Chapter 7
Molecular Breeding for Complex Adaptive Traits: How Integrating Crop Ecophysiology and Modelling Can Enhance Efficiency

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Abstract Progress in crop improvement is limited by the ability to identify favourable combinations of genotypes (G) and management practices (M) in relevant target environments (E) given the resources available to search among the myriad of possible combinations. To underpin yield advance we require prediction of phenotype based on genotype. In plant breeding, traditional phenotypic selection 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. Recent developments in the ability to inexpensively and densely map/sequence genomes have facilitated a shift from the level of the individual (genotype) to the level of the genomic region. Molecular breeding strategies using genome wide prediction and genomic selection approaches have developed rapidly. However, their applicability to complex traits remains constrained by gene-gene and gene-environment interactions, which restrict the predictive power of associations of genomic regions with phenotypic responses. Here it is argued that crop ecophysiology and functional whole plant modelling can provide an effective link between molecular and organism scales and enhance molecular breeding by adding value to genetic prediction approaches. A physiological

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framework that facilitates dissection and modelling of complex traits can inform phenotyping methods for marker/gene detection and underpin prediction of likely phenotypic consequences of trait and genetic variation in target environments. This approach holds considerable promise for more effectively linking genotype to phenotype for complex adaptive traits. Specific examples focused on drought adaptation are presented to highlight the concepts.

Keywords Genotype-to-phenotype • Phenotypic prediction • Trait physiology • QTL • Functional genomics • Crop improvement

7.1 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 the myriad of 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 have difficulty reliably predicting (and navigating 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 traditional phenotypic selection approach has been, and remains, 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 had 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. This could be described as a short ‘phenotypic distance’ (Fig. 7.1). 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).

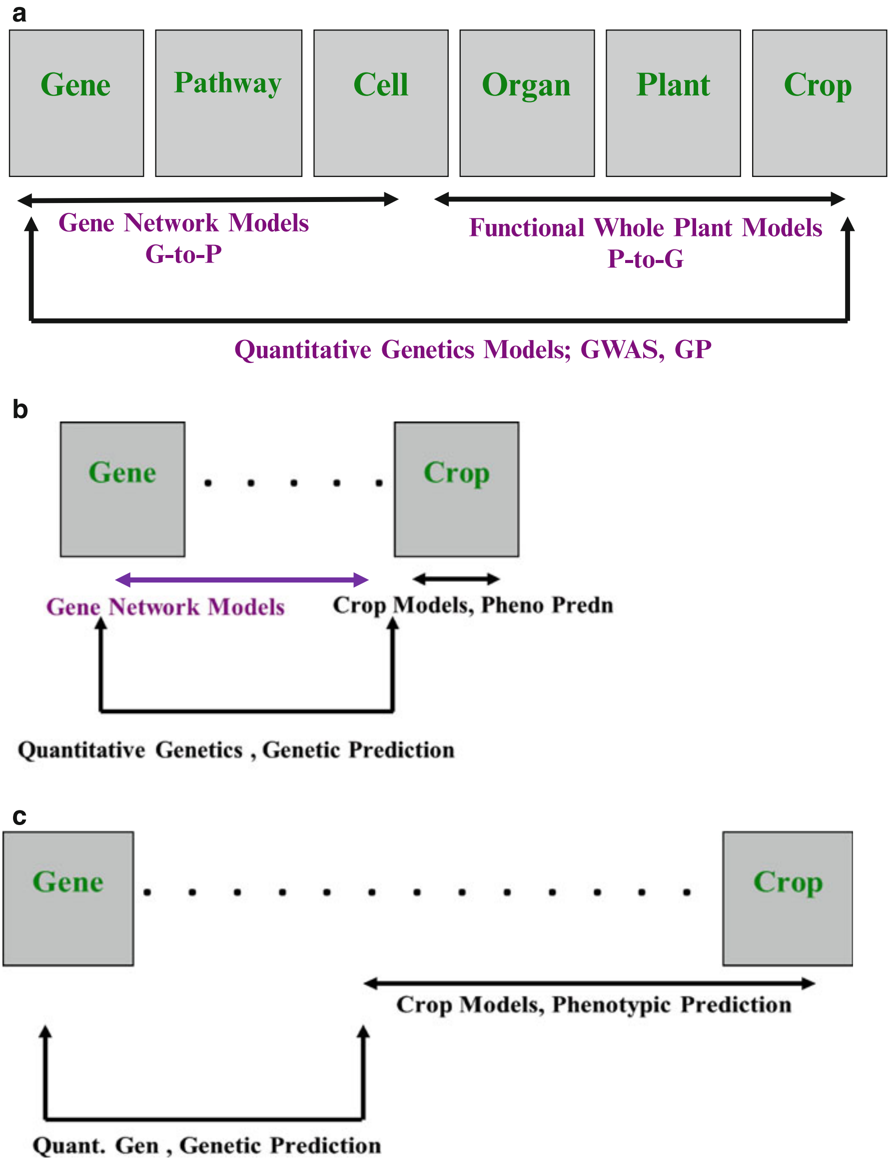

Fig. 7.1 (**a**) Approaches to G-to-P prediction, their association with levels of biological organisation, and the concepts of (b) 'short' and (c) 'long' phenotypic distance for traits that do, or do not, scale readily from molecular to whole organism scale. (**b**) Short phenotypic distance where traits scale directly from molecular to organism scale and there is a likely greater role for genetic prediction and gene network models. (**c**) Long phenotypic distance where traits do not scale readily from molecular to whole organism level and there is likely a greater role for ecophysiology and crop models

Developments in molecular genetic 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 (e.g., quantitative trait locus – *QTL*) (Hammer and Jordan 2007). The ability to inexpensively and densely map genomes has facilitated development of molecular breeding strategies (Cooper et al. 2005, 2009). However, their applicability to complex traits remains constrained 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. There is a long 'phenotypic distance' due to the extent of the biological integration required from the causal polymorphisms at genome scale to the phenotype of interest (e.g., Sinclair et al. 2004) (Fig. 7.1). 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. Continuing advances in genotyping and crop genomics (Heffner et al. 2009; Morrell et al. 2012; Morris et al. 2012) have now facilitated association mapping approaches that assess correlation of phenotype with genotype in populations or panels of unrelated individuals. Such genome wide association studies rely on advanced statistical procedures to identify associations between a phenotype and a genomic marker profile. Genomic selection involves the use of phenotypic prediction equations based on profiles of marker data from a training set of genotypes, which have been phenotyped. The predictions are then applied across breeding materials that are genotyped extensively but not phenotyped. This offers considerable potential for more rapid genetic gain in breeding. However, for complex traits, the procedure still suffers from context-dependent effects and the 'phenotypic distance' problem (Fig. 7.1). Association mapping and genomic selection rely on the stability of the relationship between a phenotype and the set of genomic markers found in the training set, which is strongly dependent on the relevance of the genotypes and environments sampled.

Here we consider concepts associated with genotype-to-phenotype (G-to-P) modelling and how whole plant/crop ecophysiology and functional whole plant modelling can provide an effective link between molecular and organism scales to enhance efficiency of molecular breeding and crop improvement. There are two main avenues highlighted. Firstly, we describe how to enhance phenotyping strategies by using ecophysiological insight derived from dynamic crop growth and development modelling. This involves dissecting complex traits to more robust targets by reducing 'phenotypic distance' and context dependencies. Secondly, we show how to use crop growth and development models for trait evaluation and phenotypic prediction. This requires robust dynamic crop growth and development models that can predict consequences of context-dependent genotype and environment effects in target production regions.

7.2 Genotype-to-Phenotype (G-to-P) Modelling

There is a range of approaches for G-to-P modelling for complex traits that can be somewhat simplistically represented in relation to broad levels of biological organisation (Fig. 7.1). Gene network models that account for gene expression dynamics and metabolic pathway interactions have potential to account for gene context dependencies but require advanced knowledge of network structure and dynamics (see Chap. 1 of this book by Baldazzi et al.). 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 where the network is well characterised and scaling is direct (van Oosterom et al. 2006; Salazar et al. 2009; Dong et al. 2012). Network models involving enzyme kinetics have also been developed for exploring aspects of starch synthesis as a means to focus efforts aimed at manipulating starch structure and functionality (Wu et al. 2013).

Functional whole plant models have potential to account for environment context dependencies as they attempt to encapsulate dynamic plant-environment interactions based on physiological understanding (Tardieu 2003; Reymond et al. 2003; Chenu et al. 2008; Yin and Struik 2008; Hammer et al. 2005, 2010). It is plausible to link the vector of coefficients defining the plant characteristics to genomic regions, but the issue of scaling from coefficient to gene level remains problematic. There are some examples where the 'metaprocesses' of ecophysiology, such as the ubiquitous canopy radiation use efficiency (RUE) (Sinclair and Muchow 1998), have been dissected to their physiological or metabolic underpinning processes, firstly via canopy photosynthesis models that are driven by photosynthesis-light response curves and canopy structure (Hammer and Wright 1994; de Pury and Farquhar 1997), and more recently by direct linkage of those models to biochemical pathway models for photosynthesis (Gu et al. 2014). Hence, as knowledge advances, there are opportunities for gene network and metabolic pathway models to interface with crop ecophysiological models and advance dynamic modelling capability to account for genetic and environmental context dependencies in G-to-P prediction.

7.3 Whole Plant Ecophysiology and 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. This is now even more prescient in the genomics era. Agronomic models contain a mix of descriptive and explanatory approaches that suffice 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/genetics with crop improvement. Recent developments within the APSIM modelling platform (Hammer et al. 2010) have focused 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. They detail a case of the stay-green phenotype in sorghum (i.e., extended retention of green leaf area during grain filling), which was generated as an emergent consequence of canopy nitrogen (N) dynamics associated with genetic differences in dwarfing. Taller genotypes grew more and required more N for structural stem tissue, leaving less available for leaves, which was more rapidly diminished by translocation to grain during grain-filling (Fig. 7.2). Hence, stay-green was generated as an emergent consequence in the shorter genotypes in response to genetic differences in plant height.

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. For example, 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) in maize have found that stable QTLs could be identified for responses of LER to temperature, vapour pressure deficit and plant 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. Some of the genomic regions associated with LER were also associated with silk extension and grain set in maize (Welcker et al. 2007). By enhancing the APSIM cereal template to operate at this level and incorporate genomic associations on LER and grain set, Chenu et al. (2009) were able to quantify impact at the crop yield level of the QTLs involved for a range of drought and climate scenarios.

7.4 Enhancing Breeding Efficiency

As indicated earlier, there are two main avenues by which crop ecophysiology and modelling can enhance breeding efficiency. The first involves use of ecophysiological insight from dynamic models to enhance phenotyping strategies by dissecting

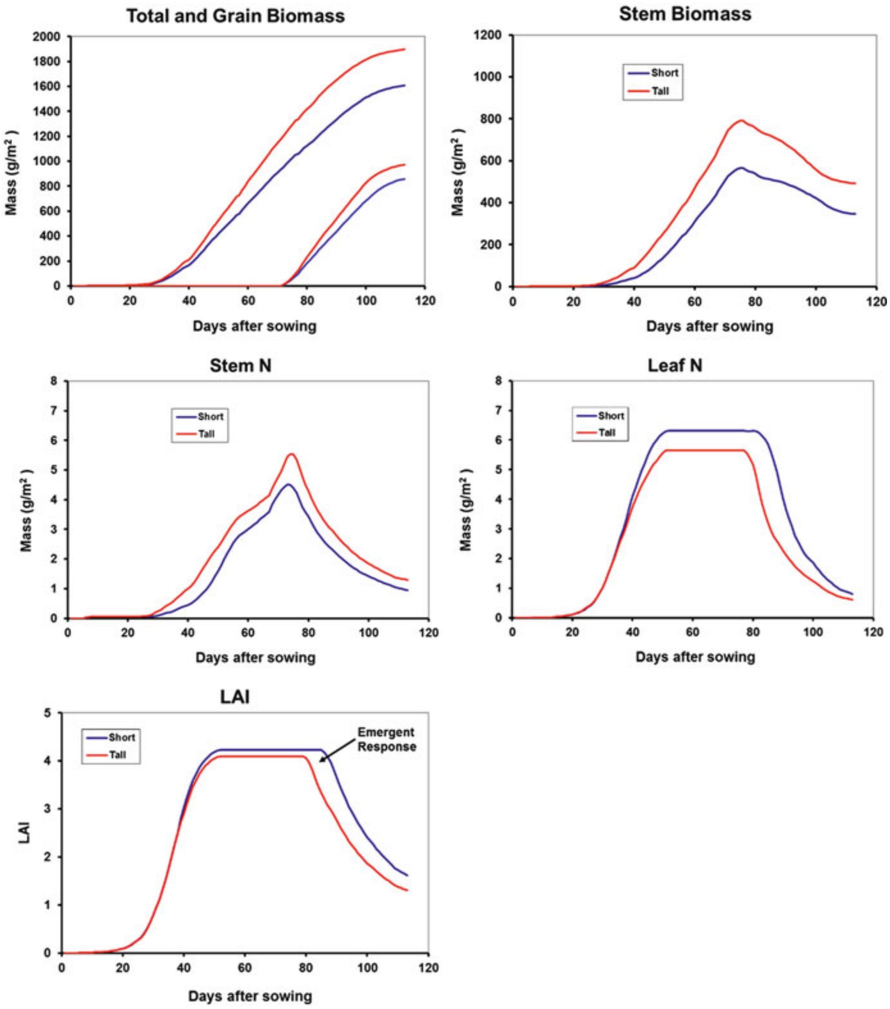

Fig. 7.2 Simulation of stay-green phenotype in sorghum as an emergent consequence of nitrogen (N) dynamics associated with differences in dwarfing genes via effects on structural N requirement for stem. Panels show organ biomass, organ N, and canopy leaf area index (LAI) simulated throughout the crop cycle for hybrids differing in height. The emergent delayed onset of senescence (i.e., 'stay-green') of the short hybrid is indicated on the panel giving the dynamics of canopy LAI. After Hammer et al. (2010)

complex traits to more robust targets that help to deal with phenotypic distance. The second involves using crop growth and development models for trait evaluation and phenotypic prediction in target production regions to help prioritise effort and assess breeding strategies. We consider an example of each.

7.4.1 Phenotyping for Drought Adaptation: Water Capture by Root Systems

The dynamics of water capture by root systems through the crop life cycle is critical to drought adaptation in water-limited environments. Slight changes in availability of soil moisture reserves associated with root system architecture, and in the timing of that availability, can have major consequences on yield in terminal drought environments, as suggested in wheat (Manschadi et al. 2006: Kirkegaard et al. 2007). In studies on sorghum in large rhizotrons, nodal root angle in young sorghum plants was shown to influence vertical and horizontal root distribution of mature plants in the soil profile and, hence, their ability to extract soil water (Singh et al. 2012). Types with narrower root angle tended to explore the soil profile more effectively at depth. These results suggested that genetic variation in nodal root angle of young sorghum plants could be a useful selection criterion for specific drought adaptation. Singh et al. (2010) had discovered this variation in nodal root angle when conducting studies on the morphological and architectural development of sorghum root systems in a small number of genotypes. They noted that due to the relatively late timing of appearance of nodal roots in sorghum, screening for genetic variation in the trait would require a small chamber system to grow plants until at least six leaves had fully expanded. They subsequently developed and implemented such a phenotyping system (Fig. 7.3) (Singh et al. 2011) and identified significant genotypic variation in the flush angle of nodal roots for a diverse set of sorghum genotypes.

Pursuing genetic variation in this trait by phenotyping mapping populations using this system, Mace et al. (2012) identified four QTLs for nodal root angle in sorghum that explained 58.2 % of the phenotypic variance and were validated across a range of diverse inbred lines. Three of the four nodal root angle QTLs showed homology to previously identified root angle QTLs in rice and maize, whereas all four QTLs co-located with previously identified QTLs for the drought adaptation trait stay-green in sorghum. Simulation studies based on possible differences in root architecture and their estimated effect on extent of water capture by root systems suggested significant yield advantage (up to 15 %) in low-yielding situations in a key sorghum production environment in NE Australia (Fig. 7.4). A putative association between nodal root angle QTLs and grain yield, which was consistent with the simulation studies, was identified through single marker analysis on field testing data from a subset of the mapping population grown in hybrid combination with three different tester lines. The identification of nodal root angle QTLs presents new opportunities for improving drought adaptation mechanisms via molecular breeding to manipulate a trait for which selection has previously been very difficult.

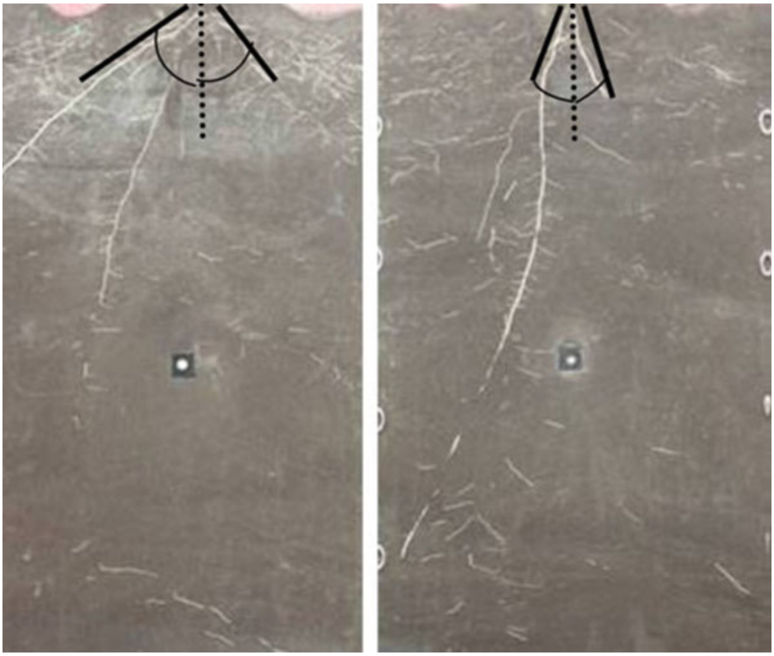

Fig. 7.3 Sorghum root angle phenotyping system. Individual plants were grown in specially designed root observation chambers until the sixth leaf had fully expanded. Each chamber consisted of two 50 cm high and 45 cm wide perspex sheets with the 3 mm gap filled with a dark, fine sandy soil so roots were clearly visible. Two genotypes divergent in angle of the first flush of nodal roots are shown. For mapping studies, chambers were stacked into tubs, covered below the plant to exclude light, and watered with a complete hydroponic solution daily. After Singh et al. (2011)

7.4.2 Phenotypic Prediction: Evaluating G × M × E Effects on Drought Adaptation

The timing of water availability through the crop life cycle is critical to drought adaptation in water-limited environments. The key principle involved is maximising the amount of water captured by the plant as transpiration (i.e., productive water use), while optimising its distribution pre- and post-anthesis. Appropriate plant trait and management system combinations for specific situations can be designed using this principle (Hammer 2006; Hammer et al. 2014). Reduced plant population and skip-row planting systems are common agronomic practices implemented with the intent of avoiding water limitation at anthesis and increasing the proportion of water use during the reproductive phase (Lyon et al. 2003; Whish et al. 2005). Genotypes expressing reduced early growth (Ray et al. 1997), early maturity (Ravi Kumar et al. 2009), or reduced tillering (van Oosterom et al. 2011; Alam et al. 2014a, b; Borrell et al. 2014a, b) can all provide a path towards soil water conservation and yield increase under drought stress (also see Chap. 5 of this book by Luquet et al.).

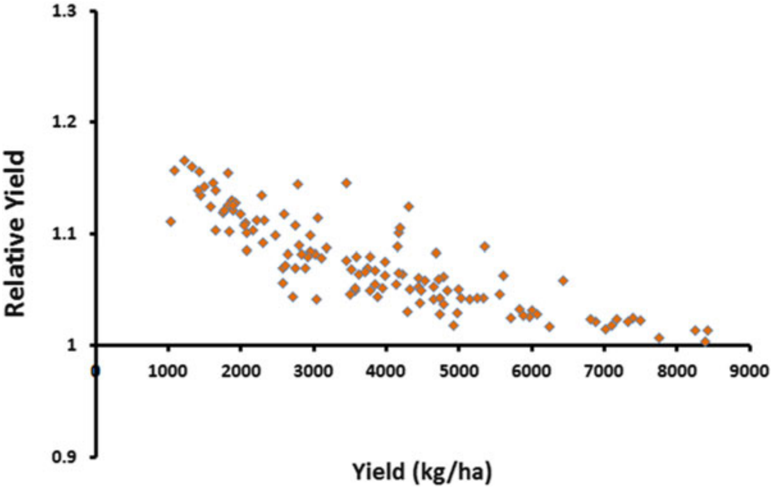

Fig. 7.4 Simulated yield of narrow root angle sorghum genotype relative to simulated yield of a standard type versus the yield of the standard type (kg ha^{-1}) for a 100-year simulation at Goondiwindi, NE Australia, assuming conventional agronomy. Each point represents 1 year of the simulation. The narrow root angle type had the same rooting depth but was assumed to access up to 15 mm extra soil water below 1 m soil depth if it was available in the soil profile

Hammer et al. (2014) reported a study that simulated the complex phenotypic adaptation landscape for combinations of these G and M factors for sorghum in the mostly water-limited production environments of north-eastern Australia, where sorghum is commonly grown as a row crop. Attributes for M employed in the simulations included three types of row configuration (solid 1 m rows; single skip row; double skip row; Whish et al. 2005) and four levels of plant density (3.5, 5.0, 6.5, 8.0 plants m^{-2}) while G attributes included nine levels of maturity (Ravi Kumar et al. 2009; Mace et al. 2013), and nine levels of tillering (Kim et al. 2010; Alam et al. 2014a, b). Levels of maturity were introduced by varying the time to floral initiation within the range −30 to +30 °Cd relative to the standard hybrid (with value 160 °Cd) using steps of 7.5 °Cd to generate the nine types. In addition to the effect on crop duration, this generates a change in total leaf number and hence modifies the pattern of leaf area development through the crop life cycle (Hammer et al. 1993). The range employed generates difference from the standard hybrid (17 leaves) within the range −1.5 to +1.5 total leaf number (Ravi Kumar et al. 2009). Levels of tillering were introduced by adding to, or subtracting from, the fertile tiller numbers assigned to the standard hybrid, within the range −2 to +2 tillers using steps of 0.5 fertile tillers to generate the nine types. For the lowest tillering type, this generates a plant that is uniculm in nearly all situations. Fertile tiller number affects maximum potential plant leaf area and hence the pattern of leaf area development through the crop life cycle (Hammer et al. 1993).

Components of the simulated yield adaptation landscapes can be viewed using heat maps of yield across a number of variables. Figure 7.5 presents yield levels for two consecutive years at one key location (Emerald) illustrating grain yield landscapes associated with variation in tillering, maturity, row configuration, and planting density. In 2005 (Fig. 7.5a), which was lower-yielding, the highest yield occurred with a low tillering, late maturing type, grown at low population in a single skip row configuration. In contrast, in 2006, with the same sowing date and soil conditions (Fig. 7.5b), yields were greater, with the maximum yield occurring with a high tillering, relatively early maturing type, grown at high population in a solid row configuration. This contrast demonstrates the instability in the adaptation landscape with different combinations of G×M being favoured depending on E, and highlights the difficulty in seeking broad adaptation in such variable production environments. Hammer et al. (2014) used the simulated phenotypic landscape to evaluate the extent of the potential advantage of a breeding strategy pursuing specific adaptation versus one pursuing broad adaptation across all environments. While significant advantages to specific adaptation were identified, this would introduce more cost and complexity to breeding.

Other recent simulation studies have also suggested that a limited maximum transpiration rate may contribute to early season water conservation, and as a consequence to improved yield under drought (Sinclair et al. 2005, 2010). The consequence of a maximum rate of transpiration is that around midday, when vapour pressure deficit (VPD) is high, plants would not lose water at an unrestricted rate (see Chap. 6 of this book by Sinclair et al.). This limitation would be manifested in decreased stomatal conductance during periods of high VPD. This behaviour would generate increased transpiration efficiency (TE, biomass accumulated per unit water transpired) for the crop because of decreased gas exchange during periods of high demand for crop water use. Experimental studies have identified a limited maximum transpiration trait in a range of species by quantifying responses to VPD (Fletcher et al. 2007; Sadok and Sinclair 2009a, b; Kholova et al. 2010; Jyostna Devi et al. 2010; Gholipoor et al. 2010, 2013; Yang et al. 2012; Choudhary and Sinclair 2014; Choudhary et al. 2014).

7.5 Implications

These examples demonstrate two of the main ways that whole plant ecophysiology and modelling can enhance molecular breeding via improved G-to-P understanding and prediction:

- Physiological dissection of complex traits in a dynamic framework – Experimental studies in controlled genetic backgrounds provide the means to determine and quantify the functional biology underpinning phenotypic differences, and thus inform high throughput phenotyping. Dynamic process concepts in crop models provide the analytical context to frame that understanding. Attributes can then be linked to genomic regions (QTLs) in a way that reduces context dependency and phenotypic distance and generates coefficients for dynamic crop models that quantify ecophysiological implications of genetic regulation.

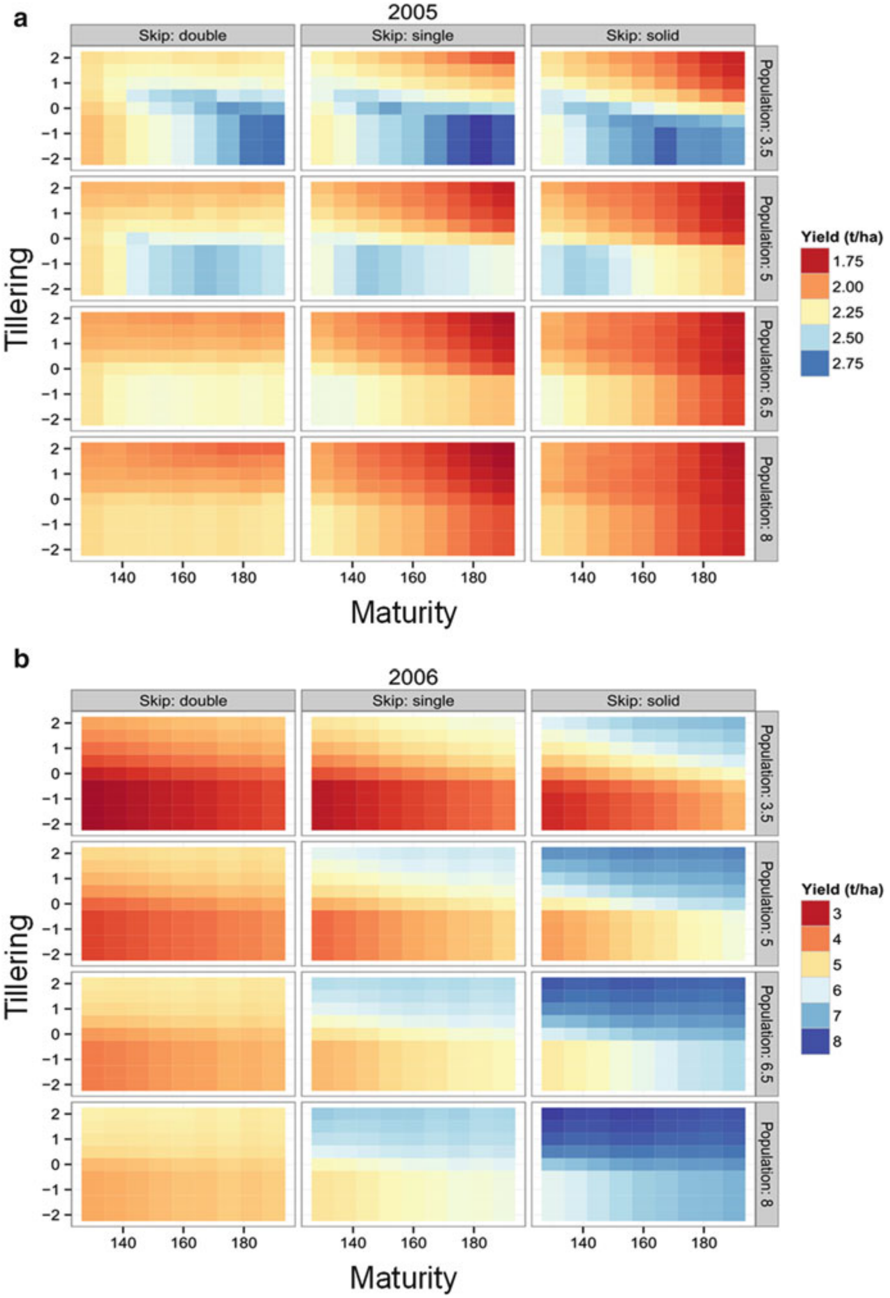

Fig. 7.5 Simulated phenotypic landscapes of sorghum grain yield (t/ha) at Emerald (NE Australia) in (**a**) 2005 and (**b**) 2006 for genotypes varying in tillering (positive values for high tillering types) and maturity (high thermal time requirement values for late maturing types – see text) and crop management varying in row configuration (double skip, single skip, and solid 1 m rows) and density (3.5–8 plants m^{-2}). After Hammer et al. (2014)

- Predicting consequences of genetic variation – Crop models with trait physiology and/or genetics embedded in their coefficient structure can be implemented in a predictive context to estimate by simulation the likely relevance of genetic variation for specific environments and management systems (i.e., G×M×E). This simulated phenotypic value has the potential to provide a basis for estimating trait value and weighting genomic regions in molecular breeding in a manner that is more robust than empirical genomic prediction approaches.

In both of these example cases, incorporating explanatory sub-models based on physiological insight into the quantitative crop model provided a basis to link changes at genomic regions directly to their emergent phenotypic consequences at the crop level via intermediary traits in a way that reduced context dependencies and phenotypic distance. Such an approach provides a pathway to effective applications in molecular breeding (Cooper et al. 2014a, b). Further, 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 (Cooper et al. 2002; Chapman et al. 2003; Hammer et al. 2005; Messina et al. 2009, 2011). In this way, whole plant physiology and modelling can provide an effective link between molecular knowledge, genotyping capacity, and the practice of crop improvement.

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