997. Plant responses to water deficit. *Trends in Plant Science* **2**:48–54.

Cabrera-Bosquet L, Fournier C, Brichet N, Welcker C, Suard B, Tardieu F. 2016. High-throughput estimation of incident light, light interception and radiation-use efficiency of thousands of plants in a phenotyping platform. *New Phytologist* **212**:269–281.

Caldeira CF, Bosio M, Parent B, Jeanguenin L, Chaumont F, Tardieu F. 2014. A hydraulic model is compatible with rapid changes in leaf elongation under fluctuating evaporative demand and soil water status. *Plant Physiology* **164**:1718–1730.

Campbell C, Atkinson L, Zaragoza-Castells J, Lundmark M, Atkin O, Hurry V. 2007. Acclimation of photosynthesis and respiration is asynchronous in response to changes in temperature regardless of plant functional group. *The New Phytologist* **176**:375–389.

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

Chenu K, Chapman SC, Tardieu F, McLean G, Welcker C, Hammer GL. 2009. Simulating the yield impacts of organ-level quantitative trait loci associated with drought response in maize: a "gene-to-phenotype" modeling approach. *Genetics* **183**:1507–1523.

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

de Wit CT, Penning de Vries FWT. 1983. Crop growth models without hormones. *Netherlands Journal of Agricultural Science* **31**:313–323.

Flack JC. 2019. Life's information hierarchy. In: Krakauer DC, ed. *Worlds hidden in plain sight: The evolving idea of complexity at the Santa Fe institute*. Santa Fe, NM: The Santa Fe Institute Press, 201–225.

Gell-Mann M, Lloyd S. 1996. Information measures, effective complexity, and total information. *Complexity* **2**:44–53.

Granier C, Inzé D, Tardieu F. 2000. Spatial distribution of cell division rate can be deduced from that of p34(cdc2) kinase activity in maize leaves grown at contrasting temperatures and soil water conditions. *Plant Physiology* **124**:1393–1402.

Hammer G, Chapman S, van Oosterom E, Podlich D. 2005. Trait physiology and crop modelling as a framework to link phenotypic complexity to underlying genetic systems. *Australian Journal of Agricultural Research* **56**:947–960.

Hammer GL, McLean G, van Oosterom E, Chapman S, Zheng BY, Wu A, Doherty A, Jordan D. 2020. Designing crops for adaptation to the drought and high-temperature risks anticipated in future climates. *Crop Science* **60**:605–621.

Hammer G, McLean G, Doherty A, van Oosterom E, Chapman S. 2019a. Sorghum crop modelling and its utility in agronomy and breeding. In: Prasad V, Ciampitti I, eds. *Sorghum: state of the art and future perspectives. Agronomy Monographs*. Madison, WI: ASA and CSSA. **58**:215–239. doi:10.2134/agronmonogr58.c10

Hammer G, Messina C, Wu A, Cooper M. 2019b. Biological reality and parsimony in crop models – why we need both in crop improvement! *In Silico Plants* **2019**:diz010; doi:10.1093/insilicoplants/diaa010.

Hammer GL, van Oosterom E, McLean G, Chapman SC, Broad I, Harland P, Muchow RC. 2010. Adapting APSIM to model the physiology and genetics of complex adaptive traits in field crops. *Journal of Experimental Botany* **61**:2185–2202.

Harrison MT, Tardieu F, Dong Z, Messina CD, Hammer GL. 2014. Characterizing drought stress and trait influence on maize yield under current and future conditions. *Global Change Biology* **20**:867–878.

Hervieux N, Dumond M, Sapala A, Routier-Kierzkowska AL, Kierzkowski D, Roeder AHK, Smith RS, Boudaoud A, Hamant O. 2016. A mechanical feedback restricts sepal growth and shape in *Arabidopsis*. *Current Biology* **26**:1019–1028.

Huang D, Wu W, Abrams SR, Cutler AJ. 2008. The relationship of drought-related gene expression in *Arabidopsis thaliana* to hormonal and environmental factors. *Journal of Experimental Botany* **59**:2991–3007.

IPCC. 2014. Summary for policymakers. In: Field CB, Barros VR, Dokken DJ, Mach KJ, Mastrandrea MD, Bilir TE, Chatterjee M, Ebi KL, Estrada YO, Genova RC, Girma B, Kissel ES, Levy AN, MacCracken S, Mastrandrea PR, White LL, eds. *Climate change 2014: impacts, adaptation, and vulnerability. Part A: global and sectoral aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge, UK and New York, NY: Cambridge University Press, 1–32.

Kim HK, van Oosterom E, Dingkuhn M, Luquet D, Hammer G. 2010. Regulation of tillering in sorghum: environmental effects. *Annals of Botany* **106**:57–67.

Kirby EJM, Appleyard M, Fellowes G. 1985. Leaf emergence and tillering in barley and wheat. *Agonomie* **5**:193–200.

Klepper B, Rickman RW, Peterson CM. 1982. Quantitative characterisation of vegetative development in small cereal grains. *Agronomy Journal* **74**:789–792.

Lacube S, Manceau L, Welcker C, Millet EJ, Gouesnard B, Palaffre C, Ribaut JM, Hammer G, Parent B, Tardieu F. 2020. Simulating the effect of flowering time on maize individual leaf area in contrasting environmental scenarios. *Journal of Experimental Botany* **71**:5577–5588.

Lafarge TA, Broad J, Hammer GL. 2002. Tillering in grain sorghum over a wide range of population densities: identification of a common hierarchy for tiller emergence, leaf area development and fertility. *Annals of Botany* **90**:87–98.

Lafarge TA, Hammer GL. 2002. Tillering in grain sorghum over a wide range of population densities: modelling dynamics of tiller fertility. *Annals of Botany* **90**:99–110.

Mairhofer S, Zappala S, Tracy SR, Sturrock C, Bennett M, Mooney SJ, Pridmore T. 2012. RooTrak: automated recovery of three-dimensional plant root architecture in soil from x-ray microcomputed tomography images using visual tracking. *Plant Physiology* **158**:561–569.

Mason MG, Ross JJ, Babst BA, Wienclaw BN, Beveridge CA. 2014. Sugar demand, not auxin, is the initial regulator of apical dominance. *Proceedings of the National Academy of Sciences of the United States of America* **111**:6092–6097.

Messina CD, Hammer GL, McLean G, Cooper M, van Oosterom EJ, Tardieu F, Chapman SC, Doherty A, Gho C. 2019. On the dynamic determinants of reproductive failure under drought in maize. *In Silico Plants* **2019**:diz003; doi:10.1093/insilicoplants/diaa003.

Messina CD, Podlich D, Dong Z, Samples M, Cooper M. 2011. Yield-trait performance landscapes: from theory to application in breeding maize for drought tolerance. *Journal of Experimental Botany* **62**:855–868.

Messina CD, Technow F, Tang T, Totir R, Gho C, Cooper M. 2018. Leveraging biological insight and environmental variation to improve phenotypic prediction: Integrating crop growth models (CGM) with whole genome prediction (WGP). *European Journal of Agronomy* **100**:151–162.

Meunier F, Couvreur V, Draye X, Zarebanadkouki M, Vanderborght J, Javaux M. 2017. Water movement through plant roots - exact solutions of the water flow equation in roots with linear or exponential piecewise hydraulic properties. *Hydrology and Earth System Sciences* **21**:6519–6540.

Millet EJ, Kruijer W, Coupel-Ledru A, Alvarez Prado S, Cabrera-Bosquet L, Lacube S, Charcosset A, Welcker C, van Eeuwijk F, Tardieu F. 2019. Genomic prediction of maize yield across European environmental conditions. *Nature Genetics* **51**:952–956.

Navarro JAR, Wilcox M, Burgueno J, Romay C, Swarts K, Trachsel S, Preciado E, Terron A, Delgado HV, Vidal V, Ortega A, Banda AE, Montiel NOG, Ortiz-Monasterio I, Vicente FS, Espinoza AG, Atlin G, Wenzl P, Hearne S, Buckler ES. 2017. A study of allelic diversity underlying flowering-time adaptation in maize landraces (vol 49, pg 476, 2017). *Nature Genetics* **49**:970-970.

Ong CK. 1983. Response to temperature in a stand of pearl millet (*Pennisetum typhoides* S.& H.). IV. Extension of individual leaves. *Journal of Experimental Botany* **34**:1731–1739.

Parent B, Tardieu F. 2012. Temperature responses of developmental processes have not been affected by breeding in different ecological areas for 17 crop species. *The New Phytologist* **194**:760–774.

Parent B, Turc O, Gibon Y, Stitt M, Tardieu F. 2010. Modelling temperature-compensated physiological rates, based on the co-ordination of responses to temperature of developmental processes. *Journal of Experimental Botany* **61**:2057–2069.

Parent B, Vile D, Violle C, Tardieu F. 2016. Towards parsimonious ecophysiological models that bridge ecology and agronomy. *The New Phytologist* **210**:380–382.

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

Penfield S. 2008. Temperature perception and signal transduction in plants. *The New Phytologist* **179**:615–628.

Perez RPA, Fournier C, Cabrera-Bosquet L, Artzet S, Pradal C, Brichet N, Chen TW, Chapuis R, Welcker C, Tardieu F. 2019. Changes in the vertical distribution of leaf area enhanced light interception efficiency in maize over generations of selection. *Plant, Cell & Environment* **42**:2105–2119.

Porter JR, Gawith M. 1999. Temperatures and the growth and development of wheat: a review. *European Journal of Agronomy* **10**:23–36.

Prusinkiewicz P, Runions A. 2012. Computational models of plant development and form. *The New Phytologist* **193**:549–569.

Ravi Kumar S, Hammer GL, Broad I, Harland P, McLean G. 2009. Modelling environmental effects on phenology and canopy development of diverse sorghum genotypes. *Field Crops Research* **111**:157–165.

Reymond M, Muller B, Leonardi A, Charcosset A, Tardieu F. 2003. 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* **131**:664–675.

Sánchez B, Rasmussen A, Porter JR. 2014. Temperatures and the growth and development of maize and rice: a review. *Global Change Biology* **20**:408–417.

Seki M, Umezawa T, Urano K, Shinozaki K. 2007. Regulatory metabolic networks in drought stress responses. *Current Opinion in Plant Biology* **10**:296–302.

Tardieu F. 2016. Too many partners in root-shoot signals. Does hydraulics qualify as the only signal that feeds back over time for reliable stomatal control? *The New Phytologist* **212**:802–804.

Tardieu F, Parent B. 2017. Predictable 'meta-mechanisms' emerge from feedbacks between transpiration and plant growth and cannot be simply deduced from short-term mechanisms. *Plant Cell and Environment* **40**:846–857.

Tardieu F, Cabrera-Bosquet L, Pridmore T, Bennett M. 2017. Plant phenomics, from sensors to knowledge. *Current Biology* **27**:R770–R783.

Tardieu F, Simonneau T, Parent B. 2015. Modelling the coordination of the controls of stomatal aperture, transpiration, leaf growth, and abscisic acid: update and extension of the Tardieu-Davies model. *Journal of Experimental Botany* **66**:2227–2237.

Tardieu F, Simonneau T, Muller B. 2018. The physiological basis of drought tolerance in crop plants : a scenario dependent probabilistic approach. *The Annual Review of Plant Biology* **69**:733–759.

Tester M, Langridge P. 2010. Breeding technologies to increase crop production in a changing world. *Science* **327**:818–822.

Tirfessa A, McLean G, Mace E, van Oosterom E, Jordan D, Hammer G. 2020. Differences in temperature response of phenological development among diverse Ethiopian sorghum genotypes are linked to racial grouping and agro-ecological adaptation. *Crop Science* **60**:977–990.

Todaka D, Zhao Y, Yoshida T, Kudo M, Kidokoro S, Mizoi J, Kodaira KS, Takebayashi Y, Kojima M, Sakakibara H, Toyooka K, Sato M, Fernie AR, Shinozaki K, Yamaguchi-Shinozaki K. 2017. Temporal and spatial changes in gene expression, metabolite accumulation and phytohormone content in rice seedlings grown under drought stress conditions. *The Plant Journal* **90**:61–78.

Usadel B, Bläsing OE, Gibon Y, Poree F, Höhne M, Günter M, Trethewey R, Kamlage B, Poorter H, Stitt M. 2008. Multilevel genomic analysis of the response of transcripts, enzyme activities and metabolites in *Arabidopsis* rosettes to a progressive decrease of temperature in the non-freezing range. *Plant, Cell & Environment* **31**:518–547.

van Eeuwijk FA, Bustos-Korts D, Millet EJ, Boer MP, Kruijer W, Thompson A, Malosetti M, Iwata H, Quiroz R, Kuppe C, Muller O, Blazakis KN, Yu K, Tardieu F, Chapman SC. 2019. Modelling strategies for assessing and increasing the effectiveness of new phenotyping techniques in plant breeding. *Plant Science* **282**:23–39.

van Oosterom EJ, Borrell AK, Deifel K, Hammer GL. 2011. Does increased leaf appearance rate enhance adaptation to postanthesis drought stress in sorghum? *Crop Science* **51**:2728–2740.

Vialet-Chabrand SRM, Matthews JSA, McAusland L, Blatt MR, Griffiths H, Lawson T. 2017. Temporal dynamics of stomatal behavior: modeling and implications for photosynthesis and water use. *Plant Physiology* **174**:603–613.

Wang F, Han T, Song Q, Yea W, Song X, Chuc J, Li J, Chen J. 2020. Rice circadian clock regulates tiller growth and panicle development through strigolactone signaling and sugar sensing. *Plant Cell* **32**:3124–3138. doi:10.1105/tpc.20.00289.

Warrington IJ, Kanemasu ET. 1983. Corn growth response to temperature and photoperiod. III. Leaf number. *Agronomy Journal* **75**:762–766.

Whittaker C, Dean C. 2017. The FLC locus: a platform for discoveries in epigenetics and adaptation. *Annual Review of Cell and Developmental Biology* **33**:555–575.

Xu ZZ, Zhou GS. 2006. Combined effects of water stress and high temperature on photosynthesis, nitrogen metabolism and lipid peroxidation of a perennial grass *Leymus chinensis*. *Planta* **224**:1080–1090.

Yin XY, Kropff MJ. 1996. The effect of temperature on leaf appearance in rice. *Annals of Botany* **77**:215–221.

Zheng B, Biddulph B, Li D, Kuchel H, Chapman S. 2013. Quantification of the effects of VRN1 and Ppd-D1 to predict spring wheat (*Triticum aestivum*) heading time across diverse environments. *Journal of Experimental Botany* **64**:3747–3761.