CHAPTER 5

AN INTEGRATED SYSTEMS APPROACH TO CROP IMPROVEMENT

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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) given the resources available to search among possible combinations in the target population of environments (E). Crop improvement can be viewed as a search strategy on a complex G×M×E adaptation or fitness landscape. Here we consider design of an integrated systems approach to crop improvement that incorporates advanced technologies in molecular markers, statistics, bio-informatics, and crop physiology and modelling. We suggest that such an approach can enhance the efficiency of crop improvement relative to conventional phenotypic selection by changing the focus from the paradigm of *identifying superior varieties* to a focus on *identifying superior combinations of genetic regions and management systems*. A comprehensive information system to support decisions on identifying target combinations is the critical core of the approach. We discuss the role of ecophysiology and modelling in this integrated systems approach by reviewing (i) applications in environmental characterization to underpin weighted selection; (ii) complex-trait physiology and genetics to enhance the stability of QTL models by linking the vector of coefficients defining the dynamic model to the genetic regions generating variability; and (iii) phenotypic prediction in the target population of environments to assess the value of putative combinations of traits and management systems and enhance the utility of QTL models in selection. We examine *in silico* evidence of the value of ecophysiology and modelling to crop improvement for complex traits and note that, while there is no definitive position, it seems clear that there is sufficient promise to warrant continued effort. We discuss criteria determining the nature of models required and argue that a greater degree of biological robustness is required for modelling the physiology and genetics of complex traits. We conclude that, while an integrated systems approach to crop improvement is in its infancy, we expect that the potential benefits and further technology developments will likely enhance its rate of development.

INTRODUCTION

Progress in crop improvement depends on identifying favourable combinations of genotypes and management practices from among innumerable possible combinations. Available resources and variability in the target environments limit this search process. Crop improvement can be viewed as a search strategy on a complex adaptation or fitness landscape, which consists of the phenotypic consequences of genotype (G) and management (M) combinations in target environments (E) (Cooper and Hammer 1996). The phenotypic consequences of only a very small fraction of all possible G×M×E combinations can be evaluated experimentally. Hence, most of the fitness landscape remains hidden to its explorer, even if the experiments remain simple and measure only yield of as many combinations as resources allow, as in standard multi-environment trials. Despite this, conventional breeding strategies based on phenotypic selection and principles of statistical quantitative genetics (Lynch and Walsh 1997) have been able to achieve sustained levels of yield improvement (Duvick et al. 2004). But to maintain this rate of advance requires increasing resources. Can an integrated approach incorporating advanced technologies in molecular markers, statistics, bio-informatics, and crop physiology and modelling enhance the efficiency of crop improvement?

The complexity of the phenotypic fitness landscape arises from G×E, M×E, G×G and G×M×E interactions. Traits associated with genetic variation (e.g., maturity, tillering) may rank differently for yield depending on environment (Hammer and Vanderlip 1989; Van Oosterom et al. 2003); management interventions (e.g., row configuration, density) may rank differently depending on environment (Whish et al. 2005); and combinations of traits and management (e.g., maturity×density) may rank differently in different environments (Wade et al. 1993). In addition, the genetic architecture of the gene network underpinning complex multi-genic adaptive traits is likely to involve varying degrees of epistatic interactions. In such situations, trait expression is governed by context dependent gene effects, i.e. interaction with other genes (Podlich et al. 2004). Such G×G interactions add substantially to genetic architecture complexity, with major implications for G×M×E interactions and rate of progress in crop improvement (Cooper et al. 2005).

It has been over a decade since the 1994 international symposium at which Cooper and Hammer (1996) advanced the concept of crop improvement as a search strategy on a G×M×E adaptation landscape and outlined a general framework for an integrated systems approach to crop improvement. Their framework incorporated simultaneous manipulation of plant genetics and crop management and considered how crop-physiological understanding and modelling might add value to existing plant-breeding methodologies. Plant breeding requires prediction of phenotype based on genotype to underpin yield advance and this provided the logical entry for advances in quantitative functional physiology.

Since the 1994 symposium there has been considerable development in these concepts and methodologies. Advances in understanding the complexities of gene-to-phenotype and phenotype-to-genotype associations for traits, and the potential to use this knowledge in plant breeding, were the subject of a symposium at the most

recent International Crop Science Congress (Brisbane, Australia, 2004: http://www.cropscience.org.au). Revised versions of invited papers to that symposium, which set out the current state of knowledge, have been published subsequently in a special issue of the Australian Journal of Agricultural Research introduced by Cooper and Hammer (2005). A number of other key review papers (Cooper et al. 2002; Hammer et al. 2002; Chapman et al. 2002; Tardieu 2003; Yin et al. 2004) cover developments in linking physiological and genetic modelling for crop improvement and in pursuing the G×M×E concept to enhance molecular breeding. In addition, there have been continuing advances in capacity for molecular genotyping and genomics approaches (Somerville and Dangl 2000; Jaccoud et al. 2001) and in statistics and bioinformatics (Van Eeuwijk et al. 2005; Verbyla et al. 2003). Such advances have enhanced the possibility for an integrated systems approach to crop improvement to link to genomic region level for complex traits. This is despite the limited progress of molecular breeding for complex traits to date due to gene and environment context dependencies (Podlich et al. 2004).

Here we consider the design and implementation of such an integrated systems paradigm for crop improvement. We assess progress from the initial concept construction in 1994 (Cooper and Hammer 1996) and focus on the linking role of crop ecophysiology and modelling to enhance the potential of molecular breeding and the efficiency of crop improvement in general. We use sorghum as a case study species, not only because it is the central focus of our crop improvement research, but also because there is advanced physiological understanding, well developed modelling capability, and a mature set of molecular technologies and genome resources, all linked to an operational breeding and crop improvement programme (Henzell and Jordan in press; Jordan et al. in press).

DESIGN OF AN INTEGRATED CROP IMPROVEMENT PROGRAMME

The central tenet of the integrated systems approach to crop improvement proposed is to change the focus from the paradigm of *identifying superior varieties* to a focus on *identifying superior combinations of genetic regions and packaging these regions into varieties*. Beyond this, it can change the focus from the breeding paradigm of *only developing superior varieties* to a crop improvement paradigm of *developing superior combinations of genetic regions and management systems to optimize resource capture and sustainability in particular cropping environments*. Key decisions in the integrated programme relate to selection of genotypes, management practices and test environments (Figure 1). A comprehensive information system supporting these decisions is the critical core of the approach.

The design of the programme involves a novel approach to integrating four relatively new technologies to enhance effectiveness in crop improvement:

- Enhanced marker technology – low-cost, high-throughput genotyping allowing all of the genotypes tested in a breeding programme to be genotyped with relatively high marker density (e.g., using DArT technology (Jaccoud et al. 2001)).

- Enhanced quantitative trait loci (QTL) detection methods – novel statistical approaches, pedigree-based methods and associative genetics to allow marker detection directly in breeding populations (Verbyla et al. 2003; Jordan et al. 2004; Van Eeuwijk et al. 2005).
- Enhanced gene-to-phenotype linkages – dynamic physiology and modelling frameworks to dissect complex traits to functional components to enhance association of phenotype with marker profiles (e.g., Leon et al. 2001; Reymond et al. 2003; Tardieu 2003; Yin et al. 2004; Messina et al. 2006).
- *In silico* evaluation – advanced modelling frameworks to characterize environments and to evaluate utility of trait and management combinations in target environments (Chapman et al. 2000a; 2000b; Hammer et al. 2005).

The proposed integration (Figure 1) provides the means to work across levels of biological organization from genetic regions to plant growth, development and yield while retaining the scale of a functional breeding and crop improvement programme. The physiology and modelling provides a 'knowledge bank' of process understanding. Modelling can generate benchmarks within the breeding-programme trialling system against which the degree of advance associated with new genetic recombinations and management systems can be assessed, despite genotype-by-management-by-environment interactions. Valuable novel combinations of regions can be identified and linked to dense marker profiles, which will be available across the breeding programme via the enhanced marker technology. The advanced statistical procedures will identify patterns of desirable genomic regions. The information accumulated in the breeding programme over time will enable
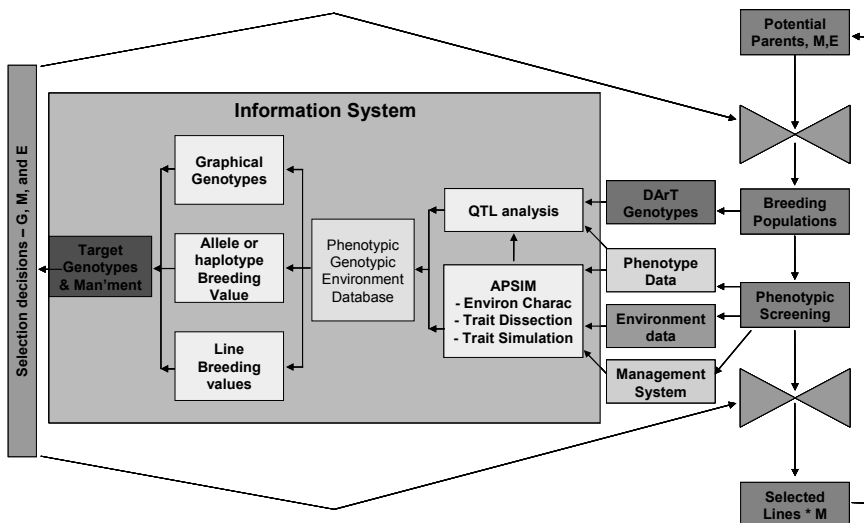

*Figure 1. Overview of an integrated crop improvement programme*

identification of key genomic regions and their value in breeding, as the genetic associations among lines will be known. Existing phenotypic information and populations generated in the breeding programme will be used in contrast to the conventional approach of developing populations specifically for mapping or validating markers. Key regions of unknown function can then be targeted for physiological analysis and modelling to build the information base. Modelling can be deployed to add value to conventional field testing by examining potential combinations of traits and management systems in a range of production environments (sites, soils, season types) via simulation analysis. Such projections of genotype and management combinations onto target environments contribute to the measures of breeding value.

## ROLE OF ECOPHYSIOLOGY AND MODELLING IN INTEGRATED CROP IMPROVEMENT

There are three general areas in which crop ecophysiology and modelling can play a role in the integrated approach to crop improvement (Figure 1): (i) characterizing environments to define the nature and frequency of challenges in the target population of environments (TPE); (ii) understanding and dissecting the physiology and genetics of complex traits; and (iii) predicting phenotypes of G×M combinations in the TPE.

Environment characterization

Using modelling to characterize environments in the TPE can assist in unravelling G×E interactions in a manner that aids selection decisions and improves the rate of yield gain in crop improvement programmes. Muchow et al. (1996) demonstrated that a sorghum simulation model (Hammer and Muchow 1994) could be used to characterize water-limited environments more effectively than indices based only on climatic data. The time course of a relative transpiration (RT) index was derived from the dynamic interactions implicit in the model. It was used to define the nature of the water limitation experienced by the crop throughout the growing season. Chapman et al. (2000a) classified environments in the TPE for sorghum in Australia based on the time course of RT and identified three distinct environment types (Figure 2). They found that the frequency of environment types at specific locations correlated with patterns of discrimination among hybrids detected in multi-environment trials (MET) at those locations. When the same simulation and classification procedure was applied to the TPE using historical climate data (Chapman et al. 2000b) they noted that changes in frequency of environment types over time periods relevant to a breeding programme affected yield likelihood and generated differing patterns of G×E (Figure 3). They suggested that weighting genotype performance by the representativeness of the selection environment in each MET with respect to the TPE would be advantageous in breeding programmes in these variable environments. Podlich et al. (1999) used breeding-system
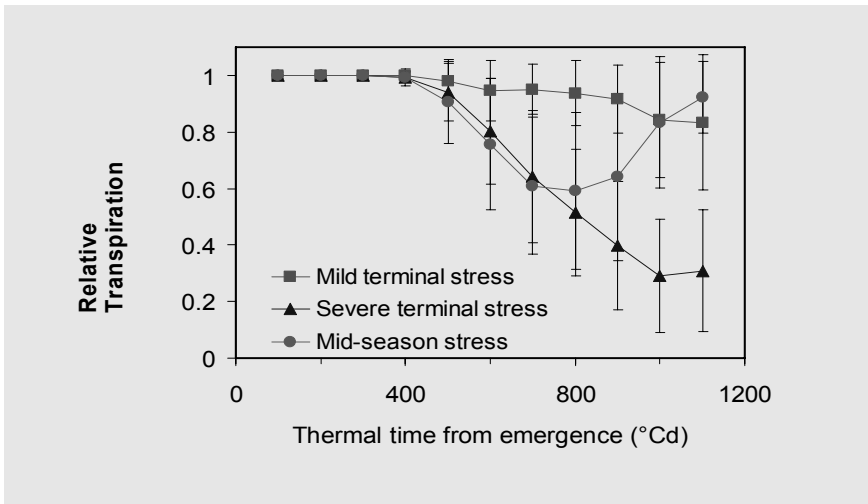
Figure 2. *Environmental characterization of sorghum production environments in Australia based on the time course of simulated relative transpiration throughout the crop life cycle (adapted from Chapman et al. 2000a)*
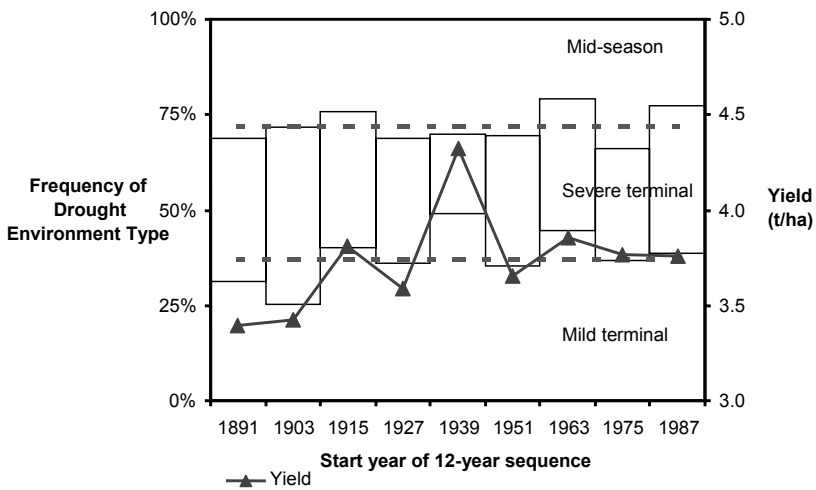
Figure 3. *Frequencies of environment types in consecutive 12-year periods during the 20th century for sorghum in Australia (adapted from Chapman et al. 2000b)*

simulation to demonstrate the advantage of such a weighted selection strategy in variable environments, especially when G×E was high (Figure 4). Löffler et al. (2005) used a simulation-based environment classification of the TPE for the Corn Belt in the US to improve cultivar performance predictability for a maize-breeding programme.
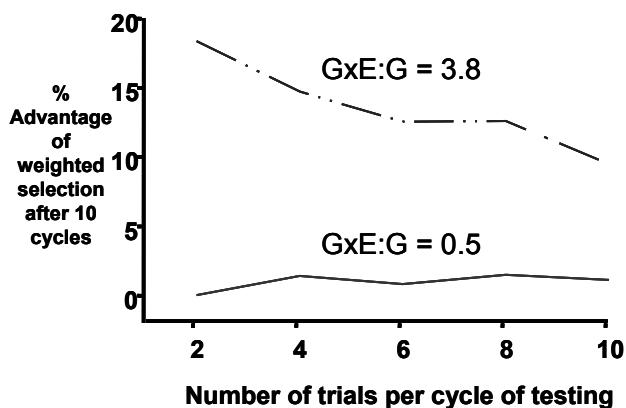
Figure 4. Percent advantage of weighted selection versus number of trials per cycle of testing in a breeding programme with high or low G×E (adapted from Podlich et al. 1999)

Complex trait physiology and genetics

A dynamic crop-modelling framework can aid understanding of the physiology and genetics of complex traits in a way that has potential to enhance efficiency in crop improvement programmes. The model provides an analytical framework to specify the functional basis underpinning phenotypic variation in a complex trait. The vector of coefficients that specify the functional and process control equations in the model is the basis for the link to genetic modes of action (i.e. QTLs or genes). The notion of using a virtual or *in silico* plant for this purpose has been discussed by Hammer et al. (2002; 2004), Tardieu (2003), Yin et al. (2004) and Dingkuhn et al. (2005).

Dissection of phenotypic variability in complex traits requires detailed experimental studies in controlled genetic backgrounds to unravel the functional biology underpinning the variability. In sorghum, studies on genotypes differing in their ability to retain green leaves during grain filling under terminal drought, known as the 'stay-green' trait (Borrell et al. 2000; 2001), have suggested that the trait arises as an emergent consequence of differences in underlying factors such as leaf size, specific leaf nitrogen, dry-matter partitioning, nitrogen uptake, and transpiration or transpiration efficiency. This understanding is being utilized in fine-mapping studies with near-isogenic lines (NILs) to isolate target genes in the genomic regions associated with the stay-green trait (Tao et al. 2000). In other studies on genotypes from a population differing in tillering (Kim et al. in press), size of leaves on the main culm and the consequent dynamics of internal plant

competition for assimilate have been identified as a likely causal factor. This is consistent with the concepts presented by Luquet et al. (2006) in modelling morphogenesis and competition among sinks in rice.

To date, however, this modelling approach to trait physiology and genetics has only been demonstrated comprehensively at organ or component level for traits such as expansive growth of leaves (Reymond et al. 2003; Tardieu 2003) and crop development (Leon et al. 2001; Yin et al. 2005; Messina et al. 2006). In these cases, coefficients defining differences among lines in process responses to environmental influences have been linked with QTL analyses. Reymond et al. (2003) combined QTL analysis with an ecophysiological model of the response of maize leaf elongation rate to temperature and water deficit by phenotyping a population and conducting the QTL analysis on the fitted model parameters. Using the derived relationships between model coefficients and QTLs, they were able to predict responses of lines with novel combinations of QTLs in a range of environments. Messina et al. (2006) achieved similar results in predicting soybean development by linking temperature and photoperiod responsiveness coefficients of a photo-thermal phenology model to allelic variants at known regulating loci. They used a study on NILs varying at these loci to derive the relationships and then applied them successfully in predicting development of other genotypes in a range of environments.

It may be possible to use a modelling approach to link more directly with gene networks controlling growth and development processes (Welch et al. 2005). Knowledge is emerging rapidly from studies on model plants to support modelling frameworks based on experimental evidence for understanding the action of gene networks at the biochemical level (e.g., Blazquez 2000). For example, Koornneef et al. (1998) presented a working model for the genetic control of flowering time in *Arabidopsis* based on extensive molecular-genetic studies to dissect this process. These studies employed a large number of mutant genotypes of *Arabidopsis* varying in time to flowering. The genetic, molecular and physiological analyses have led to elucidation of components and pathways involved. Welch et al. (2003) adapted the qualitative understanding reported for *Arabidopsis* to a quantitative predictive model of transition to flowering using a genetic neural-network approach. Morgan and Finlayson (2000) have presented a similar qualitative model for flowering in sorghum, based on their extensive studies with mutant genotypes. Beyond this, Dong (2003) developed a dynamic flowering-time model of the gene network in *Arabidopsis* that simulated the temperature- and photoperiod-dependent dynamics of mRNA expression for key genes in the network. He used controlled-environment and gene expression studies for a range of mutants to develop the model and was able to predict successfully the transition to flowering for a far wider range of G×E combinations than used in model development.

The scientific insights gained from this approach at organ or component level could be connected to more conventional crop models to explore interactions between development and growth and yield processes, thus providing an effective bridge between genetic architecture and phenotypic expression. Messina et al. (2006) connected their prediction of development in soybean based on presence of specific genetic loci to cultivar performance in breeding trials. Van Oosterom et al.

(in press) connected a simplified gene network model for photoperiod control of transition to flowering in sorghum to the APSIM generic crop-modelling platform (Wang et al. 2002) to demonstrate that an input of allelic variability could generate G×E for yield as an emergent consequence of the model dynamics. The use of modelling technologies in support of understanding the consequences of alterations of specific genes, via validated QTL models linked to model coefficients or via direct linkages to gene networks where sufficient is known, provides one of the major opportunities to utilize modelling effectively in an integrated approach to crop improvement.

Phenotypic prediction in the TPE

Using modelling to project consequences of G×M combinations in the TPE can generate information that aids selection decisions and improves the rate of yield gain in crop improvement programmes. Numerous studies have approached this by exploring putative value of potential trait variation in a range of species using a diversity of crop models (e.g., Spitters and Schapendonk 1990; Muchow et al. 1991; Aggarwal et al. 1997; Boote et al. 2001; Sinclair and Muchow 2001; Asseng and Van Herwaarden 2003; Sinclair et al. 2005) or by exploring optimization of trait and management combinations (e.g., Hammer et al. 1996). Using this approach requires confidence in the adequacy of the crop model to simulate effects of trait variation. This aspect is discussed below in considering the nature of models required to support the integrated systems approach to crop improvement. It also requires rigorous specification of soil (e.g., water-holding capacity) and climate (e.g., daily temperature and radiation) conditions for relevant production zones of the TPE as input to the simulation analysis.

An example of a model-generated G×M×E interaction relates to manipulation of tillering (G) and row spacing (M) in dryland grain sorghum production systems in Australia (Figure 5). Canopy development and consequent demand for water are affected by extent of tillering (Kim et al. in press) and row configuration (Whish et al. 2005). Figure 5 shows the results of a 50-year simulation using historical climate data for Emerald in central Queensland, Australia with the sorghum model implementation in APSIM (http://www.apsim.info/apsim/)(Wang et al. 2002). The simulation was conducted for a medium-maturing hybrid planted in early January each year assuming 80 mm of available water in a 120-cm deep vertosol soil that held a maximum of 130 mm plant-available water. In wetter higher-yielding years, the greater cover associated with solid row configuration and tillering is advantageous. But in drier, low-yielding years, the lower cover associated with uniculm plants grown in a double skip row configuration is advantageous. There is a cross-over at a yield level of about 3.5 t ha^{-1} in the standard treatment (solid row configuration and no tillers). When a random-error component is added by assuming a coefficient of variation of 12% (as per Hammer et al. 1996) and three replicates stochastically generated, the resultant 50-year MET has a highly significant G (tillering) × M (row configuration) × E (year) interaction (data not shown). Hence,

the interaction was an emergent consequence of the model dynamics generated by a change in one plant attribute and one management factor.
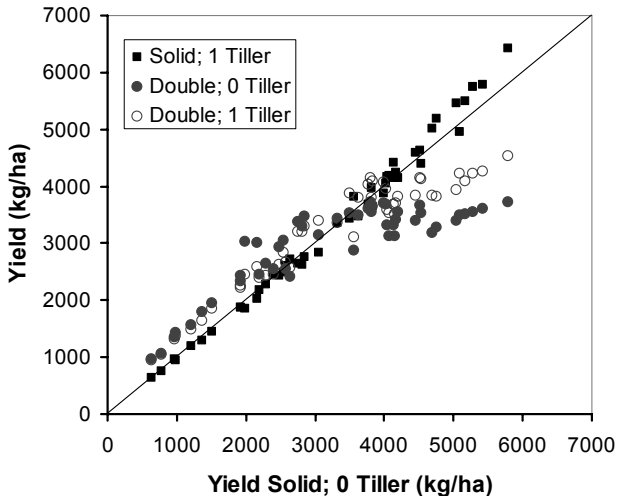

Figure 5. Simulated yield of sorghum varying in tiller number (0 or 1) and row configuration (solid or double skip) for a 50-year simulation at Emerald, Australia (for details see text). Yield for each combination each year is plotted against yield of the standard treatment (plants with no tillers grown in a solid 1m row configuration) in that year

VALUE OF ECOPHYSIOLOGY AND MODELLING IN INTEGRATED CROP IMPROVEMENT

As noted in the introduction, the key question to resolve is whether incorporating ecophysiological understanding and modelling in an integrated approach can enhance the efficiency of crop improvement. Is it possible to achieve a rate of yield improvement better than can be obtained by continued conventional empirical breeding based on phenotypic selection?

Beyond the demonstrated value of using models for environment characterization noted earlier, there is now some *in silico* evidence supporting a tentatively positive response to these questions in relation to crop improvement for complex traits (Cooper et al. 2002; Chapman et al. 2002; 2003; Hammer et al. 2005; Cooper et al. 2005). In those studies, sorghum phenotypes were simulated for a broad range of production environments in Australia based on assumed levels of variation in 15 genes controlling 4 adaptive traits. 'Virtual genotypes' were created by deriving combinations of expression states that depended on the number of positive alleles present for each trait. Expression states were then linked with crop model coefficients that quantified their physiological effects. By simulating a range of such virtual genotypes over a range of production environments, a data base of simulated phenotypes was generated. The data base of simulated phenotypes was

linked to the QU-GENE breeding-system simulation platform (Podlich and Cooper 1998) to explore effects of cycles of selection on yield gain for a range of breeding strategies. When marker-assisted selection (MAS) breeding strategies were simulated, the inclusion of marker-trait associations based on physiological knowledge and marker weights based on simulated trait value in the TPE significantly increased average rate of yield gain over MAS strategies without such knowledge and modelling capability (Figure 6). This result was dependent on (i) the assumed existence of stable QTL models that linked regions to model coefficients; and (ii) the lessening of gene and environment context dependencies of the QTLs via inherent interactions in the model dynamics that allowed robust projection of consequences of combinations onto the performance landscape in the TPE.
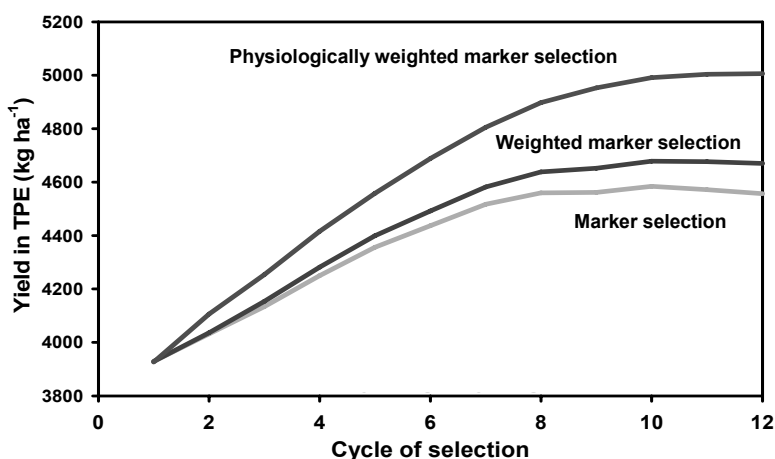
Figure 6. Average yield in the target population of environments (TPE) over 12 cycles of selection for three marker-assisted selection (MAS) scenarios for a simulated sorghum crop improvement programme. The trajectories for marker selection and weighted marker selection represent the average result over individual breeding-system simulations based on a QTL analysis from single environments. Marker selection incorporates only detection of markers, whereas weighted marker selection includes the weighting associated with each marker in the single detection environment. The trajectory for physiologically weighted marker selection represents the average result over simulations where markers have been assigned to physiological traits and marker weights have been derived from the simulated value of that trait in the entire TPE (after Hammer et al. 2005)

In a more comprehensive simulation analysis of response to breeding strategies, Cooper et al. (2005) examined a range of genetic models incorporating varying degrees of additive, epistatic and G×E effects that generated a spectrum of complexity in the resultant performance landscape. They quantified the qualitative expectation that response to phenotypic selection (PS) decreased as complexity of the genetic architecture of the trait increased. They also quantified the relative advantage of MAS over PS by simulating differences in response after 5 cycles of

selection for the same range of genetic models. They placed the sorghum example above in the context of this diverse set of situations. While the performance landscape generated in that case demonstrated a relatively high level of complexity, their analysis indicated that G×E was the major component of genetic architecture influencing complexity, and that there was only a modest advantage of the MAS strategy proposed over PS. The previous analyses (Chapman et al. 2003; Hammer et al. 2005) had emphasized that value generated from the inclusion of physiological knowledge and modelling was generated by the enhanced ability to deal with environment context dependencies (i.e., QTL×E interaction) in the use of markers. However, an optimistic view of overall value may have been presented.

Hence, while there is as yet no definitive answer to our question, it seems clear that there is sufficient promise to warrant continued effort in pursuing approaches to using physiological knowledge and modelling to enhance crop improvement for complex traits.

WHAT IS THE NATURE OF THE MODELS REQUIRED?

Many conventional agronomic models are adequate and suitable for characterizing the abiotic-stress patterns experienced by crops. The major requirements for such environment characterization are reliable predictions of ontogeny, canopy dynamics and water use. This aligns with pressures on development of agronomic models where predictive capacity for growth and yield outputs has often been more to the fore than biological robustness or mechanistic rigour in components. Predicting ontogeny establishes the developmental time base relevant to perception and effects of stresses (e.g., water limitation around flowering; high temperature during grain filling etc). Predicting canopy dynamics well is important in capturing the patterns of potential water use throughout the season. Canopy leaf area and the associated cover, in conjunction with environmental factors (e.g., radiation, vapour pressure deficit), determine demand for water. Ability of the crop to meet this demand can be related to root depth, soil water content and extraction capacity in each soil layer occupied by roots. The sunflower model of Chapman et al. (1993) details a generic water supply/demand framework of this nature but numerous other models with varying approaches (see review of Hammer et al. 2002) would be adequate for environment characterization.

A greater degree of biological robustness is required for modelling the physiology and genetics of complex traits (Hammer et al. 2002). Dissection of the underlying components associated with function and control of complex traits and projection of their effects onto the TPE requires biological realism. Models need to be sufficiently detailed so that important physiological linkages and interactions are simulated implicitly. They should incorporate a hierarchy of physiological processes and input variables based on experimental analyses (Tardieu 2003). The phenotype becomes an emergent consequence of variation in system architecture and control and its interaction with the environment. This requires that (i) the physiological modes of action of the traits are understood and quantified; and (ii) the model is sufficiently detailed and robust to simulate realistically the interactions with crop

growth and development generated by expression of the trait in any particular environment (Hammer et al. 1996). Tests of the integrative ability of the crop model to project consequences onto the TPE can range from qualitative sensibility testing of responses based on biological knowledge through to formal validation, where appropriate data are available (e.g., Messina et al. 2006). Robust models could add significant value to discussions on likely value of putative traits as breeding targets for indirect selection (e.g., Richards et al. 2002; Morgan et al. 2002) and to considerations of simpler targets/measures for the high-throughput phenotyping required for QTL modelling and forward selection in a breeding programme (e.g., Reynolds et al. 1998).

It is necessary to gain the understanding of the physiology and genetics of complex traits from studies in controlled genetic backgrounds. Tardieu (2003) used transgenic plants to link genetic responses to coefficients of a model of water flux through the plant. Messina et al. (2006) used near-isogenic lines varying at specific loci to derive coefficients for a phenology model that could then be estimated via linear functions of the alleles present. This contrasts with initial attempts to use agronomic crop models by optimizing a range of model coefficients to best fit observed phenotypic variation among sets of diverse genotypes, which had limited success (White and Hoogenboom 1996). The modest predictive capabilities found highlighted the need to understand better the physiological basis of the genetic variation involved via studies with controlled genetic backgrounds before seeking such predictive capability across diverse material.

The ability to generate stable associations between model coefficients and QTLs provides another criterion for model realism and adequacy to deal with physiology and genetics of complex traits (Welch et al. 2005). Reymond et al. (2003) were able to achieve stable QTLs for their ecophysiological model of leaf elongation rate in maize. Similarly, Messina et al. (2006) and Yin et al. (2005) found stable QTLs for photo-thermal phenology models for soybean and barley, respectively. However, Yin et al. (1999) were unable to find stable associations with QTLs for a study on specific leaf area (SLA cm^2 g^{-1}) in barley. This suggested lack of validity with which the crop model architecture and associated coefficients captured and integrated the physiological basis of the genetic variation. The barley model used in their study simulated leaf expansion as the product of carbohydrate partitioning to the leaf and SLA. Tardieu et al. (1999) presented a modelling framework to explore whether leaf expansion was a consequence of specific leaf area or *vice versa*. They were able to conclude the latter and argued that leaf expansion should be modelled independently of the plant carbon budget and that it was largely driven by temperature. Despite now having this enhanced understanding of control of leaf expansion in cereals, many crop simulation models continue to use the SLA-driven approach erroneously. However, this would likely have few consequences when using such models for agronomic or environment characterization purposes.

Kitano (2004) discusses robustness as a fundamental feature of complex evolvable systems, like biological organisms. He notes that system controls and modularity are basic features providing system robustness and that system control is the prime mechanism for coping with environmental perturbations. Attention to these aspects is likely to be important in the progression to the type of models most

suited to study of the physiology and genetics of complex traits. This notion accords with the separation of physical and control equations in plant models (Tardieu 2003) and with the motivation behind the on-going development of the APSIM modular generic crop routines (Wang et al. 2002). The latter is designed to capture advances in knowledge as they occur, while retaining parsimony in approach to the G×M×E modelling objective. Our current research is designed to test the ability of this type of model to generate more stable associations between model coefficients and QTLs.

CONCLUDING REMARKS

We suggest that an integrated systems approach to crop improvement that incorporates advanced technologies in molecular markers, statistics, bio-informatics, and crop physiology and modelling is likely to enhance the efficiency of crop improvement significantly. We discuss the design of such a system and consider the linking role of crop ecophysiology and modelling. A role of modelling in environmental characterization to support weighted selection is clear. It also seems clear that physiology and modelling will contribute significantly in the area of complex traits. The exact nature of this contribution is still emerging and is the focus of on-going research. Attention to biological robustness in modelling will likely assist in this regard. While an integrated systems approach is in its infancy, we expect that the potential benefits and further technology developments will likely enhance its rate of development. To this end, we are simultaneously pursuing the development and implementation of an integrated systems approach to crop improvement in the Australian sorghum programme.

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