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Navigating biological complexity – The challenge for the new era of crop improvement

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Introduction

Crop improvement in the first half of the 21st century is challenged to help realise the rate of productivity advance needed for global food security. Here I argue that this requires us to learn how to better *navigate biological complexity* and that crop growth and development models provide the necessary tool. This concept sits comfortably with the legacy of Farrer from the early 20th century. Farrer brought an advanced scientific approach to bear on the major issue of the day – developing locally adapted high-yielding wheat. His efforts to develop early maturing wheat with drought and rust resistances, and acceptable grain quality, underpinned emergence of the Australian wheat industry. Farrer was an exceptional scientist and innovator in plant breeding. He was studying and utilising the inheritance of traits many years before the rediscovery of Mendelian principles of genetics. He was an 'individual innovator' pursuing high impact science for sustainable agriculture and food – an approach now promoted by my own institute. But perhaps in the 21st century, a culture of collaborative connectivity is required to foster the innovation we need.

Here, I will address this argument in four steps -

- 1. Yield advance is on-going but **must** be hastened
- 2. Advance is constrained by the prediction and navigation problem in complex biological systems
- 3. Crop growth and development modelling as the navigational tool
- 4. Hastening innovation is best addressed by integration.

Yield advance is on-going but must be hastened

Since the early innovations introduced by plant breeding pioneers like Farrer, yield advance in field crops has been continuous and underpinned by innovations in agronomy and breeding. There is good evidence to support this. For example, in Australia, productivity increase in sorghum has been high by world standards at about 4% per annum over the past 2 decades (Fig. 1). This high level of yield increase has been associated with many factors – breeding (midge resistance, staygreen), surface management (minimum tillage, controlled traffic) and effective use of water (profile monitoring), agronomy (row configuration), seasonal climate forecasting (responsive management), improved management of soil fertility and weeds, and improved planting technologies. This advance has been supported by strong research and development across many disciplines in a form of 'corporate innovation'. But the disciplines have tended to operate in isolation. However, this high rate of yield advance is not being realised globally for major crop species (Fig. 2). There is evidence of reducing levels of advance, especially for rice, wheat, and barley, which are now increasing at, or below 1% per annum, with reports of little or no increase in particular regions, possibly reflecting impacts of climate change.

To maintain food security for an increasing world population in a future facing climate change, the rate of productivity increase is now challenged. World population is projected to increase from 7 to 9 billion by 2050, with most of this increase occurring in developing countries. With projected changes in diets in major developing economies, this translates to a projected 70% increase in production needed by 2050. Given

limited opportunity for growth in area cultivated, rates of productivity increase near 2% per annum will be required to meet this demand. Yield advance must be hastened. While closing yield gaps in developing world agricultural systems can contribute significantly, there is also a need for more rapid genetic advance in environmental potential yield.

Advance is constrained by the prediction and navigation problem in complex biological systems

Progress in crop improvement is constrained by a prediction problem. We need the ability to identify the favourable combinations of genotypes (G) and management practices (M) in relevant target environments (E) among all possible combinations. Phenotypic performance of the array of possible combinations forms what can be viewed as an "*adaptation landscape*". 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 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, but slow and inefficient.

The phenotypic prediction challenge faced in dealing with complex traits in breeding improved crop plants is akin to the navigation problem faced by early mariners who lacked the means to determine longitude accurately. When setting out on a journey with a map and existing knowledge, they seldom reached their desired destination via a consistent path, and sometimes did not arrive at all. This great scientific problem of the 18th century was solved by the development of tools for accurate measurement of time (and hence prediction of longitude) at sea. With reliable and robust nautical timepieces, mariners could better predict their location and voyage reliably. Today we are at a similar early stage in the exploration of biological systems. We build the genetic maps and knowledge, make phenotypic predictions, and set out on voyages. But most of these voyages do not end up at the destination we seek and are difficult to repeat. More often than we would like, the complexity of the system impairs our attempts at prediction. Our current statistical quantitative genetics tools, although effective in conventional breeding, have a limited ability to predict the phenotypic destination from the genetic map.

Rapid advances in molecular genetic technologies have allowed the focus of practical crop improvement to shift from the level of the individual (genotype) to the level of genomic region (e.g. QTL, gene). The ability to inexpensively and densely map/sequence genomes has enabled molecular breeding strategies using molecular marker and genome wide prediction approaches. However, their applicability beyond simply controlled traits is constrained by gene-gene and gene-environment interactions, which restrict robust predictive power of associations of genomic regions with phenotypic responses for complex traits, like water use efficiency or yield. Despite this limitation due to "*phenotypic distance*", it has been possible to design molecular breeding strategies using these technologies that can accelerate plant breeding. However, we need the equivalent of the mariners' timepiece to help us better navigate across the scales of biological organization from gene to phenotype for complex traits. Novel modelling approaches to predict gene-to-phenotype associations might help us to deal with this complexity and operate across scales of biological organization for breeding improved crop plants.

Crop growth and development modelling as the navigational tool

Plants are complex adaptive systems. They respond to G, M, and E factors in an integral manner at crop community level, but phenotypic responses and fitness occur at the organism/plant level. Adjustments occur at the organ level but are driven by gene networks residing at cellular level. Adaptive responses are moderated via the control of growth and morphogenesis, often via information flow through key hormones. Evolution can be viewed as a form of tinkering with these control systems.

Complex systems are admirably suited to dynamic modelling approaches. Crop growth and development models incorporate equations to predict organ and crop growth and development, resource capture, and fluxes

in the system (Fig. 3). These equations must be informed by biological knowledge and experimental data. The equations break down the phenotypic complexity into key drivers and implicitly incorporate important non-linear interactions among system components and their control. Much phenotypic complexity thus emerges as a consequence of the model dynamics. Improved phenotypic predictions via crop modelling result from an ability to deal with the complex interactions among plant growth and development processes, environmental effects and genetic controls. The coefficients of the equations thus have potential to provide robust connection points for genomic regions (Fig 3). The structure and coefficients underpinning the explanatory capability of the model must link effectively to the genomic regions associated with variability in the complex trait. To be effective, the dynamic model must improve on the existing empirical methods that operate directly from genomic region to phenotypic response. This requires close attention to biological rigour in the structure and representation of process dynamics in the model while retaining predictive capacity. This predictive capacity of the dynamic model could then be used for favourably weighting more important QTL during their selection in a marker-assisted breeding programme. The approach provides a means to focus on the value of genomic regions, even for complex traits and their combinations. It thus has the potential to change crop improvement dramatically by integrating phenotypic and molecular approaches in breeding improved crop plants.

Beyond this, the modelling approach helps identify traits likely to be effective so that phenotyping and genome wide prediction approaches can be better targeted. For example, modelling studies in sorghum and wheat have identified the significant value of small amounts of extra water extraction at depth, and its association with genetic differences in root angle of major root axes early in plant development. This has enabled development of a targeted phenotyping system for this root system trait. While there have been recent developments in high throughput phenotyping platforms using advanced imaging systems, this capability is often missing this link to the functional relevance of the target measures. Better targeting of this phenotyping capability is critical to its effective deployment. Field based phenotyping systems using sensing technologies from ground and aerial platforms offer considerable potential to link directly with crop improvement experiments. However, again, a focus on the biological interpretation of the measures is critical. Reverse engineering of crop growth and development models offers considerable potential to add value to these developments in phenotyping by helping to unravel complexity and better interpret biological causes of variation among entries.

Hastening innovation by integration

We are on the verge of a new technological era that offers considerably more. It is now possible to break down some of the biological complexity and enhance predictive power using crop physiology and modelling. The models capture the underpinning functional control of crop growth and development processes and have advanced predictive capability. They provide an avenue for linking organism and molecular scales. Novel advanced phenotyping technologies operating at high temporal and spatial resolution in breeding populations can then be targeted to provide the avenue for linkage with genomic regulation of key processes affecting crop yield.

Future innovation arises from the *integration* of these advanced technologies - genotyping power, biological knowledge of the functional dynamics of crop growth and development, advances in phenotyping technologies, and effective bioinformatics. There is need for balance in effort and funding among genotyping, phenotyping, bioinformatics, and linking modelling. This will likely evolve in a form of 'distributed innovation' across many public and private players. However, to be effective there must be collaborative connectivity. Achieving this connectivity will be as much the innovation, as developments in the component technologies, as we strive to meet the urgent need for more rapid productivity advance by better navigating biological complexity.

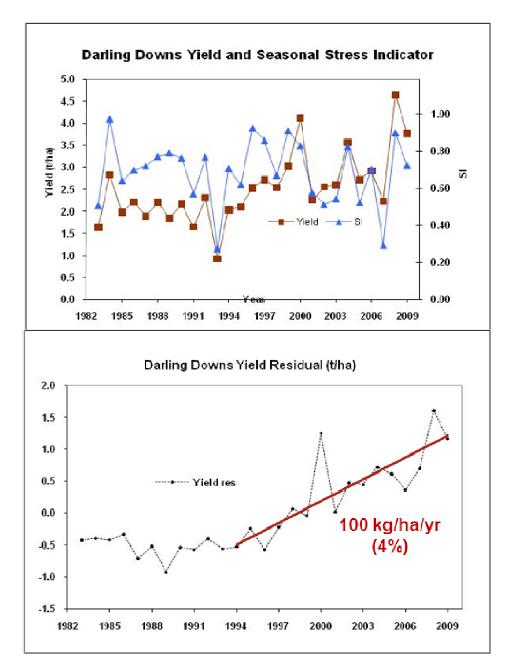


Figure 1. Top panel - Average annual grain yield (t/ha) of sorghum for the Darling Downs shire and annual seasonal water stress indicator (SI) for the period 1982-2009. Bottom panel – trend in average grain yield for the Darling Downs shire after removing effect of temporal variation in SI.

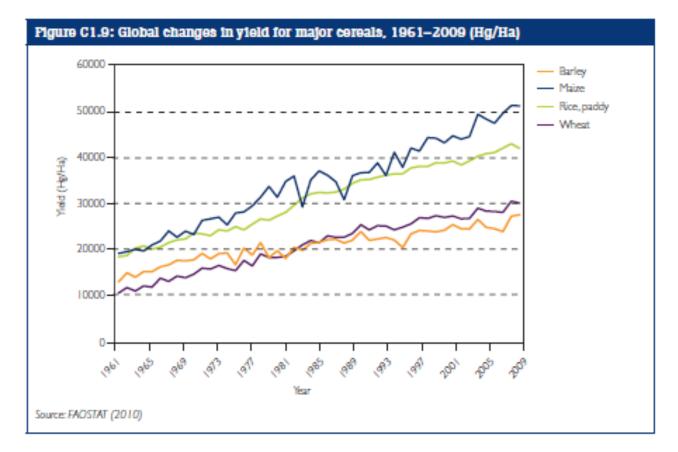


Figure 2. Average annual global grain yield (hg/ha) for major cereals for the period 1961-2009.

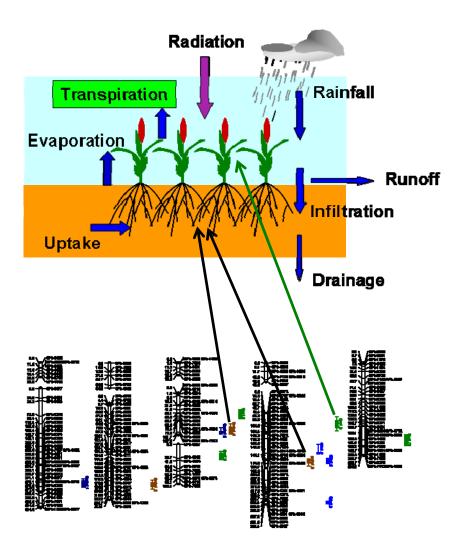


Figure 3. Schematic of processes involved in crop water balance in a crop growth and development model and their potential quantitative association with differing controlling genomic regions.