

Functional Whole Plant Modelling – The Missing Link between Molecular Biology and Crop Improvement?

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Abstract

Recent progress in molecular technologies for genome sequencing and functional genomics has not yet contributed significantly to practical crop improvement associated with key complex traits, such as water productivity. This is largely because whole plant phenotypic responses associated with complex traits do not scale directly from the level of molecular action. The complexities of interactions within the plant and of the plant with its environment confound application of molecular scale knowledge. Here, we argue that functional whole plant modelling has a critical role to play as a linking technology between phenotypic and molecular approaches to plant breeding and crop improvement. Plant models, which are simplified mathematical representations of the interacting biological and environmental components of the dynamic plant/crop system, offer potential for understanding and predicting gene-to-phenotype relationships for complex traits. However, existing descriptive agronomic models do not contain the degree of biological functional detail required. A greater emphasis on explanatory approaches via understanding the dynamics of underpinning crop growth and development processes is required. Such functional whole plant models can be used to predict trajectories of organism status throughout the crop cycle as emergent consequences of genetic (G), management (M) and environmental (E) influences. This will provide the basis to –

- dissect the functional physiology underpinning genetic variation in key adaptive traits,
- identify genomic regions in a way that reduces environment and genotype context dependencies, and
- predict crop growth and yield consequences in a manner that incorporates G*M*E effects.

A generic framework is being developed for these purposes in cereal crops. Examples of its use in linking molecular and plant scales to support crop improvement are presented.

Key Words

Genotype-to-phenotype, trait physiology, QTL, functional genomics, water productivity

Introduction

Progress in crop improvement is limited by the ability to identify favourable combinations of genotypes (G) and management practices (M) in the relevant target environments (E) given the resources available to search among possible combinations. Phenotypic performance of the array of possible combinations forms what can be viewed as an adaptation or fitness landscape (Cooper and Hammer, 1996). Crop improvement then becomes a search strategy on that complex G*M*E landscape. However, currently we cannot reliably predict (and navigate to) the desired destination on the adaptation landscape. We require prediction of phenotype based on genotype to underpin yield advance. In plant breeding, traditional empirical methods have involved measuring phenotypic performance of large segregating populations in multi-environment trials and applying rigorous statistical procedures based on quantitative genetic theory to identify superior individuals. This phenotypic selection approach has been successful for a number of crops, but cost per unit yield gain has risen substantially, interactions with management are not integrated, and genotype-by-environment interactions confound selection.

With recent progress in molecular technologies for genome sequencing and functional genomics, it has been widely expected that a gene-by-gene engineering approach would enable enhanced efficiency in

crop improvement. Indeed, there have been successes in developing plants that better resist pests or tolerate herbicides. Those cases involved single-gene transformations where plant phenotypic response scaled directly from the level of molecular action. However, little of this promise has been realised for key complex traits where relationships among components and their genetic controls involve quantitative multi-gene interactions. Integrating gene effects across scales of biological organisation in such situations is not straightforward. Complexities associated with gene interactions, mediated via transcriptional and post-transcriptional regulation, or distributed control of fluxes in plant metabolic pathways are major impediments to scaling from gene network to phenotype, so that phenotypic prediction based on a gene-by-gene approach remains elusive (Hammer et al., 2006; Benfey and Mitchell-Olds, 2008).

Developments in molecular technologies have nonetheless allowed the focus of practical crop improvement to shift from the level of the individual (genotype) to the level of genomic region (quantitative trait locus - QTL) (Hammer and Jordan, 2007). The ability to inexpensively and densely map genomes has facilitated development of molecular breeding strategies. However, their applicability to complex traits is limited by context-dependent gene effects attributed to gene-gene and gene-environment interactions, which restrict predictive power of associations of genes/genomic regions with phenotypic responses. Despite this limitation, Cooper et al. (2005) found that even though many of the context-dependent effects of genetic variation on phenotypic variation can reduce the rate of genetic progress from breeding, it is possible to design molecular breeding strategies for complex traits that on average will outperform phenotypic selection. But this would require gene-to-phenotype (G-to-P) models of the traits that were able to account for the context-dependent effects.

In this paper we overview approaches to G-to-P prediction and discuss how functional whole plant modelling can provide an effective link between molecular and organism scales to enhance crop improvement.

G-to-P Prediction and Context Dependencies

There is a range of approaches for G-to-P prediction for complex traits that can be somewhat simplistically represented in relation to broad levels of biological organisation (Fig. 1). Gene network models have potential to account for gene context dependencies but require advanced knowledge of network structure and dynamics. Model species (e.g. *Arabidopsis*) provide opportunities to capture such knowledge. However, the issue of scaling from network to whole plant phenotypic response remains, unless direct associations exist, as for example with transition to flowering (van Oosterom et al., 2006). Functional whole plant models have potential to account for environment context dependencies as they attempt to encapsulate the dynamic plant-environment interactions (Tardieu, 2003; Reymond et al., 2003; Chenu et al., 2008; Yin and Struik, 2008). It is plausible to link the vector of coefficients defining the plant model to genomic regions, but the issue of scaling from coefficient to gene level is problematic.

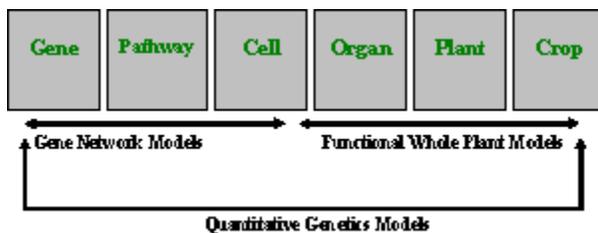


Figure 1. Approaches to G-to-P prediction and their association with level of biological organisation.

Functional Whole Plant Modelling

Plant/crop models have been used extensively to facilitate decision making by crop managers, and to aid in education, but Hammer et al. (2002) suggested that greater explanatory power was required for their effective application in understanding and advancing the genetic regulation of plant performance and

plant improvement. Agronomic models contain a mix of descriptive and explanatory approaches that suffices for their application in decision/discussion support for crop management. Adequate prediction of resource use, crop growth and yield can be obtained with algorithms that describe aspects of crop growth, such as plant leaf area as a function of thermal time or plant leaf size distribution. The coefficients of these algorithms can be mapped to genomic regions, but this is unlikely to diminish any context dependencies, i.e. the coefficients will retain the context dependencies of the phenotypic variable they describe.

A physiological framework that facilitates further dissection and modelling of traits provides an avenue to overcome this problem. By enhancing the explanatory power of the modelling approach while not introducing undue complexity, it is possible to have phenotypic attributes as emergent properties of the model dynamics. This approach holds considerable promise for effective linking of genotype to phenotype and, hence molecular biology with crop improvement (specific examples are outlined in the next section). Recent developments (see McLean et al., 2008, these proceedings) within the APSIM modelling platform (Keating et al., 2003; Wang et al., 2002) have focussed on structuring a generic cereal template to better accommodate the hierarchy of physiological determinants of crop growth and development needed for this more explanatory approach to plant modelling.

Whole Plant Modelling as the Missing Link

Robust explanatory plant models have the potential to underpin G-to-P prediction by linking their coefficients with the genomic regions known to be associated with complex traits. However, to be effective the linkage to model coefficients must reduce (or remove) the environmental and genetic context dependencies related to the phenotypic trait(s) that they generate. Two specific examples highlight the possibilities -

Leaf area development in maize

The seasonal pattern of leaf area development is critical to resource (e.g. light, water) capture, and hence to crop growth and timing of stress. Studies at organ level (Reymond et al., 2003; Tardieu et al., 2005) on leaf expansion rate (LER) have found that stable QTLs could be identified for responses of LER to temperature, vapour pressure deficit and water status, whereas QTLs for leaf area were dependent on the growing environment. Hence, by moving to the level of LER, environment context dependencies were removed. By enhancing the APSIM cereal template to operate at this level, Chenu et al. (2008, these proceedings) were able to quantify impact at the crop level of QTLs involved in leaf expansion for a range of drought and climate scenarios.

Transition to flowering in sorghum

The gene network controlling photoperiodic response of floral initiation has been studied intensively and is becoming well understood. Based on published work on gene expression dynamics for Arabidopsis and rice, van Oosterom et al. (2006) developed a simplified gene network model that mimicked the effects of allelic variants of key genes on the phenology of both long- and short-day crops under a range of daylength. Although incorporation of this network into the APSIM-sorghum crop growth simulation model required a number of assumptions to complement current knowledge gaps, the combined model was used to simulate grain yield of two allelic variants of sorghum for a number of environments at Dalby, Qld. The model was able to generate genotype-by-environment interactions for grain yield as a direct consequence of dynamic interactions between allelic variants and environmental conditions. That is gene and environment context dependencies were removed.

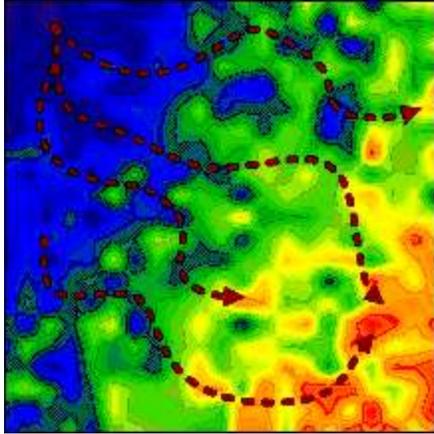


Figure 2. Breeding trajectories on the adaptation landscape associated with the simulation study for sorghum reported by Chapman et al. (2003) (after Hammer et al., 2006).

In both of these cases, incorporating explanatory sub-models into the quantitative crop model provided a basis to link changes at genomic regions directly to their emergent phenotypic consequences at the crop level in a way that reduced context dependencies. Such an approach provides a pathway to effective applications in molecular breeding (Cooper et al., 2005). The functional whole plant models can be used to explore breeding strategies by generating the adaptation landscape of possible G*M*E combinations on which breeding system simulation tools can map the trajectories resulting from specific breeding approaches (Figure 2) (Cooper et al., 2002; Chapman et al., 2003; Hammer et al., 2005; Messina et al., 2007). In this way, functional plant modelling can provide the missing link between molecular knowledge and the practice of crop improvement.

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