

Phenotyping vs Ideotyping: Opportunities and Limitations of model-assisted crop design drawing from information on genetic diversity

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Crop improvement & climate change: Place of phenotypic plasticity

Climate change and variability (CCV) is characterized by both a steady trend leading to a global warming and an increasing frequency of extreme (drought, thermal) events (IPCC 2007). Crop performance becomes more variable and in many environments will show downward trends. Because it is forecasted that this climatic trend will keep intensifying, there is a need today to breed for varieties better adapted to future cropping conditions. This is particularly urgent in developing countries where farmers mostly have limited capacity to financially bridge a failed season or the technical means to minimize the impact of climatic events on yield through improved cultural practices (Giese *et al.* 2009). Rice, the tropics’ foremost food crop, is particularly vulnerable because of its high water demand and poor drought tolerance. Sorghum is a major food crop in drought prone environments and has great potential for crop improvement for food, feed and bio-fuel production (“FFF”). These two cereals are thus of particular interest for developing new plant designs for changing environments and uses.

Marker assisted selection (MAS) will strongly contribute to and accelerate improvement of rice and sorghum because both are fully sequenced model plants and possess a great genetic diversity which is crucial to rapid progress in breeding (Cooper *et al.* 2002). To face CCV, genotypes are needed that combine high yield potential, tolerance to warmer and drier conditions and adaptive traits to tolerate highly variable environments. Inducible adaptive traits are expected to provide the plant with phenotypic plasticity that helps maintaining performance under fluctuating conditions. While breeders designed varieties with reduced phenotypic plasticity as a way to achieve an optimal plant type for favorable conditions to maximize potential productivity and fertilizer response during the green revolution, it is obvious today that this strategy is not adapted to meet forthcoming climatic challenges (Dingkuhn *et al.* 2005). Phenotypic plasticity draws from the plant’s inherent capacity to dynamically regulate its morphogenesis based on compensatory source-sink processes and to optimize its productivity under fluctuating conditions (Nicotra *et al.* 2010). Combining high yield potential with adaptive behavior to face CCV, constitutive and inducible traits need to be further combined, implying an

increase of potential Genotype X Environment interactions GxE. Care must be taken to minimize trade-offs, potentially involving 'counter-productive' plasticity through negative feedback on yield (Nicotra *et al.* 2010). Trade-offs exist not only between adaptation and yield but also among multiple yield objectives, e.g., sweet sorghum producing for 'FFF' (Gutjahr *et al.* 2010).

Plant modeling to support phenotyping and ideotyping: state of the art

Genetic analysis and breeding for complex traits such as grain yield, biomass or sugar needs to address component traits that impact on the phenotypic expression of the complex trait in a given set of environments. Component traits are expected to be genetically and physiologically simpler but their measurement must take into account GxE. Phenotyping of panels of cultivars or lines is thus extremely sensitive to the choice of environmental conditions. Molecular markers can then be derived from association mapping (providing QTLs) and can be directly used for selection, provided that probability of phenotypic expression is high. This is where the main hurdles reside: effective expression in different genetic backgrounds and different environments needs to be ascertained beforehand and requires (i) a sufficiently large and diverse panel ensuring recurrence of useful alleles in different backgrounds, and (ii) phenotyping methodology and environments expressing the useful loci/alleles. During the last decade plant physiology and modeling demonstrated their relevance in supporting the stepwise, upstream processes of molecular breeding:

i) Support for phenotyping: Plant physiology is increasingly providing applied tools for phenotyping down to the molecular scale (eg. transcriptomics: Takahashi *et al.* 2005). But still, association genetics mostly use rather crude (but economical) phenotyping tools. Behavioral, plasticity traits, conditional to environment, cannot be captured this way. Identifying their genetic basis requires pairs of environments that make such traits observable, and models that help extract the underlying reaction norm. A model formalizing the response of a simple biological process (output variable) to external variable(s) can be used to separate the G (genotypic parameters) from the E (input variables) effects (Yin *et al.* 1999). By fitting the model, G parameters can be quantified heuristically and can be considered traits in the genetic analysis. Reymond *et al.* (2003) used a simple model of maize leaf expansion rate (LER) response to soil water deficit, leaf to air vapor pressure deficit and temperature to analyze the GxE in different temperate environments. QTLs detected for model parameters were genotype specific and stable across environments; they were also confirmed in another genetic (tropical) background (Welcker *et al.* 2007). Here, QTLxE interactions were overcome by modeling that causing QTL instability if detected with directly measured. Further progress is under way in this field, eg. using architectural modeling in conjunction with image analysis, or functional-structural plant model to extract parameters of compensatory growth (Luquet *et al.* 2010).

ii) *Support for ideotyping*: The added value of elemental traits and related QTLs for breeding cannot be estimated without considering their impact on the performance of the whole plant system in a population context. This requires crop models having sufficient detail of both varietal traits and environment (including management), as well as interactions among them. The challenge is to capture the interactions realistically to account for GxE (Hammer *et al.* 2010). If adaptation to CCV is the objective, the GxE simulations must be sufficiently accurate to allow extrapolation of ideotype performance to hypothetical scenarios. By introducing the LER model of Reymond *et al.* (2003) into the APSIM crop model (Chenu *et al.* 2009), the effect of LER related QTLs on grain yield was simulated for different genotypes and drought environments, opening the door for *in silico* design of plant ideotypes. This study is probably the first real proof of concept for ideotype simulation using crop models driven by genetic parameters. Doing this for traits constituting phenotypic plasticity, however, requires models with greater physiological detail.

Can plant modeling help molecular breeding in dealing with the genetic and physiological architecture of complex traits?

An important obstacle to molecular breeding are the genetic and/or physiological linkage among traits making difficult the study of a trait without another (W. ter Steege *et al.* 2005). Many traits are not what they appear to be because there are an indirect result of other processes. Models can help explain emergent properties of the plant system difficult to apprehend experimentally (Génard *et al.* 2010). Welcker *et al.* (2007) reported that some QTLs controlling maize LER (Reymond *et al.* 2003) also control silk expansion rate, and thus ASI (Anthesis to Silking Interval), with similar allelic effects. Chenu *et al.* (2009) included into APSIM the pleiotropic effect of these QTLs on both LER and ASI. Simulation experiments showed a positive impact of QTL accelerating LER on yield under well watered conditions. Considering the pleiotropic QTL effects on LER and ASI strongly affected yield, highlighting the potential errors committed in ideotyping when the genetic architecture and physiological trade-offs of a complex trait are not accounted for. The elemental traits considered here (LER, ASI) are physiologically weakly linked as they impact on yield at different developmental stages. Complexity increases dealing with more interacting traits (Hammer *et al.* 2010), for example, that regulating plant morphogenesis (plasticity) vs. drought responses.

Plants develop according to a specific construction plan that is implemented as an orchestrated phenological process that can be more or less rigid or plastic. Besides the responses of the organogenetic process itself to stresses, it determines in a constitutive way resource use and thus, the probability and intensity of stress occurrence such as drought. It involves several traits related to the activity of the meristems having dynamic physiological feedbacks and compensations among them (Granier and Tardieu 2009): e.g., organ initiation rate, organ expansion rate and potential size, tillering, and geometric traits

such as leaf or root angle. The result is a dynamic system of assimilate sources and sinks that continuously adjusts its internal equilibrium as environment changes, buffered by transitory reserve pools. It involves physiological signaling because adjustment of organ size requires adjustment in cell number, determined by meristem activity. Tisné *et al.* (2008), on *A. thaliana*, and W. ter Steege *et al.* (2005) (on wheat) provided some first results on the genetic links between plant leaf number and leaf epidermal cell area and number. These findings indicate that the physiological linkages among morphological traits at different organizational levels (cell to plant) are subject to genetic control and not only physiological interaction. This in turn has consequences for the way traits constituting morphological plasticity can be phenotyped and modeled (Granier and Tardieu 2009). Can such traits be phenotyped separately or is a systemic approach essential?

Genetically controlled response norms thus interact with environment to generate adaptive, phenotypic plasticity. This is the concept behind the crop model *Ecomeristem* (Luquet *et al.* 2010a). It simulates plant morphogenesis in a population context at organ level, with GxE interactions through C source feedback on sinks and development processes (supply/demand). Feedbacks are tuned by G parameters. Luquet *et al.* (2010a; 2010b) used *Ecomeristem* to explore the impact of genotypic development rate (DR) on the early vigor of rice. Physiological feedbacks between DR, tillering ability, leaf size, expansion, senescence and non structural C storage were demonstrated under optimal and drought conditions, and their regulation seen as an expression of different adaptation strategies. Greenhouse observations on a panel of 200 japonica rices identified trait associations predicted by the model. Model parameters that control the elemental traits of vigor were estimated for each genotype of the panel. Genetic association mapping of genotypic parameter values will evaluate the appropriateness of using *Ecomeristem* for phenotyping of complex traits, the hypothesis being that structural-functional architecture will provide keys to the architecture of genetic control. If confirmed, the approach will allow designing ideotypes with greater confidence using models.

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