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

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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 (Violet-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

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 [Violet-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	<i>Maximum stomatal conductance</i>	<i>Leaf growth rate</i>	<i>Radiation interception efficiency</i>	<i>Grain number</i>
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. \(2019\)](#).

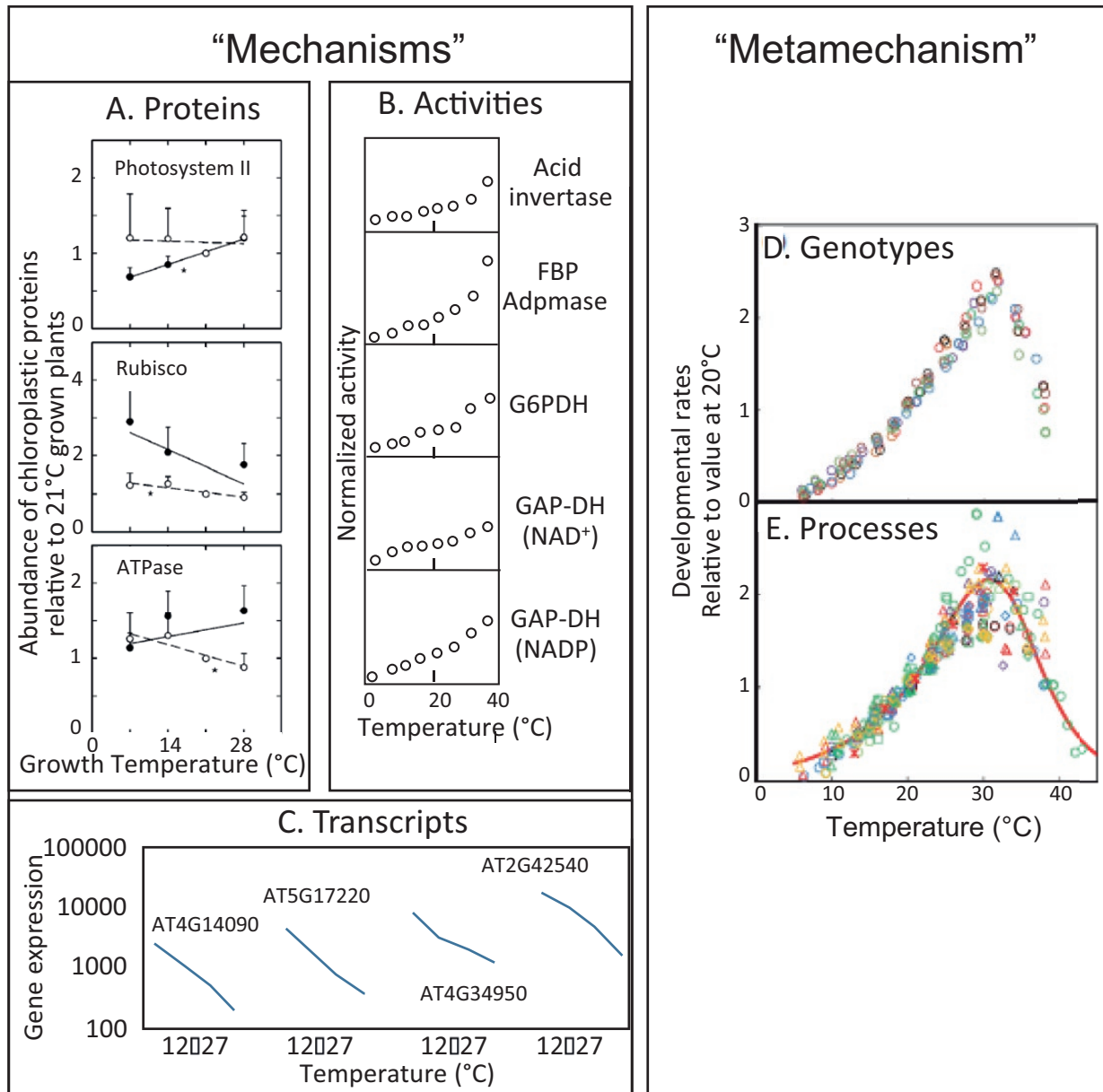


Figure 3. Complexity of temperature responses of transcripts or protein amounts, and enzyme activities (A), (B), (C), compared with the commonality of responses between genotypes (D) and between 17 developmental processes in different studies (E). (A) Amount of three proteins involved in light signalling, 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 non-stressing 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

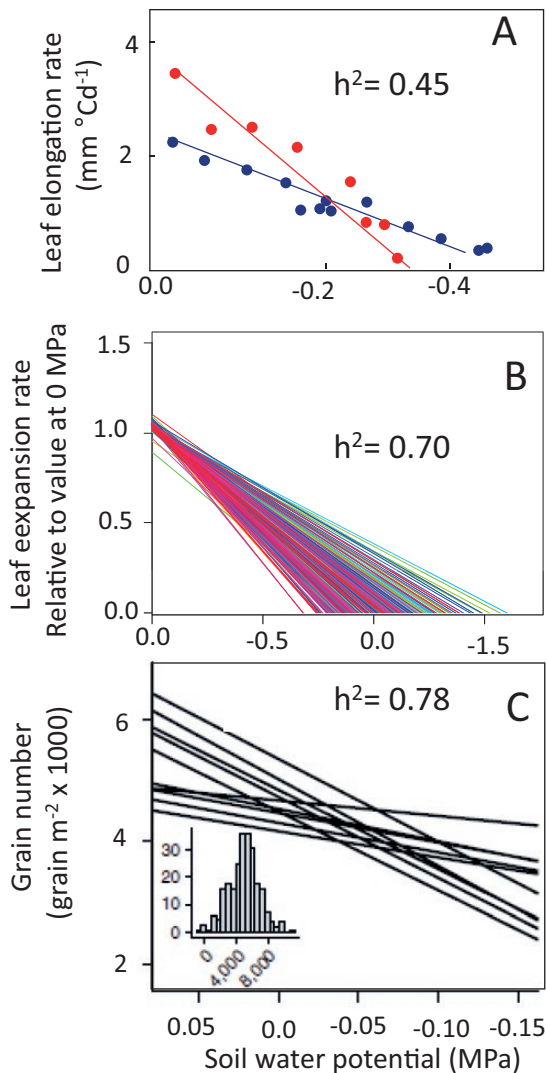


Figure 4. Response of integrated traits to soil water potential. (A) Leaf elongation rate plotted against predawn leaf water potential, a proxy of soil water status, for two genotypes (red and blue) in different experiments (Reymond *et al.* 2003), (B) whole-plant leaf expansion rate plotted against 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

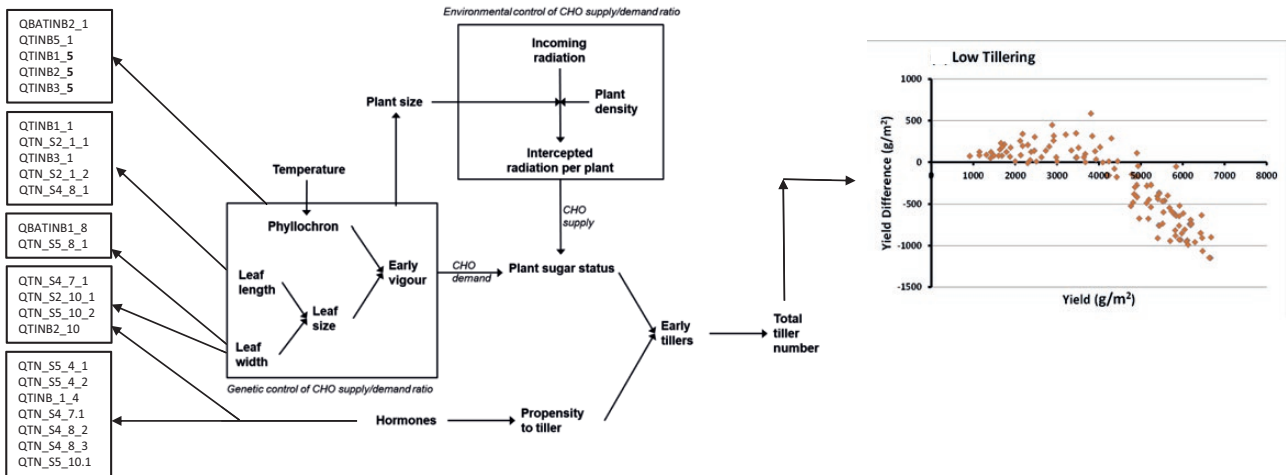


Figure 5. The interplay of environmental and genetic regulation of tillering in sorghum via internal plant competition for sugars and hormonal regulation of propensity to tiller (Alam *et al.* 2014a, 2017), the simulated consequences of reduced tillering on yield difference relative to standard tillering (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 CO₂ 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.

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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

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