

QTL × E × M: combining crop physiology and genetics

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Introduction

Knowledge on molecular biology and genetics of plants has progressed enormously. However, this knowledge has highlighted in the first place that plant metabolism and its regulation under variable and – especially in organic agriculture – often stressful environmental conditions are extremely complex. Plant and crop scientists still do not fully understand how the plant, as an autonomous organism, or a crop, as a group of mutually interacting plant individuals, is capable of managing its own complexity and how it perceives and interprets all the information it is exposed to in order to survive, propagate its genes and produces useful products for mankind. Modelling can help to bring order in that complexity – at least to some extent – because we can reduce the complex reality to a number of robust algorithms that are capable of catching the dynamics and mechanistics of the most determining processes. Dissecting complex traits with low heritability into relatively simple component traits, which are less sensitive to environmental conditions, will assist breeders in making faster breeding progress.

The new challenge

Modern crop physiology is challenged to bring the information from functional genomics to the crop level, by introducing true biological mechanisms from systems biology into crop models based on a true understanding of the organization of the crop across scales and the crop's response to environmental conditions. Crop physiology is for a greater part developing into the direction of what we call 'crop systems biology', which aims at modelling complex crop-level traits relevant to global food production and energy supply, via building the links between 'omics'-level information, underlying biochemical understanding, and physiological component processes. Essential in crop systems biology is to properly map the organization levels and the communication systems between these levels for the different key processes, from the molecule or gene, all the way up to the crop. Such an approach is clearly needed (and also suitable) when dealing with the interactions between environment (E), management (M) and genetic components (often identified as QTL), further called QTL × E × M interactions, because molecular information (in the form of QTLs for desirable traits) should be evaluated and used at a level where it really matters: where the genotype interacts with E and M. In our framework we distinguish between environment and management. Many researchers consider management as part of the environment but the distinction is useful because it stresses what is manageable (and therefore at least to some extent also predictable in a quantitative way) and what is not.

Where do we stand today?

Many relevant crop traits, such as yield and quality, are quantitative and complex. They are controlled by multiple, interacting genes whose expression may be dependent on environment. The modern molecular marker technologies enable us to dissect the variation in these complex traits into the effects of QTLs. With the progress of QTL mapping new breeding approaches such as marker-assisted selection have become possible and breeding by design has become within reach. However, we should not be too optimistic about these opportunities on the short term, since polygenic control, epistasis and QTL × E × M interactions can impede the use of these approaches. Some of these aspects require continuous

and long-lasting efforts; but for QTL \times E \times M interactions modelling may become handy in the first place.

Whole-crop physiology models are the obvious tools to dissect complex traits into manageable component traits and to describe the effects of environment and management on them in a mechanistic way. This is obviously useful for breeders as they will now have information with much less QTL \times E \times M interaction and therefore QTLs which are more robust, resulting in a more efficient breeding process. But it is also attractive for crop physiologists: until recently models were very poor in capturing the genetic component of these complex traits, let alone the QTL \times E \times M interactions. So if crop physiology and genetics are combined judiciously, crop physiology and modelling research can reinforce the genetic analysis of complex traits, thereby improving breeding efficiency, but at the same time can also create approaches with which crop physiology can use genetic information in crop models.

Because crop models represent causality between component processes and yield, they can predict crop performance beyond the environments for which the model parameters were estimated. This singular property allows the models potentially to resolve QTL \times E \times M into underlying processes on a daily basis and to predict crop performance for any genotype in any environment.

In order to realize these achievements, a model-based approach comprising of five steps is required:

1. Create a crop model that predicts complex traits based on relations between elementary processes and environmental variables.
2. Evaluate the capability of the model to predict the complex trait across a wide range of combinations.
3. Identify QTL for model-input traits using a genetic QTL approach.
4. Develop a QTL-based model whereby the original values of model input traits are replaced by QTL-based inputs.
5. Validate the QTL-based model across environments.

Examples

Examples where the approach described in the previous section has been or is being applied to analyse gene/QTL \times E \times M interactions and that demonstrate the approach of dissecting complex traits into biologically meaningful component traits in which the environmental effect is already accounted for, are:

1. QTL-based models of time to flowering for rice, barley and rapeseed, based on the response of flowering time to photoperiod and temperature as affected by, for example, sowing time or models of time to flowering in Arabidopsis based on gene networks;
2. QTL-based models of the response of elongation rate of maize leaves based on temperature, vapour pressure deficit and soil-plant-water relations as affected by irrigation schedules;
3. QTL-based models of the development over time of soil cover and of tuber formation in potato as affected by fertilizer supply;
4. QTL-based models of use efficiency of nitrogen in barley and of nitrogen and phosphorus in potato as affected by resource input and production environment (conventional versus organic; different types and levels of resource input);
5. QTL-based models of root growth and resource capture in lettuce as affected by transplant management;
6. Gene-based models of fruit growth in tomato based on cell cycling, cell division and cell elongation as affected by temperature regime and fruit load;
7. QTL-based modelling of fruit quality in peaches, based on physical, metabolic and physiological subroutines and affected by fruit load;

8. QTL-based modelling of drought tolerance in rice focusing on complex traits such as photosynthesis, chlorophyll fluorescence, yield components, and yield.

Relevance for organic agriculture

QTL-based modelling and organic agriculture can become a perfect match. In organic farming, the crop eco-physiological principles are not different from those in conventional farming but the systems are more complex, are more difficult to generalize across individual farms, and interactions (including those relating to genotype \times environment \times management) are more significant. Agronomic characteristics of organic production environments are usually much more complex than in the case of conventional agriculture because of the intrinsic variation in process rates, timing and duration (e.g. of mineralization of organic matter in dependence of physical, chemical and biological soil fertility). Moreover, organic agriculture is using an agro-ecological approach taking measures to stimulate the self-regulating ability ('autonomy') of living systems, including (agro-)ecological systems, whereas conventional systems often use external inputs which overrule this ability. Model-based systems analysis for organic agriculture can therefore be a very useful tool in quantifying agro-ecological processes and their consequences for yield, quality and other aspects of system behaviour.

As organic agriculture has fewer management means to adjust the environment to the genotype, it needs varieties that are better adapted to variable low-input (organic) growing conditions. Organic farming aims at optimizing the production system more than the individual crop and thus practices are not aimed at providing optimal amounts of resources to the individual crop but to maintaining system health. Nutrient supply and water supply are therefore less regular, less abundant, and more depending on (variable) environmental conditions, including physical, chemical, and biological soil conditions. For example, mineralization of organic matter and uptake of nutrients depend on availability of soil moisture, thus increasing variation in growth.

This means that by definition organic agriculture seeks holistic approaches and looks for varieties which fit in those approaches. Crop ideotypes for organic systems are more complex (with more trade-offs) than their counterparts in conventional agriculture. Trade-offs should be quantified preferably by modelling approaches. Moreover, organic farmers look for varieties that are robust under their conditions, i.e. show a reliability, an efficiency of functioning, and a persistence of functionality under fluctuating, unpredictable and changing conditions. A good example of robustness might be a large plasticity towards dynamic availability of nutrients and water by maintaining a suitable root architecture throughout the life cycle and a dynamic balance in shoot to root ratio, even when this would mean extra investments in root dry matter that does not contribute to the harvestable yield.

Complex and system-specific characteristics such as robustness might well have a genetic background and are therefore amenable for selection, but this still requires proof by proper research. For that robustness needs to be defined in agronomic terms and specified in crop physiological terms, resulting in those characteristics that can be broken down into component traits for which stable (i.e. environment and management independent) QTLs can be identified. Complex traits can be conceptualized within a modelling framework and tested for a diverse set of organic environments. QTLs can then be identified for these component traits.

The need to break down complex traits into manageable component traits might be against the nature of the holistic thinking in organic agriculture but is a prerequisite for effective breeding on such traits and to allow the use of marker assisted selection techniques for those traits.

In order to let QTL-based modelling contribute to designing robust varieties for organic agriculture the five steps for developing such a model explained above in the section

“Where do we stand today?” would still suffice. However, each of the steps would be extremely laborious and time- and resource-demanding given the complexity of the traits organic agriculture is looking for and in the light of the fact that we have only designed successful QTL-based models for relatively simple growth traits or relatively simple developmental traits.

Further reading

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