Modelling strategies for assessing and increasing the effectiveness of new phenotyping techniques in plant breeding

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Modelling strategies for assessing and increasing the effectiveness of new phenotyping techniques in plant breeding

Fred van Eeuwijk[1], Daniela Bustos-Korts[1], Emilie J Millet[1], Martin Boer[1], Willem Kruijer[1], Addie Thompson[2], Marcos Malosetti[1], Hiroyoshi Iwata[3], Roberto Quiroz[4], Christian Kuppe[5], Onno Muller[5], Konstantinos N. Blazakis[6], Kang Yu[7,8], Francois Tardieu[9], Scott Chapman[10]

1. Biometris, Wageningen University & Research Centre, P.O. Box 16, 6700 AC Wageningen, The Netherlands
2. Department of Plant, Soil and Microbial Sciences, Michigan State University, 1066 Bogue St, East Lansing, MI 48824 USA.
3. Department of Agricultural and Environmental Biology, Graduate School of Agricultural and Life Sciences, The University of Tokyo, 1-1-1 Yayoi, Bunkyo-ku, Tokyo 113-8657, Japan
4. International Potato Center (CIP), P.O. Box 1558, Lima 12, Peru
5. Institute for Bio-and Geosciences, IBG-2: Plant Sciences, Forschungszentrum Jülich GmbH, 52425 Jülich, Germany
6. Department of Horticultural Genetics and Biotechnology, Mediterranean Agronomic Institute of Chania (MAICh), Alsylio Agrokipiou, PO BOX 85, 73100 Chania-Crete, Greece.
7. Crop Science, Institute of Agricultural Sciences, ETH Zurich, Switzerland
8. Remote Sensing & Terrestrial Ecology, Department of Earth and Environmental Sciences, KU Leuven, Belgium
9. Laboratoire d'Ecophysiologie des Plantes sous Stress Environnementaux, UMR759, INRA, 34060 Montpellier, France
10. CSIRO Agriculture and Food, Queensland Bioscience Precinct, 306 Carmody Road, St Lucia, QLD 4067, Australia and School of Agriculture and Food Sciences, The University of Queensland, Gatton, QLD 4343, Australia

Highlights

- We present the major classes of genotype to phenotype models for predicting complex phenotypes with genotype by environment interactions in the field as functions of genotypic and environmental inputs.
- We show how existing genotype-to-phenotype models can be generalized to incorporate information obtained by new phenotyping devices and techniques for improving the prediction of primary traits like yield under field conditions.
- We demonstrate how the utility of information from new phenotyping devices and techniques can be evaluated within the context of predictive genotype-to-phenotype models

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Abstract

New types of phenotyping tools generate large amounts of data on many aspects of plant physiology and morphology with high spatial and temporal resolution. These new phenotyping data are potentially useful for a better understanding and prediction of complex traits, like yield, that are characterized by strong environmental context dependencies, *i.e.*, genotype by environment interactions. For an evaluation of the utility of new phenotyping information, we will look at how this information can be incorporated in different classes of genotype-to-phenotype (G2P) models. G2P models predict phenotypic traits as functions of genotypic and environmental inputs. In the last decade, easy access to high-density single nucleotide polymorphism markers (SNPs) and sequence information has boosted the development of a class of G2P models called genomic prediction models that predict phenotypes from genome wide marker profiles. The question now is to build G2P models that incorporate simultaneously extensive genomic information alongside with new phenotypic information. Beyond the modification of existing G2P models, new G2P paradigms are required. We present candidate G2P models for the integration of genomic and new phenotyping information and illustrate their use in examples. Special attention will be given to the modelling of genotype by environment interactions. The G2P models provide a framework for model based phenotyping and the evaluation of the utility of phenotyping information in the context of breeding programs.

Keywords

crop growth model; genomic prediction; genotype-by-environment-interaction; genotype-to-phenotype model; mixed model; multi-environment model; multi-trait model; phenotyping; phenotyping platform; physiology; plant breeding; prediction; reaction norm; response surface; statistical genetics.

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Abbreviations

APSIM: Agricultural Production Systems sIMulator

ASI: Anthesis Silking Interval

BLUP: Best Linear Unbiased Predictor

BLUE: Best Linear Unbiased Estimator

CGM: Crop Growth Model

G×E: Genotype by Environment (Interaction)

G2P: Genotype to Phenotype

LER: Leaf Elongation Rate

NDVI: Normalized Difference Vegetation Index

MET: Multi-Environment Trial

QTL: Quantitative Trait Locus

SEM: Structural Equations Model

SNP: single nucleotide polymorphism markers

SpATS: Spatial Analysis of field Trials with Splines

TPE: Target Population of Environments

VCOV: Variance-COVariance

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1. Introduction

A primary objective and problem in plant breeding remains the improvement of yield. Therefore, the utility of new genotyping and phenotyping techniques should be evaluated in the light of the additional genetic gain for yield that can be obtained by the implementation of new techniques, where cost-benefit considerations should be made in relation to the speed and cost of the additional genetic gain. Yield is an example of a complex traits characterized by the contributions of many genes with relatively small effects that show strong context dependencies in the form of epistatic and genotype by environment interactions (G×E). These context dependencies complicate the breeding process [1–3]. Improvement of yield is made in relation to a target population of environments (TPE), *i.e.* the set of conditions for which the genotypes (cultivars, varieties) are bred [3,4]. Across the TPE, typically the environmental conditions change to an extent that the phenotypic response curves of individual genotypes, the reaction norms [5,6], will show divergence, convergence, and intersection, which is an expression of G×E. Traditional phenotyping strategies consist of the evaluation of genotypes in a number of trials across a number of locations for a number of years, called multi-environment trials (METs). The hope is that the trials in the MET form a representative sample from the conditions in the TPE and that the MET provides enough information for identifying and estimating G×E patterns with enough precision to decide upon a strategy on how to handle G×E [7,8].

Early onwards it was recognized that hoping for METs to contain informative sets of environmental conditions was not an optimal strategy for developing adapted genotypes to defined biotic and abiotic stress conditions. Managed stress trials were introduced to complement classical location by year METs [8–10]. Furthermore, in many crops, physiology and physics driven measurement protocols were developed in attempts to predict the behaviour of genotypes under abiotic stress conditions [11]. Therefore, many phenotyping techniques were being used to help the breeding process attain genotypes with superior yields.

However, phenotyping as a separate discipline within plant biology is a new phenomenon. The rapid development of new phenotyping technologies has led to an enormous increase in the types and amounts of phenotypic data that can be monitored and registered. All levels of biological organisation have become accessible from within the cell up to the level of the ecosystem, and at spatial and temporal resolutions that were unthinkable before, with whole new types of processes being open to study [12,13]. New phenotyping devices occur that can be classified as: 1) high precision platforms, which are not necessarily high throughput, for

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omics, anatomical and functional traits at cell and organ level, covering short time scales [14,15]; 2) whole-plant field and controlled environment platforms for plant canopy traits [8,16,17]; 3) Networks of field experiments (METs), with high throughput phenotyping techniques across environmental ranges [18,19]. The diversity and complexity of new phenotypic data types raises the question of how to use this information efficiently to increase biological understanding of plant systems and how to improve the accuracy of prediction for complex traits like yield? Should we copy the genomic prediction paradigm and simply include all phenotypic data in our prediction models without any feature selection? Or, will we do better by selecting specific features from our phenotyping information, *i.e.*, identify those traits that are relevant for better adaptation, as proposed by [12,20].

In this paper, we will look at ways to incorporate new phenotyping data into predictive models for complex traits, where for simplicity of exposition we will focus on yield. We will describe various model classes, mainly statistical, but also crop growth models, that provide the means to evaluate and quantify the utility of new phenotyping information. We start with a presentation of a classification of phenotypic trait data according to the amount of modelling the data underwent. The next two sections, describe statistical models and crop growth models for predicting phenotypic traits from DNA profiles, environmental information, and additional phenotypic information, together with some illustrative examples. In these sections, attention will be given to some promising new G2P models and the role of modelling in relation to breeding strategies is considered. The last section presents some challenges ahead.

2. A phenotypic trait hierarchy

2.1. Traditional phenotyping

Within plant breeding and genetics, phenotyping always played an essential role. To improve phenotypes via interventions at the genetic level, we need to measure the phenotypes and genotypes precisely and cost effectively. Furthermore, we need suitable G2P models that allow us to identify the most important genetic and environmental factors driving phenotypic variation and to predict the phenotype from genetic and environmental inputs. For complex traits, G2P models will have to address explicitly the phenomenon of G×E [19,21,22]. Traditionally, for the target trait of the breeding process, yield, MET evaluations of breeding material play an important role, where the included germplasm can consist of segregating offspring populations as well as diversity panels. Some popular G2P models for MET data are the following. For

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genotype i in environment j (trial, year by location combination) a simple model is $y_{ij} = \mu_{ij} + \epsilon_{ij}$, where μ_{ij} stands for the expectation or mean of genotype i in environment j, while ϵ_{ij} represents a random residual. Roughly, in this model the expectation expresses the adaptation part of the phenotype of which we think we understand it well enough to predict it for given genotypes and environments, while the residual represents a combination of biological instability (to be modelled by genotype specific stability variances), not modelled phenotypic variation (polygenic variation), and experimental error. For the expectation, we try to find a model that makes the expectation a function of genotype specific sensitivities to environmental covariables: $\mu_{ij} = \mu(\beta_i; z_j)$, for a single environment covariable z with a value z_j in environment j to which the genotype i has a sensitivity β_i. Genetic information can be inserted by making the genotypic sensitivities functions of marker profiles, $\boldsymbol{x_i}$, $\mu_{ij} = \mu(\beta(\boldsymbol{x}_i); z_j)$. When the phenotypic responses for genotypes to the environmental covariable are linear, *i.e.*, the reaction norm is linear, then $\mu_{ij} = \mu(\beta_i; z_j) = \beta_i\, z_j$. The formulation $\mu_{ij} = \mu(\beta_i; z_j)$ allows the reaction norms also to be non-linear. In the latter case, the genotype can be characterized by multiple parameters as well, $\mu_{ij} = \mu(\boldsymbol{\beta}_i; z_j)$. For example, for a logistic dependence, $\mu_{ij} = \frac{\beta_{1i}}{(1+\exp(-\beta_{2i}(z_j - z_0))}$, with β_{1i} the plateau for the reaction norm of genotype i, β_{2i} the slope, and z_0, or β_{3i}, the value for which the response reaches half of its maximum. More flexible formulations are possible by choosing a spline basis for the environmental covariable z, $s(z_j) = \sum_v b_{iv} h_v(z_j)$, with $h_v(z_j)$ one of the elements in a set of the B-spline basis functions relevant to environment j, and b_{iv} a genotype specific spline coefficient. Then, $\mu_{ij} = \mu(\beta_i; s(z_j)) = \mu(\sum_v b_{iv} h_v(z_j))$. [23,24].

In traditional phenotyping, most resources were spent on METs to estimate yield itself, the primary trait, but it was not uncommon either to try to estimate other traits than yield, secondary phenotypes, that could be used as genotype specific covariables in prediction models for yield. For example, $\mu_{ij}^f = \mu^f(\mu_i^s; z_j)$, with μ_{ij}^f the expectation for the focus trait (target trait, primary trait, highest order trait), $\mu^f(a; b)$ a function to generate the expectation for the focus trait with a genotypic input a and an environmental input b, μ_i^s is the genotype specific expectation for a secondary trait measured under controlled conditions and z_j is an environmental characterisation. This type of G2P model will also be suitable to incorporate new phenotyping information. However, the new secondary phenotyping information has higher spatial and temporal resolution than the more traditional secondary phenotyping information, it can come

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from many biological levels of organization, and the number of secondary phenotypes can be huge. We will give examples of such secondary phenotypes below. Therefore, it is not obvious which secondary phenotypes are useful for predicting yield and how the secondary phenotypes should enter existing G2P models. In statistical terms, within a high dimensional regression context, we have simultaneously a covariable subset selection problem and a functional form or transformation problem. Furthermore, our current G2P models may have to be modified to benefit from the large quantity of secondary phenotyping information.

To facilitate the development of a new G2P framework that can incorporate both large quantities of secondary phenotyping information as well as genomic information and environmental characterizations, we want to introduce a conceptual classification of new phenotyping traits. Advanced statistical and crop growth modelling methods will be required to generalize prediction and inference from the genotypes and environmental conditions included in METs to a wider set of genotypes representing the full collection of selection candidates and a wider set of environmental conditions representing the TPE. **Table 1** shows how raw secondary phenotyping data are elaborated and converted into genotype specific covariables that enter G2P for yield. This conversion consists of a number of discrete modelling steps that transform large numbers of basic and raw secondary phenotype data with low predictive power and utility into relatively few genotype specific parameters with high predictive power.

[Table 1 here]

2.2. Feature extraction

Let us define a typical phenotypic observation or measurement as $y_{ir}^{k}(t_{im})$, for trait k $(= 1 \dots n_T)$ genotype i $(= 1 \dots n_G)$ for the r-th replicate $(r = 1 \dots n_R)$ at time point t_{im}, $m = 1 \dots n_{M_{ik}}$. The observation $y_{ir}^{k}(t_{im})$ can be interpreted as a raw data point. Alternative modelling steps add value to the data and aggregate information from raw data points into model parameters. The raw data are null level traits, they are not aggregated over time or environmental gradients and no value addition by modelling has taken place. In a sequence of modelling efforts, the raw data are converted into parameters, higher level traits, that integrate data over time and environmental gradients to become predictors of complex traits like yield.

Modern phenotyping devices and techniques can produce large numbers of variables that each by themselves not necessarily relate in a one-to-one fashion to phenotypic traits of interest. So an important first step in phenotyping is to extract from large numbers of variables those features that are potentially useful for modelling biological and genetic processes and structures. Imaging has become an important secondary phenotyping technique that generates large amounts of information of which only a part will be relevant for phenotypic prediction. There are several methods to extract the features from images (**Fig. 1)**. As images are usually quite noisy, pre-processing and feature-extraction methods are a key first step to produce phenotypic information with improved signal to noise ratios that at a later stage may prove to be useful for predicting a target trait [25,26].

[Figure 1 here]

Strategies to obtain trait information from images might involve segmentation [27,28], tracking procedures to deal with the problem of occlusions between plant organs [29] and using signal intensity at specific wavelengths (or indices derived from these intensities) as a proxy to plant traits. Common proxies using this approach are the normalized difference vegetation index (NDVI) to characterize biomass accumulation dynamics or canopy temperature to identify drought-tolerant genotypes [18,28,30,31]. An alternative is to identify morphological changes in sequential images (*e.g.* time to flowering) and segment specific organs (*e.g.* spikes) or organ surfaces (*e.g.* canopy drought stress [32]).

2.3. Correcting for experimental design factors and spatial variation

The extraction of features from the ample information generated by new phenotyping devices contains aspects of covariable subset selection, transformation and noise reduction. The result of this process is a set of secondary phenotypic traits for which it later on remains to be shown that they are useful for the prediction of primary traits. A first modelling step is now to estimate genotype and treatment means correcting for experimental design factors and spatial variation. Such an analysis is usually done per trait so that we can simplify the model to $y_{ir}(t_{im}) = \mu_i(t_{im}) + \epsilon_{ir}(t_{im})$, with $\mu_i(t_{im})$ the genotype specific expectation for the trait in its dependence on time, while $\epsilon_{ir}(t_{im})$ is a residual. When all genotypes are observed at the same times, we can write $y_{ir}(t) = \mu_i(t) + \epsilon_{ir}(t)$, where we want to estimate $\mu_i(t)$. In principle, when correcting for design and spatial variation we should take into account the dependence in

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time between the observations on the same genotype and plant, but such an analysis is immediately non-trivial. Therefore, analyses are often performed per time point. Effectively we then fit the model $y_{ir} = \mu_i + \epsilon_{ir}$ for each time point, which is equivalent to an analysis of variance, or a mixed model with autoregressive formulations for the dependence in row and column directions [33]. A recently proposed alternative is a mixed model with a two dimensional P-spline basis for spatial variation [34,35]. This spline approach has the advantage of avoiding the difficult model selection step. An example using the so-called SpATS model is given in (**Fig. 2**). The corresponding R-package SpATS is available on CRAN (https://cran.r-project.org/package=SpATS), and produces adjusted means (Best Linear Unbiased Predictions, BLUPs, or Best Linear Unbiased Estimates, BLUEs) as well as generalized heritabilities [36,37]. SpATS is flexible and user-friendly and performs comparably to more elaborate spatial models that require for each experiment a model selection process [34]. The absence of a model selection requirement allows a fully automatic implementation of this method for the analysis of field trial and platform experiments, especially convenient for the analysis of time series of phenotyping data obtained by the use of High Throughput Phenotyping devices. As an example, **Fig. 2** shows the Arabidopsis data coming from the Phenovator platform [38] for the light-use efficiency of PSII of 344 Arabidopsis accessions [39].

[Figure 2 here]

2.4. Dynamic modelling of spatially adjusted secondary phenotypes

Adjustment of genotypic and treatment means for experimental design and spatial variation was done per time point above. The next step is to model the genotypic means (or treatment means of any type) as adjusted for experimental design and spatial variation in relation to time, where these genotypic means are treated as if they were observations themselves, $y_i(t) = \mu_i(t) + \epsilon_i(t)$, with $y_i(t)$ actually being the estimated genotypic mean of the previous modelling step (see section 2.3), which we can write as $y_i(t) \coloneqq \widehat{\mu_i}$ at time *t*.

Models for $\mu_i(t)$ can be parametric, $\mu_i(t) = \mu(t; \boldsymbol{\theta_i})$, with $\boldsymbol{\theta_i}$ a parameter vector for genotype *i* that describes the dependence of its dynamic phenotype $y_i(t)$ on time. Common functions to model trait dynamics are the logistic, Gompertz and exponential growth functions [40–43]. For a logistic relation to time the model would be $\mu_i(t) = \frac{\theta_{1i}}{(1+\exp(-\theta_{2i}(t-\theta_{3i}))}$ with θ_{1i} the upper asymptote, θ_{2i} the slope at the mid-point (where $y_i(t)$ reaches half of the asymptote), and θ_{3i} the time at which the mid-point is reached [41,44]

Fig. 3 illustrates the dynamics of leaf length of two genotypes that have been phenotyped over time, with both genotypes grown under three levels of temperature and two levels of water stress. The leaf elongation dynamics are summarized by a logistic curve. Genotype G1 is not very sensitive to temperature (reflected in the three red curves running close to each other, **Fig. 3A**), but very sensitive to water stress (reflected in the two blue curves running far apart from each other). In contrast, genotype G2 is sensitive to temperature, but not so much to water stress. By fitting a logistic curve we can extract slope parameters (leaf elongation rate) that are at this stage both genotype and environment specific.

Parametric models for $\mu_i(t)$ may be too restrictive to capture the dynamics of traits like canopy temperature, leaf area or senescence. A more flexible alternative for modelling trait dynamics is offered by P-splines [23,24]. For example, P-splines were used to model haulm senescence in potato and identify QTLs for the genotype-dependent slopes [45]. The use of splines can be extended to genomic prediction models for incorporating information from canopy temperature and NDVI over time [46].

In this context of dynamic models for phenotypes, we mention further the work on function-valued trait models, in which explicit mathematical functions describe trait dynamics during the growing season [47]. Genotype specific curve parameters as conditioned by the environment were modelled in relation to a genetic basis within a functional mapping framework by [42,48,49].

Some phenotypic traits are repeatedly measured over time without the genotype specific expectation changing over time. This brings us in the classical repeated measurements situation, $y_i(t) = \mu_i + \epsilon_i(t)$, where for the residual term a correlation structure should be defined that allows for deceasing correlation between time points with increasing separation [50,51]. For example, repeated measures on NDVI were analysed by a multi-trait model with a special structure for the auto-correlation between successive measurements [46].

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The curve parameters, $\boldsymbol{\theta_i}$, represent traits of a higher level or order than the initial time dependent trait $y_i(t)$. They represent an integration over time of this lower level trait. New phenotyping technologies facilitate the characterization of growth and development during the growing season. High temporal resolution of measurements is achieved for secondary traits that are at a lower biological organization level than target or focus traits: leaf and stem size, biomass and disease scores [52,53]. Modelling the dynamics of such lower and intermediate level traits fits into a strategy to replace large amounts of data by limited numbers of genotype specific parameters. These parameters are often rates, like leaf elongation rate. The estimates for the time dynamics parameters can once again form the starting point of a new round of modelling when these parameters are seen as functions of environmental gradients (see next section 3.5)

[Figure 3 here]

2.5. Modelling phenotypes in relation to environmental gradients

In section 2.4 we estimated genotype specific parameters that summarized dynamical behaviour of secondary phenotypes. These parameters were not only genotype specific, but also environment specific. Assume we have also environmental characterizations for the conditions under which the curve parameters were estimated, collected for each experiment or trial in a vector $\boldsymbol{z}_j$. Let the slopes for genotype *i* in environment *j*, θ_{2i}, simply be redefined as a new phenotype, y_{ij}. A model for this phenotype is: $y_{ij} = \mu_{ij} + \epsilon_{ij}$. When we want to express the dependence of the phenotype, for example the curve parameter from section 2.4, on a set of environmental characterizations, we write, $y_{ij} = \mu(\boldsymbol{\beta}_i; \boldsymbol{z}_j) + \epsilon_{ij}$, with $\boldsymbol{\beta}_i$ genotype specific sensitivities to a set of environmental characterizations contained in $\boldsymbol{z}_j$. The function $\mu(a; b)$ generates a genotype and environment specific expectation from a genotype specific input *a* and environment specific input *b*. In its simplest version, a linear regression with one environmental characterization, $y_{ij} = \beta_i z_j + \epsilon_{ij}$.

The genotype specific sensitivities of curve parameters, $\boldsymbol{\beta}_i$, represent again a higher level of integration of phenotypic information. When we consider the dependence of curve parameters on environmental conditions, we effectively have integrated across temporal and environmental gradients. Examples of such high level traits are the physiological parameters that predict yield across environments [53–55]. In **Fig. 4A** and **4B**, they would correspond to the sensitivities of leaf elongation rate (a higher order trait) to temperature and water stress. The sensitivities to multiple environmental covariables can be incorporated in a higher level prediction model for yield.

High precision platform and to some extent whole plant platform measurements aim at the phenotyping of higher-order traits that are expected to show a reduced complexity for the control of G×E because, as they represent sensitivities, their nature already embodies the genotypic response across environmental conditions. The information on the genetic and environmental controls of higher order traits is expected to be transferable to field conditions and to help in predicting yield across the TPE when inserted in appropriate G2P models like factorial regression models, multi-trait models, and crop growth models [56,57]. Evaluations of diversity panels on phenotyping platforms can involve single evaluations at a defined time under controlled environmental conditions. More often these platforms are used to measure time series on multiple traits measured jointly across a range of environmental conditions, thereby allowing analysis of G×E and calculation of higher order phenotypic traits [57–59].

[Figure 4 here]

2.6. Integrating multiple higher order traits in prediction models for the target trait

The structure of G×E observed for the target trait in the TPE and its underlying environmental drivers have a large influence on which phenotypic traits need to be estimated at various biological levels for a successful prediction of the target trait across environmental gradients. When we have an a priori idea of a statistical or physiological prediction model, the structure of such a model can guide us in which secondary traits to concentrate on for measurements at a phenotyping platform. As an illustration, we consider a crop growth model (CGM) that predicts a target trait from small sets of genotype specific inputs and environmental characterizations [60,61]. The inputs for the CGM were at the genotypic side, the physiological parameters total leaf number (TLN, a low level trait), area of largest leaf (AM, a low level trait), solar radiation use efficiency (SRE, a higher order trait), and thermal units to physiological maturity (MTU, an intermediate level trait). For the environmental side of the model, the important inputs were daily average temperature (Temp) and solar radiation (Rad). The structure of the CGM was: $y_{ij}^{f} = \mu^{CGM}(\boldsymbol{y}_i^{s}; \boldsymbol{z}_j) + \epsilon_{ij}$, with y_{ij}^{f} the focus trait, yield, for genotype

i in environment j, $\boldsymbol{y}_i^s$ the input vector of secondary phenotypes (TLN, AM, SRE, MTU), $\boldsymbol{z}_j$ the input vector of relevant environmental characterizations (Temp, Rad), and $\mu^{CGM}(a; b)$ the CGM function that converts genotype specific inputs and environmental inputs in to predictions for the target trait.

In the original study [61], only meteorological data from the weather station Champaign (Illinois) were used to estimate predictions $\hat{y}_{ij}^f$, whereas for additional calculations we used the information of another 19 weather stations in Illinois. After the integration over time and the meteorological characterizations by the CGM, the results of our calculations show non-linear responses for the target trait, $\hat{y}_{ij}^f$, in relation to the environmental covariables latitude and longitude (**Fig. 5A**). The impression is raised that at a suitable statistical model would be $y_{ij}^f = \mu^{Stat}(\boldsymbol{\beta_i}; \boldsymbol{z}_j) + \epsilon_{ij}$, with $\boldsymbol{z}_j$ is latitude and longitude, and $\boldsymbol{\beta_i}$ the genotype specific curve parameters that describe the dependence on latitude and longitude. Both the CGM and statistical prediction model may produce acceptable accuracies (correlation between observed and prediction yield). The difference between both approaches may reside in the robustness of the predictions with respect to the specification of the training set of environmental conditions.

The simulated heritability in our example was 0.85 per location, as in the original study [61]. **Fig. 5A** shows the two-dimensional response surface for yield in 2012 for one of the parents of the simulated DH population [61]), where a mixed model two-dimensional P-spline method was used to fit the spatial trend [62]. **Fig. 5B** shows the response curves for four genotypes as function of latitude, for predictions with the same longitude as Champaign. The early mature genotype (TLN=6) is performing best at high latitude, while the other three genotypes show non-linear response curves.

[Figure 5 here]

2.7. A reference framework for evaluating the prospects of secondary phenotyping information for improving the prediction of target traits.

In earlier sections, we have introduced a number of G2P models that predict target traits from genotype specific and environmental inputs. Furthermore, a number of these models offered possibilities for incorporating secondary phenotyping information. Within the framework of a G2P model the contribution of secondary phenotyping to prediction of the target trait can be assessed in a number of ways. In later sections, a number of examples will be given of possible improvements by the introduction of secondary phenotyping information into G2P models. The situation we envision for our modelling purposes is the following. We have at our disposal a set of field experiments for a target trait that belong to a MET that is supposed to represent the TPE. The target trait is estimated only once, at harvest, and no dynamical information is available for the target trait. We have measurements with phenotyping tools in one or more trials of the MET as well as on possible phenotyping platforms. With respect to secondary phenotyping, we may want to compare different technologies as well as sampling and measurement schemes.

For statistical G2P models, and ignoring the time dependency of the focus or target trait, we can think of observations for genotype *i* in environment *j*, y_{ij}^{f}, and we want to predict yield from genetic and environmental information, as well as from secondary phenotyping information:

$$y_{ij}^{f} = \mu\left(G(\boldsymbol{x}_i), E\left(\boldsymbol{z}_j\right), P(\boldsymbol{y}_{ij}^{s})\right) + \epsilon_{ij}^{f}$$

in which $\mu\left(G(\boldsymbol{x}_i), E\left(\boldsymbol{z}_j\right), P(\boldsymbol{y}_{ij}^{s})\right)$ is a function that generates the expectation for the target phenotype on the basis of three arguments: 1) a genotype related function, *G(.)*, working on genotype specific genetic information, which can include marker information (SNPs, sequence profile), contained in the input vector $\boldsymbol{x}_i$; 2) an environment related function, *E(.)*, working on environment specific information contained in the vector $\boldsymbol{z}_j$ consisting of summaries for meteorological, soil and management variables; 3) a phenotype related function *P(.)* working on secondary phenotypic information, $\boldsymbol{y}_{ij}^{s}$, with $s \in S$, the set of secondary phenotypes, which can be genotype specific or, more often, can depend on a combination of genotype and environment (**Figs. 3, 4 and 5**).

In many statistical-genetic G2P models, the functions *G(.)* and *E(.)* are simply identity functions and a dependence on higher order traits is absent, while the function $\mu\left(G(\boldsymbol{x}_i), E\left(\boldsymbol{z}_j\right), P(\boldsymbol{y}_{ij}^{s})\right)$ is a multiplication of genotypic and environmental information. For example, $\mu\left(G(\boldsymbol{x}_i), E\left(\boldsymbol{z}_j\right), P(\boldsymbol{y}_{ij}^{s})\right) = \mu\left(G(\boldsymbol{x}_i), E\left(\boldsymbol{z}_j\right)\right) = \mu\left(x_i; z_j\right) = \theta x_i z_j$, with x_i a count for the number of minor alleles for a marker in a quantitative trait locus (QTL) or candidate gene (between 0 and 2), and z_j an environmental covariable like the average temperature in a critical developmental stage, and θ is the QTL allele substitution effect that scales with the environment

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[19,21,22,63–65]. Traditional G2P models need to be generalized to accommodate secondary phenotypic information. Various options will be discussed in the remainder of this paper.

Traditional statistical models for MET data do not contain dynamical aspects, developmental time is not explicitly present in such models. In contrast, CGMs have the dynamics of development as the core of their model formulation. One possible mathematical-statistical description of a CGM is as follows. Assume we consider yield as the focus trait, *f*, for genotype *i* in environment *j* at time T_j (harvest time in environment *j*, taken to be the same for all genotypes):

$$y_{ij}^{f}(T_j) = \int_0^{T_j} \mathfrak{F}_t \left[\left(\boldsymbol{y}^{s\in S_P}(\boldsymbol{x}_i) \right);\ \left(\boldsymbol{y}^{s\in S_I}(\boldsymbol{x}_i, \boldsymbol{z}(t_{\boldsymbol{j}})) \right) \right] dt + \epsilon_{ij}^{f},$$

In a crop growth model, yield depends on two sets of underlying or component traits: 1) physiological parameters that are functions of DNA variation, represented by a SNP vector, $\boldsymbol{x}_i$, that have no environmental and no time dependence, $\left(\boldsymbol{y}^{s\in S_P}(\boldsymbol{x}_i) \right)$, with the secondary phenotypes, denoted by *s*, belonging to the set S_P set of physiological parameters; 2) intermediate traits with G×E that are SNP, environment and time dependent, $\left(\boldsymbol{y}^{s\in S_I}(\boldsymbol{x}_i, \boldsymbol{z}(t_{\boldsymbol{j}})) \right)$ with S_I the set of intermediate traits. The environment dependence of the intermediate traits is expressed by a dependence on a vector of time varying environmental variables, $\boldsymbol{z}(t_{\boldsymbol{j}})$. So, the focus trait is typically evaluated at a single time point at the end of the growing season, at harvest time, $t = T_j$, and is a dynamical function $\int_0^{T_j} \mathfrak{F}_t [[;]] dt$ integrating over time, with as arguments physiological parameters, intermediate traits, and environmental information. We add an error term ϵ_{ij}^{f} as a simple way of introducing some stochasticity into the system.

For physiological parameters, S_P, think of resource capture (*e.g.*, leaf angle, root architecture), conversion efficiency (*e.g.*, light use efficiency, water use efficiency) and biomass allocation to yield (*e.g.*, harvest index). For environmental variables, think of the amount of resource (*e.g.*, light, water, nutrients) and conditions as temperature and CO_2 [3,20,66,67]. The combination of CGMs for yield with QTL or genomic prediction models for component traits is described in multiple papers [53,61,68–74]. The attraction of such G2P models is that they in theory allow to predict phenotypes for combinations of new genotypes and environments from marker profiles and environmental characterizations.

In the case of statistical models, for the estimation of parameters, a loss function can be defined on the discrepancy between observations on the primary trait for MET data representing the TPE and the predictions of the G2P model [75]. A loss function puts weights on the discrepancies $(y_{ij} - \hat{y}_{ij})$ during the estimation of model parameters. The choice of loss function determines the estimation and inference procedure including the model building. A well-known loss function is least squares, where parameters are estimated to minimize $\left(y_{ij} - \hat{y}_{ij}\right)^2$. An alternative estimation and inference procedure is based on maximization of (residual) maximum likelihood [76]. Given a G2P model for a primary trait and an inference procedure we can investigate to which extent the insertion of secondary phenotyping information itself or features extracted from secondary information into the G2P model leads to a smaller residual variance or higher likelihood.

Another popular way of assessing the quality of secondary phenotyping information is by the correlation between observed and predicted primary trait values, *i.e.* $\text{corr}\left(y_{ij}; \hat{y}_{ij}\right)$, where this correlation is often calculated as part of a cross validation process. Utility of phenotyping information can then be established by inspecting these correlations for different G2P models. This cross validation approach can be applied to both statistical and crop growth models.

For CGMs genotype specific information on a number of physiological parameters may be required that can be difficult to obtain. Phenotyping platforms may then produce direct estimates for such parameters or approximations to such parameters. In such cases, the contribution of secondary phenotyping to genetic gain may be less straightforward to assess. In general, any correlation of secondary phenotypes to genotype specific inputs for G2P models will contribute to genetic gain, where higher level phenotypes will be more useful than lower level phenotypes because they are closer to the target trait, their phenotypic distance to the target trait is smaller [77]. Just like any correlation of secondary traits with G2P inputs will be useful, so will QTLs that are shared between secondary traits and G2P inputs.

In this paper, with respect to G2P models to consider, we will focus on linear mixed models (LMMs) and crop growth models (CGMs), although we will also address Bayesian approaches. We will describe G2P models for a primary trait like yield and illustrate how these models help in assessing the usefulness of phenotyping strategies.

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3. Statistical G2P models

3.1. A correlated response framework connecting measurements on plant platforms and field observations

Consider the simple case that a secondary trait is measured on a precision or whole-plant platform, y^s, to serve as an estimate for a similar and/or related trait in the field, y^f. Best is to think of a higher order trait like genotype specific physiological parameter that expresses the sensitivity to a certain environmental condition or factor and that we can estimate earlier, easier, more precisely or more cheaply under controlled conditions. We want to use the platform estimate to predict a similar and/or related environmental sensitivity for fields belonging to the TPE, where the TPE can be represented by a series of experiments belonging to a MET.

The singularity of the platform and the field trait is a convenient opportunity to apply classical quantitative genetic theory on correlated responses as a framework to assess the utility of phenotyping. Realistically, the single trait on the platform may be a higher order secondary trait, a function of platform traits like a genotype specific summary across multiple measuring times or environments, a principal component calculated from a set of platform traits, or a selection index calculated to maximize the selection response for a trait in the field/TPE. The single trait in the TPE can again be a function of a number of field traits, *i.e.* a summary statistic like a genotypic mean, a sensitivity to an environmental gradient, or a selection index calculated from the experiments in a MET.

Let us assume that the trait as measured on the platform will consist of an intercept, genetic part and an error part, $y_i^s = \mu_i^s + G_i^s + \epsilon_i^s$, similarly so for the trait in the field/MET/TPE, $y_i^f = \mu_i^f + G_i^f + \epsilon_i^f$. We assume that the TPE is known and the field experiments in the MET represent a random draw from the TPE, so experiments are exchangeable and G×E is a source of error variation, and no repeatable interactions can be identified. For the latter case, a regression approach is a more suitable than a correlation approach.

We may want to select genotypes on superior performances in the platform response, anticipating that the correlated selection response for the field trait will be larger than when selecting directly on the field response itself. Using indirect selection response theory we can say that this approach makes sense when the genetic correlation between platform and field,

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$\rho^{(s,f)}$ is high, *i.e.*, the same genetic basis is involved, and the heritability on the platform, $h^{2,s} = \frac{V_{G^s}}{V_{y^s}} = \frac{V_{G^s}}{V_{G^s} + V_{\epsilon^s}}$, is higher than the heritability in the field, $h^{2,f} = \frac{V_{G^f}}{V_{G^f} + V_{\epsilon^f}}$. More precisely, when the condition is fulfilled that $\rho^{2,(s,f)} h^{2,s} > h^{2,f}$ it makes sense to select on the platform representation of the trait in place of the field trait itself. The heritability at the platform may be higher because the conditions at the platform can be better controlled or more replicates can be taken, hence the error variance, V_{ϵ^s}, is smaller than the error variance in the field, V_{ϵ^f}. Additionally, the genetic variance at the platform, V_{G^s}, can be increased by choosing environmental conditions that are more strongly discriminating between genotypes and it is larger than the genetic variance in the field, V_{G^f}. The genetic correlation between platform and field depends on the extent to which the conditions in the field induce the same genes or QTLs to be expressed as on the platform, where the sign of the QTL effects should coincide and the magnitude of the effects should be proportional between platform and field.

For a full evaluation of correlated responses versus direct responses, economic considerations for measurements on platforms and fields should be included as well. In that case, a selection index with economic weights is recommended. For example, economic weighting coefficients were included for the combination of several primary traits for sugar cane (biomass yield, sugar and fibre content)[78,79]. The index can also consider traits (*e.g.* physiological measurements) that do not have a direct economic impact, but correlate with economically important traits. In sugarcane for example, it was found that across diverse genotypes, the secondary phenotype mid-season plant stomatal conductance was highly correlated with total biomass yield, and this trait could be used as a proxy during the earlier stages of selection when genotype numbers are high, and plots are small, such that biomass yield *per se* is not reliable [80]. (Although the secondary trait is here not measured on a platform but in the field, the logic of correlated response remains valid.)

When multiple measurements of the same trait under different environmental conditions are taken on the platform and the field, the framework can be extended to include G×E in either or both of platform and field. For that situation, the expressions for the heritabilities and the genetic correlation need to be modified. If we assume that repeated platform and field experiments can be interpreted as coming from a specific distribution of platforms, respectively, field experiments, then the error variances for platform and field in the expressions above should be replaced by $\frac{V_{GE^s}}{n_{e^s}} + \frac{V_{\epsilon^s}}{n_{e^s} n_{r^s}}$, with V_{GE^s} the genotype by experiment interaction (G×E) variance for repeated experiments at the platform, n_{e^s} the number of experiments at the platform, V_{ϵ^s} is now the intra block variance for the platform (assuming a randomized complete blocks design was used), and n_{r^s} the number of replicates per platform experiment. Similar quantities can be defined for the field. Depending on the magnitude of the genotype by experiment interactions and the intra block errors, one can balance the number of experiments and replicates per experiment to find an efficient allocation of resources in which the platform heritability reaches a certain desired value. Whether this number of experiments and replicates is feasible will depend on additional information known to the breeder, where economic arguments will play an important role.

The size of the error variance is thus largely under control of the breeder. This is to a lesser extent the case for the value of the genetic variance and the correlation between platform and field. The magnitude of these genetic parameters will depend on the timing of measurement and the method of measurement on platform and field as well as on the environmental conditions up to the measurements [81].

3.2. Illustrative examples correlated response framework for high precision and whole-plant platforms to predict phenotypes in the field

Grain yield in maize depends on the ability of leaves and silks to maintain growth under fluctuating environmental conditions, especially under drought. Characterizing growth of leaves and silks under a range of environmental conditions in the field is a difficult task. Platforms have the advantages of facilitating more frequent and detailed measurements and also offer larger possibilities of controlling the environmental conditions than field experiments. For that reason, they are an interesting alternative to characterize relevant traits for drought adaptation in maize. For example, platform phenotypes have been used to estimate leaf elongation rate per unit of thermal time and the slope of leaf elongation to evaporative demand and soil water status [52]. QTLs of maximum leaf elongation rate on the platform co-located with QTLs of the anthesis-silking interval in well-watered fields, with alleles conferring high leaf elongation rate conferring a low anthesis-silking interval. The QTLs of the response of leaf elongation rate to water deficit at the platform co-located with QTLs of anthesis-silking interval in water deficit fields. For these QTLs, the allele conferring a larger anthesis-silking interval in the field (hence a reduced silk elongation rate) was also the one leading to a smaller leaf elongation rate on the platform. This suggested that common genetic mechanisms are shared

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between the growth of reproductive organs in the field and leaf growth on the platform. These conclusions were further supported by a metaQTL analysis in which QTLs for maximum leaf elongation rate on the platform co-located with QTLs involved in the growth of shoots, roots, but also reproductive organs in controlled conditions and fields [82,83]. Further, the sensitivity of leaf growth to soil water deficit at the phenotyping platform was related to the sensitivity of maize grain number to soil water deficit around flowering time in the field [84]. A more detailed characterization of the sensitivity of leaf growth to environmental conditions was demonstrated and a model to predict leaf area in the field, as a function of leaf length and width and their respective sensitivities to intercepted light and evaporative demand has been proposed [57]. Platform and field data were used to calculate the genotypic sensitivity of leaf elongation to evaporative demand and of leaf width to intercepted radiation, respectively. The advantage of combining platform and field data is that the platform allowed a larger temporal resolution in the phenotypic and environmental measurements (leaf elongation rate, air temperature, air humidity and leaf temperature were measured every 15 min) and it also allowed to impose more specific levels of water limitation (and soil water potential higher than -0.05 MPa via automatic irrigation). The response of leaf elongation rate (leaf 6) to leaf-to-air vapour pressure deficit was estimated by using data at the time step of 15 min during daily peaks of vapour pressure deficit. The equations for the sensitivities of leaf elongation to evaporative demand and of leaf width to intercepted radiation were tested in an external data set, a network of 15 field experiments. Equations to predict leaf length and width resulted in an accurate prediction of individual leaf area in the whole field dataset ($R^2 = 0.62$). QTL allelic effects underlying leaf width and length were smaller in the platform than in the field, but they were clearly correlated between platform and field experiments. Thus, although there was G×E between platform and field experiments, the correlated QTL effects would still allow to use platform data to improve selection for leaf area in field conditions [57].

Another example of the use of indirect selection for field conditions based on traits measured in controlled conditions is the following. Nine early vigour characteristics of wheat F2:4 plants grown in trays (coleoptile tiller frequency, number of primary tillers, number of main stem leaves, breadth of leave 2, leave 3, mean leaf breadth, length of leaf 2, specific leaf area, plant leaf area and biomass) were evaluated to improve biomass production in the field for F2:6 plants [85]. Tray performance was a good predictor of field performance for leaf breadth and length, leaf area, and plant biomass. Genetic correlation between traits measured on the trays and biomass in the field was highest for biomass (r = 0.61), suggesting that early biomass measured

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on the trays was a good predictor for early biomass in the field. Other traits measured on the trays that showed a moderate to high genetic correlation with field biomass were plant leaf area (r = 0.59), length of leaf 2 (r = 0.43), length of leaf 3 (r = 0.41) and mean leaf breadth (r = 0.40). The most promising for indirect selection were mean leaf breadth and breadth of leaf 2, with a relative gain from indirect selection that was 61 and 60% of the gain to be obtained from directly selecting for biomass in the field. Although plant leaf area on the tray showed a larger genetic correlation with field biomass than mean leaf breadth and breadth of leaf 2, it had a lower heritability ($H^2_{plant\ leaf\ area} = 0.30$, $H^2_{mean\ leaf\ breadth} = 0.82$, and $H^2_{breadth\ leaf\ 2} = 0.76$) reducing its potential to be used for indirect selection (relative gain from indirect selection for leaf area on the tray was 55%). This example illustrates the importance of jointly considering the magnitude of genetic correlations between traits measured on the platforms and those in the field and trait heritability to assess the potential of traits to aid selection for early biomass in the field. One aspect that would need to be further assessed in this study [85] is whether selection for early biomass is indeed correlated to yield at the end of the growing season. Only if the correlation between early biomass and yield is reasonably large, it would be advantageous to use early biomass measured in the trays as early selection trait. In the previous example, all phenotyping was done by hand, which is a time-consuming process. However, thanks to imaging technologies, the approach could be scaled up to a breeding programme. For example, the dynamics of early growth for individual plants grown in greenhouse trays could be characterized with multi-view images [86]. Examples presented above are summarized in Table 2.

[Table 2 here]

3.3. A multi-trait prediction framework for yield using high throughput phenotyping information

HTP devices in the forms of sensors, drones, unmanned aerial vehicles generate high dimensional secondary phenotypic data for experiments that are part of METs representing the TPE. The HTP information is used to approximate yield related traits and components over the growing season. The HTP information is introduced in the form of additional traits alongside yield in multi-trait G2P models.

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A multi-trait mixed model for genotype *i* and trait *k* can be defined as follows $y_i^k = \mu_i^k + G_i^k + \epsilon_i^k$, with μ_i^k the fixed intercept for trait *k*, and G_i^k the random trait-specific genetic effect for genotype *i* and trait *k*, while ϵ_i^k is a residual. The random genetic effects G_i^k will have a multivariate normal matrix distribution with mean zero and variance-covariance matrix (VCOV) $\boldsymbol{\Sigma}$: $\{G_i^k\} \sim MVN(\mathbf{0}, \boldsymbol{\Sigma})$ (Cullis et al., 2005). The VCOV for the genetic effects, $\boldsymbol{\Sigma}$, has a special structure that can be interpreted as a product of a VCOV defined on the genotypes, $\boldsymbol{\Sigma}^G$, where pedigree and/or marker information determine correlations between genotypes, and another VCOV defining the genetic variances and correlations between traits, $\boldsymbol{\Sigma}^T$, where each trait has its unique genetic variance and each pair of traits has its unique genetic correlation. The above multi-trait model is customarily turned into a multi-trait genomic prediction model by defining the matrix $\boldsymbol{\Sigma}^G$ in terms of similarities between marker profiles of genotypes [87].

A multi-trait model can be generalized to multiple environments: $y_{ij}^k = \mu_{ij}^k + G_{ij}^k + \epsilon_{ij}^k$ with intercept μ_{ij}^k and a random genetic effect G_{ij}^k and a residual ϵ_{ij}^k. The VCOV for the genetic effects has a multi-variate normal distribution with zero mean and will have to represent the trait by environment variances and correlations. In the context of genomic prediction models for multi-environment data with G×E, VCOV structures for the environments have been described [88,89]. The VCOV for environments can be based on similarity in environmental characterization between environments, a generalization of the fixed factorial regression models, see next section, like in [89,90] and [91]. For the simultaneous modelling of VCOV structures for genotypes, environments and traits, see [92].

For the identification of multi-trait mixed models one can use log-likelihood ratio tests to compare different VCOV structures for G_i^k or G_{ij}^k (see [93]) where the differences relate to how to combine pedigree and marker information for the genotypes in $\boldsymbol{\Sigma}^G$ [94–96], which traits to include alongside yield in $\boldsymbol{\Sigma}^T$, and how to efficiently represent the relations between environments in a VCOV for environments, $\boldsymbol{\Sigma}^E$, and/or which environmental characterizations to use to calculate environmental correlations [89]. To test the utility of secondary phenotyping information, log-likelihood ratio tests can compare the fit of multi-trait models with differing sets of secondary traits. See also [97]. If these tests cannot be applied, because the VCOV models are not nested, then information criteria like AIC or BIC may be used [98,99]. Of course, models can also look at the predictive ability of models with different sets of secondary phenotypes.

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The most common multi-trait prediction scenario considers yield and basic phenotypes measured simultaneously at the end of the growing season (*e.g.* [100,101]). A second (and less explored) scenario combines information from yield measured at harvest with low level phenotypes measured over multiple time points during the growing season, or with higher order traits that summarize the response of low level traits over time. Incorporating the genotype specific responses during the growing season into a prediction model provides a better insight in the traits underlying adaptation to particular growing conditions [8,72,102].

3.4. Illustrative examples of multi-trait prediction to incorporate high precision and whole-plant platforms

One example for multi-trait prediction is the use of aerial measurements of canopy temperature, and green and red normalized difference vegetation index (NDVI) as secondary phenotypes to increase accuracy for grain yield in wheat [30]. In [30], single trait predictions were compared with multi-trait predictions across environments differing for the level of drought and temperature stress. In this example, prediction accuracy for yield increased by 70%, averaged across environments. The benefit from modelling multiple traits simultaneously was similar for all environmental conditions.

An important issue to be considered when doing multi-trait prediction in multiple environments is to which extent those secondary phenotypes are related to phenology. Correcting for days to heading improved single-trait prediction accuracies across environments, suggesting that the G×E variance for grain yield corrected for days to heading is lower than that of uncorrected grain yield [30]. For both within- and across-environment prediction, correcting for days to heading reduced the genetic correlations between grain yield and the secondary traits, which in turn reduced the accuracy gained from including secondary trait data. A strategy to take full advantage of secondary trait data while avoiding indirect selection on a phenological trait may be to include data on the phenological trait in a multivariate prediction model alongside with any available secondary traits, and then use the multivariate BLUPs to calculate a selection index with yield and the phenological trait weighted appropriately [30].

3.5. Factorial regression incorporating platform traits for prediction of yield in the field

In a factorial regression approach for platforms, we have to assume for statistical reasons that platform traits are measured without error, which in practice means little error, and can therefore

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be used as genotypic covariables in factorial regression models to predict yield for the field. Typically on a platform, a set of genotypes is measured and the secondary phenotypes become genotype specific covariables. However, by a smart use of platforms to measure development-related traits, it is also possible to define genotype and environment specific covariables (see example below). The prediction models can be of different classes. Simplest are regression models in which either genotype or genotype by environment specific covariables are introduced to predict a target trait. The complexity of the factorial regression model depends on the number and type of genotypic and environmental covariables that are included in the fixed part of the model and the assumptions that are made with respect to the structuring of the random residual.

A simple statistical model for the value of a primary field trait (yield) for genotype *i* in environment *j* is: $y_{ij}^{f} = \mu_j^{f} + g_i^{f} + ge_{ij}^{f} + \epsilon_{ij}^{f}$, with μ_j^{f} a fixed environmental intercept, g_i^{f} a fixed genetic main effect, ge_{ij}^{f} fixed G×E, and ϵ_{ij}^{f} a random residual, which can be structured in various ways. To start, for the G×E term, the purpose will be to identify genotypic covariables that can be combined with environmental covariables and leave a proportionality constant to be estimated, $ge_{ij}^{f} = \sum_{c \in C, d \in D} \theta_{cd} y(\boldsymbol{x}_i)_c^{s} z_{jd}^{e} + \delta_{ij}^{f}$, with $y(\boldsymbol{x}_i)_c^{s}$ a genotype specific predictor measured at the phenotyping platform with a genetic basis contained in $\boldsymbol{x}_i$, z_{jd}^{e} an environmental characterization, and θ_{cd} a scaling constant for the product $y(\boldsymbol{x}_i)_c^{s} z_{jd}^{e}$ that requires estimation. Lastly, δ_{ij}^{f} represents a lack of fit term. The full sets of genotypic and environmental covariables are denoted by *C* and *D*, respectively. Although the genotypic specific platform traits can be related to their genetic basis by fitting a QTL or genomic prediction model this extra step of modelling is optional in that the field trait can be predicted directly from the platform traits at the phenotypic level as well as from their predictions from a genetic model. The use of a genetic model for the platform traits allows extending the selection set of genotypes by predicting platform trait values for non-phenotyped genotypes (at the platform). The genotypic and environmental covariables can include quadratic and cross product terms as well to allow the fitting of response surfaces. Another useful generalization is to allow the covariables to be expressed with respect to a spline basis.

The approximation of the field response G×E model term by products of platform genotypic covariables and field environmental characterization covariables can equally be applied to the total of genotype dependent terms as follows: $g_i^{f} + ge_{ij}^{f} = \sum_{c \in C, d \in D} \theta_{cd} y(\boldsymbol{x}_i)_c^{s} z_{jd}^{e} + \delta_{ij}^{f}$.

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For the fitting of predictive models of the above types linear mixed models, penalized regressions and Bayesian approaches are required that allow for the modelling of the residual terms δ_{ij}^{f} and ϵ_{ij}^{f} with general variance-covariance structures allowing for kinship relationships between genotypes and heterogeneity of variance and correlation for environments. An important problem is the selection of predictive genotypic and environmental covariables in variable selection procedures. For penalized regression the choice of penalties requires attention, which translates to the choice of priors in the Bayesian context. The complicating issue is the simultaneous selection or penalization of information in the genotypic and environmental direction.

Selection of predictive environmental covariables becomes even more difficult - yet even more vital - when considering high-frequency data obtained from sensors. Weather stations and soil moisture probes report environmental conditions throughout the growing season, on a daily, hourly, or even more frequent basis. These characterizations potentially can be incorporated as environmental covariables after variable selection or as principal components after dimensionality reduction, but then the G×E interactions at any given time point of observation will be lost.

3.6. Illustrative examples of factorial regression incorporating platform information

To build factorial regression models for prediction of yield in the TPE, a platform may be used to estimate genotype specific phenologies. Subsequently, for individual genotypes the time spent in different phenological stages can be calculated. The next step is to calculate summary statistics for environmental variables like minimum, maximum and average temperature, rainfall, radiation, and further variables for each genotype in each developmental stage. The assigned value for an environmental covariable in environment *j* for a genotype *i* in a particular growth stage depends on the beginning and end time of that growth stage for that genotype in that environment. Therefore, the covariable should be indexed by genotype, *i*, and environment, *j*, as well as the covariable itself, *d*: z_{ijd}. G×E can be modelled in terms of such genotype specific environmental covariables as $ge_{ij} = \sum_{d \in D} \beta(\boldsymbol{x}_i)_d z_{ijd}$, with the genotypic sensitivities, $\beta(\boldsymbol{x}_i)_d$, being a (possible) function of a SNP profile. In maize, the progression of phenological stages closely follows thermal time, with a nearly constant leaf appearance rate [102]. Thermal time based on meristem temperature can be used to calculate leaf stages at the platform and in the field, provided that the leaf emission rates are the same. Leaf stages

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correspond to developmental stages of the ear [103] and can be used to define phenological periods. So, measuring leaf appearance at the platform allows to define the length of phenological stages in the field and to calculate the environmental conditions working at a particular genotype in a field experiment. In that way, environmental covariables can be calculated that are genotype and environment specific. With respect to those covariables, genotypic sensitivities are estimated. For the maize panel, three environmental covariables could be identified that explained a substantial part of the G×E [19]. These sensitivities could successfully be predicted from marker profiles in a genomic prediction. Therefore, the G×E in this example could be predicted from marker data and environmental covariables by using a factorial regression model. The platform served to estimate the length of genotype specific phenological stages and environmental characterizations.

3.7. Structural equations and network models

Structural equation models (SEMs) are an alternative class of statistical models describing the relations between primary traits and secondary traits [104]. In their simplest form, SEMs describe functional relations among traits in a single environment and at a single time point. The response for genotype *i* and trait *k* is then modelled as $y_i^k = \mu^k + \sum_{v \in pa(k)} \lambda_v^k \, y_i^k + \epsilon_i^k$, where μ^k is a trait specific intercept, $pa(v)$ is the set of parents of trait *k* (*i.e.* the traits affecting trait *k*), and the λ_v^k's are path coefficients, describing the strength of the relations. In the classical SEM literature [105], the functional relations are linear and the errors Normal, but generalizations are possible [106]. See *e.g.* [107] for a non-linear example in rice. SEMs are conceptually similar to factorial regression and crop growth models (in the sense that a primary trait is modelled in terms of component traits), but are more suitable for modelling additional levels of biological variation: the components can in turn depend on metabolites, methylation, proteins, gene expression, etc. The main advantage of structural models over regression models is the ability to predict the behaviour of the system after an intervention (*i.e.* selection decision), which mathematically is defined as a change in one or several of the structural equations. This property makes SEMs a tool for ideoptype design, helping breeders to define a selection strategy.

While SEMs rely on functional relations specified beforehand, methods for causal inference aim to learn relations between traits from observational data, which is of particular interest for traits that are only partially understood [108]. The earliest causal inference methods such as the

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PC-algorithm learn relations by estimating and comparing all the relevant conditional (in)dependencies between variables [109]. Under certain assumptions (notably the absence of feedback loops and latent variables) this gives the partially directed graph that is most consistent with the data.

In the context of G2P models, causal inference methods have been used to model relations between traits at several biological levels and QTLs [110–117], or between random genetic effects [118,119]. Several causal inference methods have also been used to estimate causal effects among yeast traits, outperforming regression approaches [120,121].

More recent causal inference approaches rely on invariance or time-course data [122,123]. Although longitudinal networks have shown promise in other fields [124], they have not yet been assessed in the context of plant breeding, making them worthwhile for exploration in further research. Another important open question is the extension to structural models for multiple environments. Variation in genetic correlations between traits across environmental conditions is an important form of G×E [92,125,126]. Network models could make such changes visible in a biologically meaningful way.

4. Crop growth models as G2P models

4.1. A crop growth modelling framework aiming at prediction

The G2P models in section 3 are all static, the time dimension proper to growth and development can only be incorporated in a limited and somewhat artificial way. Crop growth models (CGMs) present a class of G2P models that integrate genetic and environmental variables in a natural way over time [53,61,127,128]. This solves several problems. First, the need for dimensionality reduction or variable selection of environmental covariables is eliminated. Second, the interaction of the crop with the environment across time is automatically accounted for. This essentially eliminates the need to correct for flowering time, as phenology is incorporated into the model. Finally, it takes advantage of previously determined biological interactions and observations of plant growth and development to estimate the target (such as yield) from a set of higher order traits [129]. The higher order traits used to parameterize the CGM for the target trait may exhibit higher heritability and stability across environments than the target trait itself, and therefore selection on those secondary traits

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may be more efficient than selection on the target trait itself, as long as the physiological processes are properly modelled [129].

In section 2.7, we described a CGM for a target trait *f* for genotype *i* in environment *j* as follows

$$y_{ij}^{f}(T_j) = \int_0^{T_j} \mathfrak{F}_t \left[\left(\boldsymbol{y}^{s \in S_P}(\boldsymbol{x}_i) \right);\ \left(\boldsymbol{y}^{s \in S_I}(\boldsymbol{x}_i, \boldsymbol{z}(t_{\boldsymbol{j}})) \right) \right] dt + \epsilon_{ij}^{f}.$$

The target trait, yield, depends on physiological parameters without environment and time dependence, $\left(\boldsymbol{y}^{s \in S_P}(\boldsymbol{x}_i) \right)$, and intermediate traits with G×E that are environment and time dependent, $\left(\boldsymbol{y}^{s \in S_I}(\boldsymbol{x}_i, \boldsymbol{z}(t_{\boldsymbol{j}})) \right)$. The time varying environmental variables, $\boldsymbol{z}(t_{\boldsymbol{j}})$ determine the environment dependence of the intermediate traits. The secondary traits are functions of SNP variation via the argument $\boldsymbol{x}_i$, the SNP profile. The target trait is evaluated at the end of the growing season, for $t = T_j$. The dynamical function $\int_0^{T_j} \mathfrak{F}_t [[;]] dt$ integrates physiological and intermediate traits over time,

For most commonly used models, the time dimension is expressed at a daily time step, although hourly time steps have been recently proposed for sugar cane [130] and potato [131]. Therefore, most CGMs are not continuous time but discrete time models. Models combining processes occurring at different times scales and with facilities for feedback loops between physiological parameters and intermediate traits can generate reproducible emergent properties at plant level [12,55].

For the estimation of parameters in a CGMs, Bayesian approaches are attractive [132,133]. Bayesian approaches have powerful capability to optimize multiple parameters in a nonlinear and complex model and to quantify the uncertainty in estimated parameters and predictions. Good demonstrations of Bayesian approaches in the integration of CGMs and genomic prediction models are [61,134,135]. The Bayesian framework enables information sharing between genotypes, which can contribute to the improvement of prediction accuracy. Moreover, the integration may enable the dissection of a target trait that has nonlinear relationship with genome-wide markers into component traits which are controlled in purely linear way [61]. Another advantage of Bayesian approaches is the possibility to use expert knowledge of breeders and/or historical experimental data as prior information.

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Modelling can also be useful to evaluate the design of phenotyping strategies and the efficiency of resource allocation. Key design issues concern the number and type of environments to include in METs and the number and type of genotypes and traits that can be phenotyped. Other relevant design issues are how to choose the selection intensity on individual traits to arrive at the realisation of an ideotype, and how frequent and how precise phenotyping methods needs to be to increase prediction accuracy.

4.2. Construction of a training set of environments

When G×E is present in the TPE, the choice of which environments to use for phenotyping becomes crucial to obtain high prediction accuracies, as the environments used for training should represent well the environmental conditions in which future varieties will be grown [91]. The structure of G×E has a large influence on whether it is convenient to obtain field phenotyping information from METs (relying on the natural year-to-year variation to represent the range of environmental conditions relevant to the TPE), or whether it is necessary to use managed stress environments to ensure that all relevant levels of environmental variation are covered. The choice for one or the other strategy will depend on how well locations in an average year represent the whole range of environmental conditions and on the estimated year-to-year variation [8,136,137].

Crop growth models offer a valuable tool to characterize the G×E structure and to separate repeatable from non-repeatable G×E components. For example, the crop growth model APSIM was used to classify environments according to their water-deficit patterns [138] and to give an impression of the repeatability of a given water-deficit pattern at a given location, across years. The APSIM model has also been used to define the drought patterns of maize in Europe [139]. These results were used to develop a detailed QTL model with environment dependent QTL expression. Combining the drought patterns with temperature variation resulted into six different environmental scenarios that were introduced as a classifying factor in a multi-environment QTL model [19]. Such an approach allows to identify the most likely water-stress scenario in a particular location and the QTL-alleles that should be selected. The CGM output can also be used to develop statistical criteria to optimize METs to increase prediction accuracy for the target trait [140] or to characterize genotype-by-environment-by-management interactions, helping breeders, physiologists and agronomists to better understand the drivers of genotype adaptation [129,141].

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4.3. Construction of a training set of genotypes

The parametrization of statistical and crop growth models requires intensive phenotyping efforts. In place of measuring expensive physiological traits on all genotypes of a selection set, one can try to estimate these parameters on a reduced training set of genotypes and then predict the parameters for the total of the selection set of genotypes by QTL or genomic prediction models. For the construction of a training set of genotypes that well represent the selection set, a diversity analysis based on molecular markers is useful. See [142–144] for examples of strategies to select genotypes for the training set. Alternatively, and relying only on phenotypic data, principal components analysis of morpho-physiological traits can be used to identify an appropriate training set for estimating growth model parameters. For an example in sweet potato germplasm, see [145].

4.4. Ideotype construction and identification of selection targets

Once the major environments types encountered in the TPE are identified and characterized, it is necessary to identify which traits are more likely to improve adaptation to a specific environment. Traits differ in their influence on grain yield and this influence might change from one environment type to the next. CGMs offer the opportunity to evaluate the effect of explicitly breeding to modify specific traits underlying yield, allowing breeders to design an ideotype that is best adapted to each environment type [77,129,141]. Most of the suitable CGMs are structural models, considering the resource capture and allocation, without taking into account the spatial arrangement and geometry of each plant organ. There is another type of models (the functional-structural plant models, FSPM), which incorporate the 3-D spatial arrangement of plant organs by explicitly modelling plant architecture [146–150].

The mechanistic model GECROS has been used to evaluate the impact of increased photosynthesis on rice biomass production [151]. The GECROS model considers the relationships between traits at different levels of organization over time, enabling to upscale from a basic process as photosynthesis to its effects at a whole crop level. A similar CGM aiming to scale up from photosynthesis to canopy level is the Diurnal Canopy Photosynthesis Simulator (DCaPS), implemented as a web-application [152]. The DCaPS package allows to assess likely canopy-level consequences of changes in photosynthetic properties, connecting photosynthesis with crop growth and development.

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Virtual phenotyping using a functional structural plant modelling (FSPM) approach can help to support the decision cycle of plant performance analysis by integrating different traits into a spatial-temporal whole plant simulation [146–150]. For example, an optimization procedure was applied to the functional–structural plant model MAppleT to evaluate which parameter combinations would allow to identify the trait combinations leading to the optimal phenotypes for the target trait [153].

4.5. Evaluating the impact of phenotyping schedule on prediction accuracy

The approach to characterize G×E using CGM [138,154,155] can be extended by combining the APSIM model with knowledge from quantitative genetics, simulating an explicit genetic basis for the APSIM parameters that are segregating in the population [156]. Such an approach would simulate trait dynamics across environments, characterizing G×E patterns and the change of trait correlations over time. For example, a wheat diversity panel segregating for 12 parameters of APSIM-wheat over 84 environments in the Australian wheat belt was simulated [156] (a subset of the environments shown in [138,157]). The output of these simulations allowed to evaluate the potential of biomass measured during the growing season to improve yield predictions with a multi-trait genomic prediction model. A further opportunity offered by the combination of statistical genetic models and CGMs is the evaluation of the impact of phenotyping frequency and the size of measurement error on trait heritability and prediction accuracy for the target trait. In such a way, an approach that combines CGMs like APSIM-wheat with a quantitative genetic basis potentially allows to evaluate phenotyping and selection strategies across environments.

5. Challenges ahead

This paper has discussed a number of G2P modelling approaches to take into consideration the different sources of phenotypic information and their underlying G×E structure. Unfortunately, the fast implementation of phenotyping technologies has not necessarily been accompanied by a proportional implementation of facilities for data storage and data interoperability. In the same manner, protocols for the design of experiments specifically in phenotyping platforms are not yet applied satisfactorily everywhere. In this regard, European initiatives as EMPHASIS (https://www.plant-phenotyping.org/Data_Policy) and EPPN^{2020} (https://eppn2020.plant-phenotyping.eu/) will play a central role in the successful implementation and dissemination of phenotyping technologies into breeding programmes by standardizing the phenotyping designs, phenotyping/envirotyping protocols and data storage.

Throughout this paper, we have discussed a number of G2P models that can be used to predict phenotypes across environments and will help to obtain a larger response to selection. Although the central role of G2P models for genetic gain is not under discussion, little will be gained from these models, without their implementation in an effective pipeline that facilitates the integration of data pre-processing, prediction and decision support tools [158]. This aspect of an effective implementation of G2P models is still at an early stage, but its development promises to play a central role in the years to come.

6. Concluding remarks

- Additional phenotyping can be done at growth chambers, platforms, managed environment trials or a sample of (field) multi-environment trials.
- Genotype-to-phenotype modelling (G2P) plays a central role in enabling breeders to combine the different sources of phenotypic and genotypic information and assisting them in the design of phenotyping strategies.
- Modelling steps involve image pre-processing, correcting for spatial trends within each trial (low level traits), dynamical modelling of genotypic responses within environments against time thereby producing intermediate order traits, modelling dynamics parameters in their dependence on environmental gradients and calculate sensitivities (higher order traits), and combining the information of multiple higher order traits with environmental data to predict the target trait.
- G2P models for the target trait from underlying component traits involve statistical models like multi-trait models, factorial regression models, and crop growth models.
- Design issues that can be addressed with G2P models involve the decision of which environments and genotypes to use for phenotyping, which traits to prioritize in which environment type (ideotype design) and what kind of phenotyping schedule to use in terms of measurement frequency and precision to increase prediction accuracy for the target trait.

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References

[1] M. Cooper, Complex Trait Genetics and Gene-to-Phenotype Models, Aust. J. Agric. Res. 56 (2004) 895–918.

[2] D.W. Podlich, C.R. Winkler, M. Cooper, Mapping As You Go. An Effective Approach for Marker Assisted Selection of Complex Traits, (2004) 1560–1571. doi:10.2135/cropsci2004.1560.

[3] M. Cooper, G.L. Hammer, Plant Adaptation and Crop Improvement, CAB International, Wallingford, UK, 1996.

[4] R.E. Comstock, R.H. Moll, Genotype-Environment Interactions, in: W.D. Hanson, H.F. Robinson (Eds.), Stat. Genet. Plant Breed. A Symp. Work., National Academy of Sciences-National Research Council, 1963: pp. 164–196.

[5] R. Woltereck, Weitere experimentelle Untersuchungen über Artveränderung, speziel über das Wesen quantitativer Artunterschiede bei Daphnien, Verhandlungen Der Dtsch. Zool. Gesellschaft. (1909) 110–173.

[6] T.J. DeWitt, S.M. Scheiner, Phenotypic plasticity: functional and conceptual approaches, Oxford University Press Oxford, 2004.

[7] M. Cooper, I.H. DeLacy, Relationships among analytical methods used to study genotypic variation and genotype-by-environment interaction in plant breeding multi-environment experiments, Theor. Appl. Genet. 88 (1994) 561–572. doi:10.1007/BF01240919.

[8] M. Cooper, C.D. Messina, D. Podlich, L.R. Totir, A. Baumgarten, N.J. Hausmann, D. Wright, G. Graham, Predicting the future of plant breeding: complementing empirical evaluation with genetic prediction, Crop Pasture Sci. 65 (2014) 311–336. doi:http://dx.doi.org/10.1071/CP14007.

[9] M. Cooper, D.R. Woodruff, R.L. Eisemann, P.S. Brennan, I.H. DeLacy, A selection strategy to accommodate genotype-by-environment interaction for grain yield of wheat: managed-environments for selection among genotypes, 90 (1995) 492–502. doi:10.1007/bf00221995.

[10] G.J. Rebetzke, K. Chenu, B. Biddulph, C. Moeller, D.M. Deery, A.R. Rattey, D. Bennett, E.G. Barrett-Lennard, J.E. Mayer, A multisite managed environment facility for targeted trait and germplasm phenotyping, Funct. Plant Biol. 40 (2012) 1–13. doi:http://dx.doi.org/10.1071/FP12180.

[11] G.L. Hammer, S. Chapman, E. van Oosterom, D.W. Podlich, Trait physiology and crop modelling as a framework to link phenotypic complexity to underlying genetic

Comment citer ce document :
van Eeuwijk, F., Bustos-Korts, Millet, Boer, Kruijer, Thompson, A., Malosetti, Iwata, H.,
Quiroz, R., Kuppe, C., Muller, Blazakis, K. N., Yu, K., Tardieu, F., Chapman, S. (2019). Modelling
strategies for assessing and increasing the effectiveness of new phenotyping techniques in plant
breeding. Plant Science, 282, 23-39. . DOI : 10.1016/j.plantsci.2018.06.018

systems, Aust. J. Agric. Res. 56 (2005) 947–960. doi:http://dx.doi.org/10.1071/AR05157.

[12] F. Tardieu, L. Cabrera-Bosquet, T. Pridmore, M. Bennett, Plant Phenomics, From Sensors to Knowledge, Curr. Biol. 27 (2017) R770–R783. doi:10.1016/j.cub.2017.05.055.

[13] J.L. Araus, S.C. Kefauver, M. Zaman-Allah, M.S. Olsen, J.E. Cairns, Translating High-Throughput Phenotyping into Genetic Gain, Trends Plant Sci. xx (2018) 1–16. doi:10.1016/j.tplants.2018.02.001.

[14] A.-R. Ballester, Y. Tikunov, J. Molthoff, S. Grandillo, M. Viquez-Zamora, R. de Vos, R.A. de Maagd, S. van Heusden, A.G. Bovy, Identification of Loci Affecting Accumulation of Secondary Metabolites in Tomato Fruit of a Solanum lycopersicum × Solanum chmielewskii Introgression Line Population, Front. Plant Sci. 7 (2016) 1–14. doi:10.3389/fpls.2016.01428.

[15] Y. Xu, C. Xu, S. Xu, Prediction and association mapping of agronomic traits in maize using multiple omic data, Heredity (Edinb). (2017) 1–11. doi:10.1038/hdy.2017.27.

[16] V.S. Weber, J.L. Araus, J.E. Cairns, C. Sanchez, A.E. Melchinger, E. Orsini, Prediction of grain yield using reflectance spectra of canopy and leaves in maize plants grown under different water regimes, F. Crop. Res. 128 (2012) 82–90. doi:http://dx.doi.org/10.1016/j.fcr.2011.12.016.

[17] L. Cabrera-Bosquet, C. Grieder, S. Alvarez Prado, C. Sánchez, J.L. Araus, Kernel δ18O reflects changes in apical dominance and plant transpiration in tropical maize, J. Agron. Crop Sci. 203 (2017) 277–285. doi:10.1111/jac.12196.

[18] T. Duan, S.C. Chapman, Y. Guo, B. Zheng, Dynamic monitoring of NDVI in wheat agronomy and breeding trials using an unmanned aerial vehicle, F. Crop. Res. 210 (2017) 71–80. doi:https://doi.org/10.1016/j.fcr.2017.05.025.

[19] E. Millet, C. Welcker, W. Kruijer, S. Negro, S. Nicolas, S. Praud, N. Ranc, T. Presterl, R. Tuberosa, Z. Bedo, X. Draye, B. Usadel, A. Charcosset, F. van Eeuwijk, F. Tardieu, A. Coupel-Ledru, C. Bauland, Genome-wide analysis of yield in Europe: allelic effects as functions of drought and heat scenarios, Plant Physiol. 172 (2016) pp.00621.2016. doi:10.1104/pp.16.00621.

[20] G.A. Slafer, R. Savin, V.O. Sadras, Coarse and fine regulation of wheat yield components in response to genotype and environment, F. Crop. Res. 157 (2014) 71–83. doi:http://dx.doi.org/10.1016/j.fcr.2013.12.004.

[21] F.A. van Eeuwijk, M.C.A.M. Bink, K. Chenu, S.C. Chapman, Detection and use of

Comment citer ce document :
van Eeuwijk, F., Bustos-Korts, Millet, Boer, Kruijer, Thompson, A., Malosetti, Iwata, H., Quiroz, R., Kuppe, C., Muller, Blazakis, K. N., Yu, K., Tardieu, F., Chapman, S. (2019). Modelling strategies for assessing and increasing the effectiveness of new phenotyping techniques in plant breeding. Plant Science, 282, 23-39. , DOI : 10.1016/j.plantsci.2018.06.018

QTL for complex traits in multiple environments, Curr. Opin. Plant. Biol. 13 (2010) 193–205. doi:10.1016/j.pbi.2010.01.001.

[22] F.A. van Eeuwijk, D. V Bustos-Korts, M. Malosetti, What Should Students in Plant Breeding Know About the Statistical Aspects of Genotype × Environment Interactions?, Crop Sci. 56 (2016) 2119–2140. doi:10.2135/cropsci2015.06.0375.

[23] P.H.C. Eilers, B.D. Marx, Flexible Smoothing with B-splines and Penalties, Stat. Sci. 11 (1996) 89–102. doi:10.2307/2246049.

[24] P.H.C. Eilers, B.D. Marx, M. Durbán, Twenty years of P-splines, SORT-Statistics Oper. Res. Trans. 39 (2015) 149–186.

[25] F. Perez-Sanz, P.J. Navarro, M. Egea-Cortines, Plant phenomics: An overview of image acquisition technologies and image data analysis algorithms, Gigascience. 6 (2017) 1–18. doi:10.1093/gigascience/gix092.

[26] S. Liu, F. Baret, B. Andrieu, P. Burger, M. Hemmerlé, Estimation of wheat plant density at early stages using high resolution imagery, Front. Plant Sci. 8 (2017). doi:10.3389/fpls.2017.00739.

[27] H. Scharr, M. Minervini, A.P. French, C. Klukas, D.M. Kramer, X. Liu, I. Luengo, J.M. Pape, G. Polder, D. Vukadinovic, X. Yin, S.A. Tsaftaris, Leaf segmentation in plant phenotyping: a collation study, Mach. Vis. Appl. 27 (2016) 585–606. doi:10.1007/s00138-015-0737-3.

[28] C. Grieder, A. Hund, A. Walter, Image based phenotyping during winter: a powerful tool to assess wheat genetic variation in growth response to temperature, Funct. Plant Biol. 42 (2015) 387–396. http://dx.doi.org/10.1071/FP14226.

[29] X. Yin, X. Liu, J. Chen, D.M. Kramer, Joint Multi-Leaf Segmentation, Alignment and Tracking from Fluorescence Plant Videos, arXiv:1505.00353v2. (2017). http://arxiv.org/abs/1505.00353.

[30] J. Rutkoski, J. Poland, S. Mondal, E. Autrique, L.G. Pérez, J. Crossa, M. Reynolds, R. Singh, Canopy Temperature and Vegetation Indices from High-Throughput Phenotyping Improve Accuracy of Pedigree and Genomic Selection for Grain Yield in Wheat, G3 Genes|Genomes|Genetics. 6 (2016) 2799–2808. doi:10.1534/g3.116.032888.

[31] A.B. Potgieter, B. George-Jaeggli, S.C. Chapman, K. Laws, L.A. Suárez Cadavid, J. Wixted, J. Watson, M. Eldridge, D.R. Jordan, G.L. Hammer, Multi-Spectral Imaging from an Unmanned Aerial Vehicle Enables the Assessment of Seasonal Leaf Area Dynamics of Sorghum Breeding Lines, Front. Plant Sci. 8 (2017) 1–11.

Comment citer ce document :
van Eeuwijk, F., Bustos-Korts, Millet, Boer, Kruijer, Thompson, A., Malosetti, Iwata, H., Quiroz, R., Kuppe, C., Muller, Blazakis, K. N., Yu, K., Tardieu, F., Chapman, S. (2019). Modelling strategies for assessing and increasing the effectiveness of new phenotyping techniques in plant breeding. Plant Science, 282, 23-39. . DOI : 10.1016/j.plantsci.2018.06.018

doi:10.3389/fpls.2017.01532.

[32] H.S. Naik, J. Zhang, A. Lofquist, T. Assefa, S. Sarkar, D. Ackerman, A. Singh, A.K. Singh, B. Ganapathysubramanian, A real-time phenotyping framework using machine learning for plant stress severity rating in soybean, Plant Methods. 13 (2017) 23. doi:10.1186/s13007-017-0173-7.

[33] B. Cullis, B. Gogel, A. Verbyla, R. Thompson, Spatial Analysis of Multi-Environment Early Generation Variety Trials, Biometrics. 54 (1998) 1–18. doi:10.2307/2533991.

[34] J.G. Velazco, M.X. Rodríguez-Álvarez, M.P. Boer, D.R. Jordan, P.H.C. Eilers, M. Malosetti, F.A. van Eeuwijk, Modelling spatial trends in sorghum breeding field trials using a two-dimensional P-spline mixed model, Theor. Appl. Genet. 130 (2017) 1375–1392. doi:10.1007/s00122-017-2894-4.

[35] M.X. Rodríguez-Álvarez, M.P. Boer, F.A. van Eeuwijk, P.H.C. Eilers, Correcting for spatial heterogeneity in plant breeding experiments with P-splines, Spat. Stat. 23 (2018) 52–71. doi:10.1016/j.spasta.2017.10.003.

[36] M.X. Rodríguez-Álvarez, M.P. Boer, F.A. van Eeuwijk, P.H.C. Eilers, Correcting for spatial heterogeneity in plant breeding experiments with P-splines, Spat. Stat. (2017). doi:10.1016/j.spasta.2017.10.003.

[37] B.R. Cullis, A.B. Smith, N.E. Coombes, On the design of early generation variety trials with correlated data, J Agric Biol Env. Stat. 11 (2006) 381–393. doi:10.1198/108571106x154443.

[38] P.J. Flood, W. Kruijer, S.K. Schnabel, R. van der Schoor, H. Jalink, J.F.H. Snel, J. Harbinson, M.G.M. Aarts, Phenomics for photosynthesis, growth and reflectance in Arabidopsis thaliana reveals circadian and long-term fluctuations in heritability, Plant Methods. 12 (2016) 14. doi:10.1186/s13007-016-0113-y.

[39] R. van Rooijen, W. Kruijer, R. Boesten, F.A. van Eeuwijk, J. Harbinson, M.G.M. Aarts, Natural variation of YELLOW SEEDLING1 affects photosynthetic acclimation of Arabidopsis thaliana, Nat. Commun. 8 (2017) 1421. doi:10.1038/s41467-017-01576-3.

[40] C.X. Ma, G. Casella, R. Wu, Functional mapping of quantitative trait loci underlying the character process: a theoretical framework, Genetics. 161 (2002) 1751–1762. http://www.ncbi.nlm.nih.gov/pubmed/12196415%5Cnhttp://www.ncbi.nlm.nih.gov/pmc/articles/PMC1462199/pdf/12196415.pdf.

[41] R. Wu, C.-X. Ma, R.C. Littell, S.S. Wu, T. Yin, M. Huang, M. Wang, G. Casella, A logistic mixture model for characterizing genetic determinants causing differentiation

Comment citer ce document :
van Eeuwijk, F., Bustos-Korts, Millet, Boer, Kruijer, Thompson, A., Malosetti, Iwata, H.,
Quiroz, R., Kuppe, C., Muller, Blazakis, K. N., Yu, K., Tardieu, F., Chapman, S. (2019). Modelling
strategies for assessing and increasing the effectiveness of new phenotyping techniques in plant
breeding. Plant Science, 282, 23-39. , DOI : 10.1016/j.plantsci.2018.06.018

in growth trajectories., Genet. Res. 79 (2002) 235–45. doi:10.1017/s0016672302005633.

[42] M. Malosetti, R.G.F. Visser, C. Celis-Gamboa, F.A. Eeuwijk, QTL methodology for response curves on the basis of non-linear mixed models, with an illustration to senescence in potato, Theor. Appl. Genet. 113 (2006) 288–300. doi:10.1007/s00122-006-0294-2.

[43] J. a. Bac-Molenaar, C. Granier, J.J.B. Keurentjes, D. Vreugdenhil, Genome wide association mapping of time-dependent growth responses to moderate drought stress in Arabidopsis, Plant. Cell Environ. (2015) 88–102. doi:10.1111/pce.12595.

[44] G.B. West, J.H. Brown, B.J. Enquist, A general model for ontogenetic growth, Nature. 413 (2001) 628–631.

[45] P. Hurtado, S. Schnabel, A. Zaban, M. Veteläinen, E. Virtanen, P.C. Eilers, F. Eeuwijk, R.F. Visser, C. Maliepaard, Dynamics of senescence-related QTLs in potato, Euphytica. 183 (2012) 289–302. doi:10.1007/s10681-011-0464-4.

[46] J. Sun, J.E. Rutkoski, J.A. Poland, J. Crossa, J.-L. Jannink, M.E. Sorrells, Multitrait, Random Regression, or Simple Repeatability Model in High-Throughput Phenotyping Data Improve Genomic Prediction for Wheat Grain Yield, Plant Genome. (2017). doi:10.3835/plantgenome2016.11.0111.

[47] J.R. Stinchcombe, M. Kirkpatrick, Genetics and evolution of function-valued traits: understanding environmentally responsive phenotypes, Trends Ecol. Evol. 27 (2012) 637–647. doi:10.1016/j.tree.2012.07.002.

[48] R. Wu, M. Lin, Functional mapping-how to map and study the genetic architecture of dynamic complex traits, Nat Rev Genet. 7 (2006) 229–237. http://dx.doi.org/10.1038/nrg1804.

[49] Z. Li, M.J. Sillanpää, Dynamic Quantitative Trait Locus Analysis of Plant Phenomic Data, Trends Plant Sci. 20 (2015) 822–833. doi:10.1016/j.tplants.2015.08.012.

[50] S. Macgregor, S.A. Knott, I. White, P.M. Visscher, Quantitative trait locus analysis of longitudinal quantitative trait data in complex pedigrees, Genetics. 171 (2005) 1365–1376. doi:10.1534/genetics.105.043828.

[51] M.S. Lund, P. Sorensen, P. Madsen, F. Jaffrezic, Detection and modelling of time-dependent QTL in animal populations, Genet. Sel. Evol. 40 (2008) 177–194. doi:10.1051/gse:2007043.

[52] C. Welcker, B. Boussuge, C. Bencivenni, J.M. Ribaut, F. Tardieu, Are source and sink strengths genetically linked in maize plants subjected to water deficit? A QTL study of

the responses of leaf growth and of Anthesis-Silking Interval to water deficit, J. Exp. Bot. 58 (2007) 339–349. doi:10.1093/jxb/erl227.

[53] K. Chenu, S.C. Chapman, F. Tardieu, G. McLean, C. Welcker, G.L. Hammer, Simulating the Yield Impacts of Organ-Level Quantitative Trait Loci Associated With Drought Response in Maize: A “Gene-to-Phenotype” Modeling Approach, Genetics. 183 (2009) 1507–1523. doi:10.1534/genetics.109.105429.

[54] F. Tardieu, Virtual plants: modelling as a tool for the genomics of tolerance to water deficit, Trends Plant Sci. 8 (2003) 9–14. doi:http://dx.doi.org/10.1016/S1360-1385(02)00008-0.

[55] F. Tardieu, B. Parent, Predictable “meta-mechanisms” emerge from feedbacks between transpiration and plant growth and cannot be simply deduced from short-term mechanisms, Plant Cell Environ. 40 (2017) 846–857. doi:10.1111/pce.12822.

[56] B. Parent, F. Shahinnia, L. Maphosa, B. Berger, H. Rabie, K. Chalmers, A. Kovalchuk, P. Langridge, D. Fleury, Combining field performance with controlled environment plant imaging to identify the genetic control of growth and transpiration underlying yield response to water-deficit stress in wheat, J. Exp. Bot. 66 (2015) 5481–5492. doi:10.1093/jxb/erv320.

[57] S. Lacube, C. Fournier, C. Palaffre, E.J. Millet, F. Tardieu, B. Parent, Distinct controls of leaf widening and elongation by light and evaporative demand in maize, Plant Cell Environ. 40 (2017) 2017–2028. doi:10.1111/pce.13005.

[58] K. Neumann, C. Klukas, S. Friedel, P. Rischbeck, D. Chen, A. Entzian, N. Stein, A. Graner, B. Kilian, Dissecting spatiotemporal biomass accumulation in barley under different water regimes using high-throughput image analysis, Plant, Cell Environ. 38 (2015) 1980–1996. doi:10.1111/pce.12516.

[59] L. Cabrera-Bosquet, C. Fournier, N. Brichet, C. Welcker, B. Suard, F. Tardieu, High-throughput estimation of incident light, light interception and radiation-use efficiency of thousands of plants in a phenotyping platform, New Phytol. 212 (2016) 269–281. doi:10.1111/nph.14027.

[60] R.C. Muchow, T.R. Sinclair, J.M. Bennett, Temperature and Solar Radiation Effects on Potential Maize Yield across Locations, Agron. J. 82 (1990) 338–343. doi:10.2134/agronj1990.00021962008200020033x.

[61] F. Technow, C.D. Messina, L.R. Totir, M. Cooper, Integrating crop growth models with whole genome prediction through approximate Bayesian computation, PLoS One. 10 (2015) 1–20. doi:10.1371/journal.pone.0130855.

Comment citer ce document :
van Eeuwijk, F., Bustos-Korts, Millet, Boer, Kruijer, Thompson, A., Malosetti, Iwata, H., Quiroz, R., Kuppe, C., Muller, Blazakis, K. N., Yu, K., Tardieu, F., Chapman, S. (2019). Modelling strategies for assessing and increasing the effectiveness of new phenotyping techniques in plant breeding. Plant Science, 282, 23-39. , DOI : 10.1016/j.plantsci.2018.06.018

[62] M.X. Rodríguez-Álvarez, D.J. Lee, T. Kneib, M. Durbán, P. Eilers, Fast smoothing parameter separation in multidimensional generalized P-splines: the SAP algorithm, Stat. Comput. 25 (2015) 941–957. doi:10.1007/s11222-014-9464-2.

[63] M.P. Boer, D. Wright, L. Feng, D.W. Podlich, L. Luo, M. Cooper, F.A. van Eeuwijk, A Mixed-Model Quantitative Trait Loci (QTL) Analysis for Multiple-Environment Trial Data Using Environmental Covariables for QTL-by-Environment Interactions, With an Example in Maize, Genetics. 177 (2007) 1801–1813. doi:10.1534/genetics.107.071068.

[64] M. Malosetti, J.-M. Ribaut, F.A. van Eeuwijk, The statistical analysis of multi-environment data: modeling genotype-by-environment interaction and its genetic basis, Front. Physiol. 4 (2013) 1–17. doi:10.3389/fphys.2013.00044.

[65] M.P.M. Thoen, N.H. Davila Olivas, K.J. Kloth, S. Coolen, P.P. Huang, M.G.M. Aarts, J.A. Bac-Molenaar, J. Bakker, H.J. Bouwmeester, C. Broekgaarden, J. Bucher, J. Busscher-Lange, X. Cheng, E.F. Fradin, M.A. Jongsma, M.M. Julkowska, J.J.B. Keurentjes, W. Ligterink, C.M.J. Pieterse, C. Ruyter-Spira, G. Smant, C. Testerink, B. Usadel, J.J.A. van Loon, J.A. van Pelt, C.C. van Schaik, S.C.M. van Wees, R.G.F. Visser, R. Voorrips, B. Vosman, D. Vreugdenhil, S. Warmerdam, G.L. Wiegers, J. van Heerwaarden, W. Kruijer, F.A. van Eeuwijk, M. Dicke, Genetic architecture of plant stress resistance: Multi-trait genome-wide association mapping, New Phytol. 213 (2017) 1346–1362. doi:10.1111/nph.14220.

[66] S. Ceccarelli, E. Acevedo, S. Grando, Breeding for yield stability in unpredictable environments: single traits, interaction between traits, and architecture of genotypes, Euphytica. 56 (1991) 169–185. doi:10.1007/BF00042061.

[67] V.O. Sadras, D. Calderini, Crop Physiology: Applications for Genetic Improvement and Agronomy, Elsevier Science, 2014.

[68] X. Yin, S.D. Chasalow, C.J. Dourleijn, P. Stam, M.J. Kropff, Coupling estimated effects of QTLs for physiological traits to a crop growth model: predicting yield variation among recombinant inbred lines in barley, Heredity (Edinb). 85 (2000) 539–549. doi:10.1046/j.1365-2540.2000.00790.x.

[69] X. Yin, P. Stam, M.J. Kropff, A.H.C.M. Schapendonk, Crop Modeling, QTL Mapping, and Their Complementary Role in Plant Breeding , Agron. J. 95 (2003) 90–98. doi:10.2134/agronj2003.9000.

[70] X. Yin, P.C. Struik, F.A. van Eeuwijk, P. Stam, J. Tang, QTL analysis and QTL-based prediction of flowering phenology in recombinant inbred lines of barley, J. Exp. Bot. 56 (2005) 967–976. doi:10.1093/jxb/eri090.

Comment citer ce document :
van Eeuwijk, F., Bustos-Korts, Millet, Boer, Kruijer, Thompson, A., Malosetti, Iwata, H.,
Quiroz, R., Kuppe, C., Muller, Blazakis, K. N., Yu, K., Tardieu, F., Chapman, S. (2019). Modelling
strategies for assessing and increasing the effectiveness of new phenotyping techniques in plant
breeding. Plant Science, 282, 23-39. , DOI : 10.1016/j.plantsci.2018.06.018

[71] M. Reymond, B. Muller, A. Leonardi, A. Charcosset, F. Tardieu, Combining Quantitative Trait Loci Analysis and an Ecophysiological Model to Analyze the Genetic Variability of the Responses of Maize Leaf Growth to Temperature and Water Deficit, Plant Physiol. 131 (2003) 664–675. doi:10.1104/pp.013839.

[72] F. Tardieu, M. Reymond, B. Muller, C. Granier, T. Simonneau, W. Sadok, C. Welcker, Linking physiological and genetic analyses of the control of leaf growth under changing environmental conditions, Aust. J. Agric. Res. 56 (2005) 937–946. doi:http://dx.doi.org/10.1071/AR05156.

[73] F.A. van Eeuwijk, M. Malosetti, X. Yin, P.C. Struik, P. Stam, Statistical models for genotype by environment data: from conventional ANOVA models to eco-physiological QTL models, Aust. J. Agric. Res. 56 (2005) 883–894. doi:http://dx.doi.org/10.1071/AR05153.

[74] M. Bogard, C. Ravel, E. Paux, J. Bordes, F. Balfourier, S.C. Chapman, J. Le Gouis, V. Allard, Predictions of heading date in bread wheat (Triticum aestivum L.) using QTL-based parameters of an ecophysiological model, J. Exp. Bot. 65 (2014) 5849–5865. doi:10.1093/jxb/eru328.

[75] T. Hastie, R. Tibshirani, J. Friedman, The elements of statistical learning, Second, Springer, 2009.

[76] S.R. Searle, G. Casella, C.E. McCulloch, Variance Components, Wiley, 2009. https://books.google.nl/books?id=mkCSOOzHMngC.

[77] G. Hammer, C. Messina, E. van Oosterom, S. Chapman, V. Singh, A. Borrell, D. Jordan, M. Cooper, Molecular Breeding for Complex Adaptive Traits: How Integrating Crop Ecophysiology and Modelling Can Enhance Efficiency BT - Crop Systems Biology: Narrowing the gaps between crop modelling and genetics, in: X. Yin, P.C. Struik (Eds.), Springer International Publishing, Cham, 2016: pp. 147–162. doi:10.1007/978-3-319-20562-5_7.

[78] P. Jackson, T. McRae, M. Hogarth, Selection of sugarcane families across variable environments I. Sources of variation and an optimal selection index, F. Crop. Res. 43 (1995) 109–118. doi:10.1016/0378-4290(95)00039-S.

[79] P. Jackson, X.M. Wei, F. Atkin, Optimal selection indices in early stage trials in sugarcane breeding programs, 37th Annu. Conf. Aust. Soc. Sugar Cane Technol. ASSCT 2015. 37 (2015) 244–251. https://www.scopus.com/inward/record.uri?eid=2-s2.0-84978525380&partnerID=40&md5=839ac63638643eece05eb3a5817ebb0f.

[80] J. Basnayake, P.A. Jackson, N.G. Inman-Bamber, P. Lakshmanan, Sugarcane for

water-limited environments. Variation in stomatal conductance and its genetic correlation with crop productivity, J. Exp. Bot. 66 (2015) 3945–3958. doi:10.1093/jxb/erv194.

[81] H. Poorter, F. Fiorani, R. Pieruschka, T. Wojciechowski, W.H. van der Putten, M. Kleyer, U. Schurr, J. Postma, Pampered inside, pestered outside? Differences and similarities between plants growing in controlled conditions and in the field, New Phytol. 212 (2016) 838–855. doi:10.1111/nph.14243.

[82] G. Dignat, C. Welcker, M. Sawkins, J.M. Ribaut, F. Tardieu, The growths of leaves, shoots, roots and reproductive organs partly share their genetic control in maize plants, Plant. Cell Environ. 36 (2013) 1105–1119. doi:10.1111/pce.12045.

[83] C. Welcker, W. Sadok, G. Dignat, M. Renault, S. Salvi, A. Charcosset, F. Tardieu, A Common Genetic Determinism for Sensitivities to Soil Water Deficit and Evaporative Demand: Meta-Analysis of Quantitative Trait Loci and Introgression Lines of Maize, Plant Physiol. 157 (2011) 718–729. doi:10.1104/pp.111.176479.

[84] R. Chapuis, C. Delluc, R. Debeuf, F. Tardieu, C. Welcker, Resiliences to water deficit in a phenotyping platform and in the field: How related are they in maize?, Eur. J. Agron. 42 (2012) 59–67. doi:10.1016/j.eja.2011.12.006.

[85] G.J. Rebetzke, R.A. Richards, Genetic Improvement of Early Vigour in Wheat, Aust. J. Agric. Res. 50 (1999) 291–301. doi:10.1071/A98125.

[86] T. Duan, S.C. Chapman, E. Holland, G.J. Rebetzke, Y. Guo, B. Zheng, Dynamic quantification of canopy structure to characterize early plant vigour in wheat genotypes, J. Exp. Bot. 67 (2016) 4523–4534. doi:10.1093/jxb/erw227.

[87] Y. Jia, J.-L. Jannink, Multiple-Trait Genomic Selection Methods Increase Genetic Value Prediction Accuracy, Genetics. 192 (2012) 1513–1522. doi:10.1534/genetics.112.144246.

[88] J. Burgueño, G. de los Campos, K. Weigel, J. Crossa, Genomic Prediction of Breeding Values when Modeling Genotype x Environment Interaction using Pedigree and Dense Molecular Markers, Crop Sci. 52 (2012) 707–719. doi:10.2135/cropsci2011.06.0299.

[89] D. Jarquín, J. Crossa, X. Lacaze, P. Cheyron, J. Daucourt, J. Lorgeou, F. Piraux, L. Guerreiro, P. Pérez, M. Calus, J. Burgueño, G. Campos, A reaction norm model for genomic selection using high-dimensional genomic and environmental data, Theor Appl Genet. 3 (2013) 1–13. doi:10.1007/s00122-013-2243-1.

[90] N. Heslot, D. Akdemir, M. Sorrells, J.-L. Jannink, Integrating environmental covariates and crop modeling into the genomic selection framework to predict genotype by

Comment citer ce document :
van Eeuwijk, F., Bustos-Korts, Millet, Boer, Kruijer, Thompson, A., Malosetti, Iwata, H., Quiroz, R., Kuppe, C., Muller, Blazakis, K. N., Yu, K., Tardieu, F., Chapman, S. (2019). Modelling strategies for assessing and increasing the effectiveness of new phenotyping techniques in plant breeding. Plant Science, 282, 23-39. , DOI : 10.1016/j.plantsci.2018.06.018

environment interactions, Theor. Appl. Genet. (2013) 1–18. doi:10.1007/s00122-013-2231-5.

[91] M. Malosetti, D. Bustos-Korts, M.P. Boer, F.A. van Eeuwijk, Predicting Responses in Multiple Environments: Issues in Relation to Genotype × Environment Interactions, Crop Sci. 56 (2016) 2210–2222. doi:10.2135/cropsci2015.05.0311.

[92] M. Malosetti, J. Ribaut, M. Vargas, J. Crossa, F. Eeuwijk, A multi-trait multi-environment QTL mixed model with an application to drought and nitrogen stress trials in maize (Zea mays L.), Euphytica. 161 (2008) 241–257. doi:10.1007/s10681-007-9594-0.

[93] F.N. Gumedze, T.T. Dunne, Parameter estimation and inference in the linear mixed model, Linear Algebra Appl. 435 (2011) 1920–1944.

[94] J. Crossa, G. de los Campos, P. Perez, D. Gianola, J. Burgueño, J.L. Araus, D. Makumbi, R.P. Singh, S. Dreisigacker, J.B. Yan, V. Arief, M. Banziger, H.J. Braun, Prediction of Genetic Values of Quantitative Traits in Plant Breeding Using Pedigree and Molecular Markers, Genetics. 186 (2010) 713-U406. doi:10.1534/genetics.110.118521.

[95] A. Legarra, I. Aguilar, I. Misztal, A relationship matrix including full pedigree and genomic information., J. Dairy Sci. 92 (2009) 4656–4663. doi:10.3168/jds.2009-2061.

[96] I. Misztal, Properties of random regression models using linear splines, J. Anim. Breed. Genet. 123 (2006) 74–80. doi:10.1111/j.1439-0388.2006.00582.x.

[97] R. Cheng, J. Borevitz, R.W. Doerge, Selecting informative traits for multivariate quantitative trait locus mapping helps to gain optimal power, Genetics. 195 (2013) 683–691. doi:10.1534/genetics.113.155937.

[98] G. Verbeke, G. Molenberghs, Linear Mixed Models for Longitudinal Data, Springer New York, 2009. https://books.google.nl/books?id=ha8_AAAAQBAJ.

[99] S. Müller, J.L. Scealy, A.H. Welsh, Model Selection in Linear Mixed Models, Stat. Sci. 28 (2013) 135–167. doi:10.1214/12-STS410.

[100] M.L. Makgahlela, E.A. Mäntysaari, I. Strandén, M. Koivula, U.S. Nielsen, M.J. Sillanpää, J. Juga, Across breed multi-trait random regression genomic predictions in the Nordic Red dairy cattle, J. Anim. Breed. Genet. 130 (2013) 10–19. doi:10.1111/j.1439-0388.2012.01017.x.

[101] A.W. Schulthess, Y. Wang, T. Miedaner, P. Wilde, J.C. Reif, Y. Zhao, M.L. Makgahlela, E.A. Mäntysaari, I. Strandén, M. Koivula, U.S. Nielsen, M.J. Sillanpää, J. Juga, Multiple-trait- and selection indices-genomic predictions for grain yield and

protein content in rye for feeding purposes, Theor. Appl. Genet. 129 (2015) 273–287. doi:10.1007/s00122-015-2626-6.

[102] K. Chenu, S.C. Chapman, G.L. Hammer, G. McLean, H.B.H. Salah, F. Tardieu, Short-term responses of leaf growth rate to water deficit scale up to whole-plant and crop levels: an integrated modelling approach in maize, Plant Cell Environ. 31 (2008) 378–391. doi:10.1111/j.1365-3040.2007.01772.x.

[103] P. Girardin, Ecophysiologie du maïs: fonctionnement de la plante et de la culture, Association générale des producteurs de maïs, 2000.

[104] S. Wright, Correlation and Causation, J. Agric. Res. (1921) 557–585.

[105] K.A. Bollen, Structural Equations with Latent Variables, 1st ed., Wiley-Interscience, 1989. http://www.worldcat.org/isbn/0471011711.

[106] B. Shipley, Cause and correlation in biology: A user’s guide to path analysis, structural equations and causal inference, 2nd ed., Cambridge University Press, Cambridge, USA, 2016.

[107] A. Onogi, O. Ideta, T. Yoshioka, K. Ebana, M. Yamasaki, H. Iwata, Uncovering a Nuisance Influence of a Phenological Trait of Plants Using a Nonlinear Structural Equation: Application to Days to Heading and Culm Length in Asian Cultivated Rice, PLoS One. 11 (2016) 1–17. doi:10.1371/journal.pone.0148609.

[108] J. Pearl, Causality, Causality, by Judea Pearl, pp.~400.~ISBN 0521773628.~Cambridge, UK: Cambridge University Press, March 2000., 2000. http://adsabs.harvard.edu/cgi-bin/nph-bib_query?bibcode=2000caus.book.....P.

[109] P. Spirtes, C. Glymour, R. Scheines, Causation, Prediction, and Search, Second Edition (Adaptive Computation and Machine Learning), second edi, A Bradford Book, 2001.

[110] S.M. Welch, J.L. Roe, Z. Dong, A Genetic Neural Network Model of Flowering Time Control in, Agron. J. 95 (2003) 71–81. doi:10.2134/agronj2003.7100.

[111] S.M. Welch, Z. Dong, J.L. Roe, S. Das, Flowering time control: gene network modelling and the link to quantitative genetics, Aust. J. Agric. Res. 56 (2005) 919–936. http://dx.doi.org/10.1071/AR05155.

[112] E.C. Neto, C.T. Ferrara, A.D. Attie, B.S. Yandell, Inferring Causal Phenotype Networks From Segregating Populations, Genetics. 179 (n.d.) 1089–1100.

[113] E.C. Neto, M.P. Keller, A.D. Attie, B.S. Yandell, Causal Graphical Models in Systems Genetics. A Unified framework for joint inference of causal network and genetic architecture for correlated phenotypes, Ann. Appl. Stat. 4 (2010) 320–339.

[114] M. Scutari, P. Howell, D.J. Balding, I. Mackay, Multiple Quantitative Trait Analysis

Using Bayesian Networks, Genetics. 198 (2014) 129–137. doi:10.1534/genetics.114.165704.

[115] H. Wang, F.A. van Eeuwijk, A New Method to Infer Causal Phenotype Networks Using QTL and Phenotypic Information, PLoS One. 9 (2014) e103997. http://dx.doi.org/10.1371%2Fjournal.pone.0103997.

[116] H. Wang, J. Paulo, W. Kruijer, M. Boer, H. Jansen, Y. Tikunov, B. Usadel, S. van Heusden, A. Bovy, F. van Eeuwijk, Genotype-phenotype modeling considering intermediate level of biological variation: a case study involving sensory traits, metabolites and QTLs in ripe tomatoes, Mol. Biosyst. 11 (2015) 3101–3110. doi:10.1039/C5MB00477B.

[117] Z. Dong, O. Danilevskaya, T. Abadie, C. Messina, N. Coles, M. Cooper, A gene regulatory network model for Floral transition of the shoot apex in maize and its dynamic modeling, PLoS One. 7 (2012). doi:10.1371/journal.pone.0043450.

[118] B.D. Valente, G.J.M. Rosa, G. De Los Campos, D. Gianola, M.A. Silva, Searching for recursive causal structures in multivariate quantitative genetics mixed models, Genetics. 185 (2010) 633–644. doi:10.1534/genetics.109.112979.

[119] K. Töpner, G.J.M. Rosa, D. Gianola, C.-C. Schön, Bayesian Networks Illustrate Genomic and Residual Trait Connections in Maize (Zea mays L.), G3 Genes|Genomes|Genetics. 7 (2017) 2779–2789. doi:10.1534/g3.117.044263.

[120] M.H. Maathuis, D. Colombo, M. Kalisch, P. Bühlmann, Predicting causal effects in large-scale systems from observational data, Nat. Methods. 7 (2010) 247–248.

[121] N. Meinshausen, A. Hauser, J.M. Mooij, J. Peters, P. Versteeg, P. Bühlmann, Methods for causal inference from gene perturbation experiments and validation, Proc. Natl. Acad. Sci. 113 (2016) 7361–7368.

[122] J. Peters, P. Bühlmann, N. Meinshausen, Causal inference using invariant prediction: identification and confidence intervals, arXiv Prepr. arXiv1501.01332v3. (2015).

[123] J. Peters, D. Janzing, B. Schölkopf, Elements of Causal Inference: Foundations and Learning Algorithms, MIT Press, 2017.

[124] S. De Vos, K.J. Wardenaar, E.H. Bos, E.C. Wit, M.E.J. Bouwmans, P. De Jonge, An investigation of emotion dynamics in major depressive disorder patients and healthy persons using sparse longitudinal networks, PLoS One. 12 (2017) 1–18. doi:10.1371/journal.pone.0178586.

[125] N.A. Alimi, M.C.A.M. Bink, J.A. Dieleman, J.J. Magán, A.M. Wubs, A. Palloix, F.A. van Eeuwijk, Multi-trait and multi-environment QTL analyses of yield and a set of

Comment citer ce document :
van Eeuwijk, F., Bustos-Korts, Millet, Boer, Kruijer, Thompson, A., Malosetti, Iwata, H., Quiroz, R., Kuppe, C., Muller, Blazakis, K. N., Yu, K., Tardieu, F., Chapman, S. (2019). Modelling strategies for assessing and increasing the effectiveness of new phenotyping techniques in plant breeding. Plant Science, 282, 23-39. , DOI : 10.1016/j.plantsci.2018.06.018

physiological traits in pepper, Theor. Appl. Genet. 126 (2013) 2597–2625. doi:10.1007/s00122-013-2160-3.

[126] N.A. Alimi, Statistical methods for QTL mapping and genomic prediction of multiple traits and environments: case studies in pepper, 2016. http://edepot.wur.nl/390205.

[127] S.C. Chapman, G.L. Hammer, D.W. Podlich, M. Cooper, Linking bio-physical and genetic models to integrate physiology, molecular biology and plant breeding, in: M. Kang (Ed.), Quant. Genet. Genomics, Plant Breed., CAB International , Wallingford UK, 2002: pp. 167–187.

[128] C.D. Messina, F. Technow, T. Tang, R.L. Totir, C. Gho, M. Cooper, Leveraging biological insight and environmental variation to improve phenotypic prediction: Integrating crop growth models (CGM) with whole genome prediction (WGP), Eur. J. Agr. (2018). https://doi.org/10.1016/j.eja.2018.01.007.

[129] G. Hammer, G. McLean, A. Doherty, E. van Oosterom, S. Chapman, Sorghum Crop Modeling and Its Utility in Agronomy and Breeding, in: Sorghum State Art Futur. Perspect., American Society of Agronomy and Crop Science Society of America, Inc., Madison, WI, 2016. doi:10.2134/agronmonogr58.2014.0064.

[130] N.G. Inman-Bamber, P.A. Jackson, C.J. Stokes, S. Verrall, P. Lakshmanan, J. Basnayake, Sugarcane for water-limited environments: Enhanced capability of the APSIM sugarcane model for assessing traits for transpiration efficiency and root water supply, F. Crop. Res. 196 (2016) 112–123. doi:10.1016/j.fcr.2016.06.013.

[131] R. Quiroz, H. Loayza, C. Barreda, C. Gavilán, A. Posadas, D.A. Ramírez, Linking process-based potato models with light reflectance data: Does model complexity enhance yield prediction accuracy?, Eur. J. Agron. 82 (2017) 104–112. doi:10.1016/j.eja.2016.10.008.

[132] M. Van Oijen, J. Rougier, R. Smith, Bayesian calibration of process-based forest models: bridging the gap between models and data, Tree Physiol. 25 (2005) 915–927. doi:10.1093/treephys/25.7.915.

[133] T. Iizumi, M. Yokozawa, M. Nishimori, Parameter estimation and uncertainty analysis of a large-scale crop model for paddy rice: Application of a Bayesian approach, Agric. For. Meteorol. 149 (2009) 333–348. doi:10.1016/j.agrformet.2008.08.015.

[134] A. Onogi, M. Watanabe, T. Mochizuki, T. Hayashi, H. Nakagawa, T. Hasegawa, H. Iwata, Toward integration of genomic selection with crop modelling: the development of an integrated approach to predicting rice heading dates, Theor. Appl. Genet. 129 (2016) 805–817. doi:10.1007/s00122-016-2667-5.

Comment citer ce document :
van Eeuwijk, F., Bustos-Korts, Millet, Boer, Kruijer, Thompson, A., Malosetti, Iwata, H.,
Quiroz, R., Kuppe, C., Muller, Blazakis, K. N., Yu, K., Tardieu, F., Chapman, S. (2019). Modelling
strategies for assessing and increasing the effectiveness of new phenotyping techniques in plant
breeding. Plant Science, 282, 23-39. , DOI : 10.1016/j.plantsci.2018.06.018

[135] M. Cooper, F. Technow, C. Messina, C. Gho, L. Radu Totir, Use of crop growth models with whole-genome prediction: Application to a maize multienvironment trial, Crop Sci. 56 (2016) 2141–2156. doi:10.2135/cropsci2015.08.0512.

[136] H. Campos, M. Cooper, G.O. Edmeades, C. Löffler, J.R. Schussler, M. Ibañez, Changes in Drought Tolerance in Maize Associated With Fifty Years of Breeding for Yield in the U . S . Corn Belt 1, Maydica. 51 (2006) 10–11.

[137] G.J. Rebetzke, A.R. Rattey, G.D. Farquhar, R.A. Richards, A. (Tony) G. Condon, Genomic regions for canopy temperature and their genetic association with stomatal conductance and grain yield in wheat, Funct. Plant Biol. 40 (2012) 14–33. http://dx.doi.org/10.1071/FP12184.

[138] K. Chenu, R. Deihimfard, S.C. Chapman, Large-scale characterization of drought pattern: a continent-wide modelling approach applied to the Australian wheatbelt – spatial and temporal trends, New Phytol. 198 (2013) 801–820. doi:10.1111/nph.12192.

[139] M.T. Harrison, F. Tardieu, Z. Dong, C.D. Messina, G.L. Hammer, Characterizing drought stress and trait influence on maize yield under current and future conditions, Glob. Chang. Biol. 20 (2014) 867–878. doi:10.1111/gcb.12381.

[140] R. Rincent, E. Kuhn, H. Monod, F.-X. Oury, M. Rousset, V. Allard, J. Le Gouis, Optimization of multi-environment trials for genomic selection based on crop models, Theor. Appl. Genet. (2017) 1–18. doi:10.1007/s00122-017-2922-4.

[141] G.L. Hammer, G. McLean, S. Chapman, B. Zheng, A. Doherty, M.T. Harrison, E. van Oosterom, D. Jordan, Crop design for specific adaptation in variable dryland production environments, Crop Pasture Sci. 65 (2014) 614–626. http://dx.doi.org/10.1071/CP14088.

[142] R. Rincent, D. Laloë, S. Nicolas, T. Altmann, D. Brunel, P. Revilla, V.M. Rodríguez, J. Moreno-Gonzalez, A. Melchinger, E. Bauer, C.-C. Schoen, N. Meyer, C. Giauffret, C. Bauland, P. Jamin, J. Laborde, H. Monod, P. Flament, A. Charcosset, L. Moreau, Maximizing the Reliability of Genomic Selection by Optimizing the Calibration Set of Reference Individuals: Comparison of Methods in Two Diverse Groups of Maize Inbreds (Zea mays L.), Genetics. 192 (2012) 715–728. doi:10.1534/genetics.112.141473.

[143] D. Bustos-Korts, M. Malosetti, S. Chapman, B. Biddulph, F. van Eeuwijk, Improvement of Predictive Ability by Uniform Coverage of the Target Genetic Space, G3 Genes|Genomes|Genetics. 6 (2016) 3733–3747. doi:10.1534/g3.116.035410/-/DC1.

[144] J. Isidro, J.-L. Jannink, D. Akdemir, J. Poland, N. Heslot, M. Sorrells, Training set

Comment citer ce document :
van Eeuwijk, F., Bustos-Korts, Millet, Boer, Kruijer, Thompson, A., Malosetti, Iwata, H.,
Quiroz, R., Kuppe, C., Muller, Blazakis, K. N., Yu, K., Tardieu, F., Chapman, S. (2019). Modelling
strategies for assessing and increasing the effectiveness of new phenotyping techniques in plant
breeding. Plant Science, 282, 23-39. . DOI : 10.1016/j.plantsci.2018.06.018

optimization under population structure in genomic selection, Theor. Appl. Genet. 128 (2015) 145–158. doi:10.1007/s00122-014-2418-4.

[145] D.A. Ramírez, C. Gavilán, C. Barreda, B. Condori, G. Rossel, R.O.M. Mwanga, M. Andrade, P. Monneveux, N.L. Anglin, D. Ellis, R. Quiroz, Characterizing the diversity of sweetpotato through growth parameters and leaf traits: Precocity and light use efficiency as important ordination factors, South African J. Bot. 113 (2017) 192–199. doi:10.1016/j.sajb.2017.08.009.

[146] J.A. Postma, C. Kuppe, M.R. Owen, N. Mellor, M. Griffiths, M.J. Bennett, J.P. Lynch, M. Watt, OpenSimRoot: widening the scope and application of root architectural models, New Phytol. 215 (2017) 1274–1286. doi:10.1111/nph.14641.

[147] A. Dathe, J.A. Postma, M.B. Postma-Blaauw, J.P. Lynch, Impact of axial root growth angles on nitrogen acquisition in maize depends on environmental conditions, Ann. Bot. 118 (2016) 401–414. doi:10.1093/aob/mcw112.

[148] Y.L. Chen, V.M. Dunbabin, J.A. Postma, A.J. Diggle, K.H.M. Siddique, Z. Rengel, Modelling root plasticity and response of narrow-leafed lupin to heterogeneous phosphorus supply, Plant Soil. 372 (2013) 319–337. doi:10.1007/s11104-013-1741-x.

[149] P.C. Struik, Botany Bridging the genotype – phenotype gap in 3D, J. Exp. Bot. (2016) 4427–4430. doi:10.1093/jxb/erw264.

[150] V.M. Dunbabin, J.A. Postma, A. Schnepf, L. Pagès, M. Javaux, L. Wu, D. Leitner, Y.L. Chen, Z. Rengel, A.J. Diggle, Modelling root-soil interactions using three-dimensional models of root growth, architecture and function, Plant Soil. 372 (2013) 93–124. doi:10.1007/s11104-013-1769-y.

[151] J. Gu, X. Yin, T.J. Stomph, P.C. Struik, Can exploiting natural genetic variation in leaf photosynthesis contribute to increasing rice productivity? A simulation analysis, Plant, Cell Environ. 37 (2014) 22–34. doi:10.1111/pce.12173.

[152] A. Wu, A. Doherty, G.D. Farquhar, G.L. Hammer, Simulating daily field crop canopy photosynthesis: An integrated software package, Funct. Plant Biol. 45 (2018) 362–377. doi:10.1071/FP17225.

[153] V. Picheny, P. Casadebaig, R. Trépos, R. Faivre, D. Da Silva, P. Vincourt, E. Costes, Using numerical plant models and phenotypic correlation space to design achievable ideotypes, Plant Cell Environ. 40 (2017) 1926–1939. doi:10.1111/pce.13001.

[154] S.C. Chapman, M. Cooper, G.L. Hammer, Using crop simulation to generate genotype by environment interaction effects for sorghum in water-limited environments, Aust. J. Agric. Res. 53 (2002) 379–389. doi:http://dx.doi.org/10.1071/AR01070.

Comment citer ce document :
van Eeuwijk, F., Bustos-Korts, Millet, Boer, Kruijer, Thompson, A., Malosetti, Iwata, H., Quiroz, R., Kuppe, C., Muller, Blazakis, K. N., Yu, K., Tardieu, F., Chapman, S. (2019). Modelling strategies for assessing and increasing the effectiveness of new phenotyping techniques in plant breeding. Plant Science, 282, 23-39. , DOI : 10.1016/j.plantsci.2018.06.018

[155] K. Chenu, M. Cooper, G.L. Hammer, K.L. Mathews, M.F. Dreccer, S.C. Chapman, Environment characterization as an aid to wheat improvement: interpreting genotype–environment interactions by modelling water-deficit patterns in North-Eastern Australia, J. Exp. Bot. 62 (2011) 1743–1755. doi:10.1093/jxb/erq459.

[156] D. Bustos-Korts, M. Malosetti, S.C. Chapman, K. Chenu, M. Boer, F.A. van Eeuwijk, A protocol combining statistical and crop growth modelling to evaluate phenotyping strategies useful for selection under different drought patterns, Wageningen University, 2017. doi:10.18174/421321.

[157] P. Casadebaig, B. Zheng, S. Chapman, N. Huth, R. Faivre, K. Chenu, Assessment of the potential impacts of plant traits across environments by combining global sensitivity analysis and dynamic modeling in wheat, PLoS One. (2016). doi:10.1371/journal.pone.0146385.

[158] S.J.C. Janssen, C.H. Porter, A.D. Moore, I.N. Athanasiadis, I. Foster, J.W. Jones, J.M. Antle, Towards a new generation of agricultural system data, models and knowledge products: Information and communication technology, Agric. Syst. 155 (2017) 200–212. doi:10.1016/j.agsy.2016.09.017.

Comment citer ce document :
van Eeuwijk, F., Bustos-Korts, Millet, Boer, Kruijer, Thompson, A., Malosetti, Iwata, H., Quiroz, R., Kuppe, C., Muller, Blazakis, K. N., Yu, K., Tardieu, F., Chapman, S. (2019). Modelling strategies for assessing and increasing the effectiveness of new phenotyping techniques in plant breeding. Plant Science, 282, 23-39. , DOI : 10.1016/j.plantsci.2018.06.018

Comment citer ce document :
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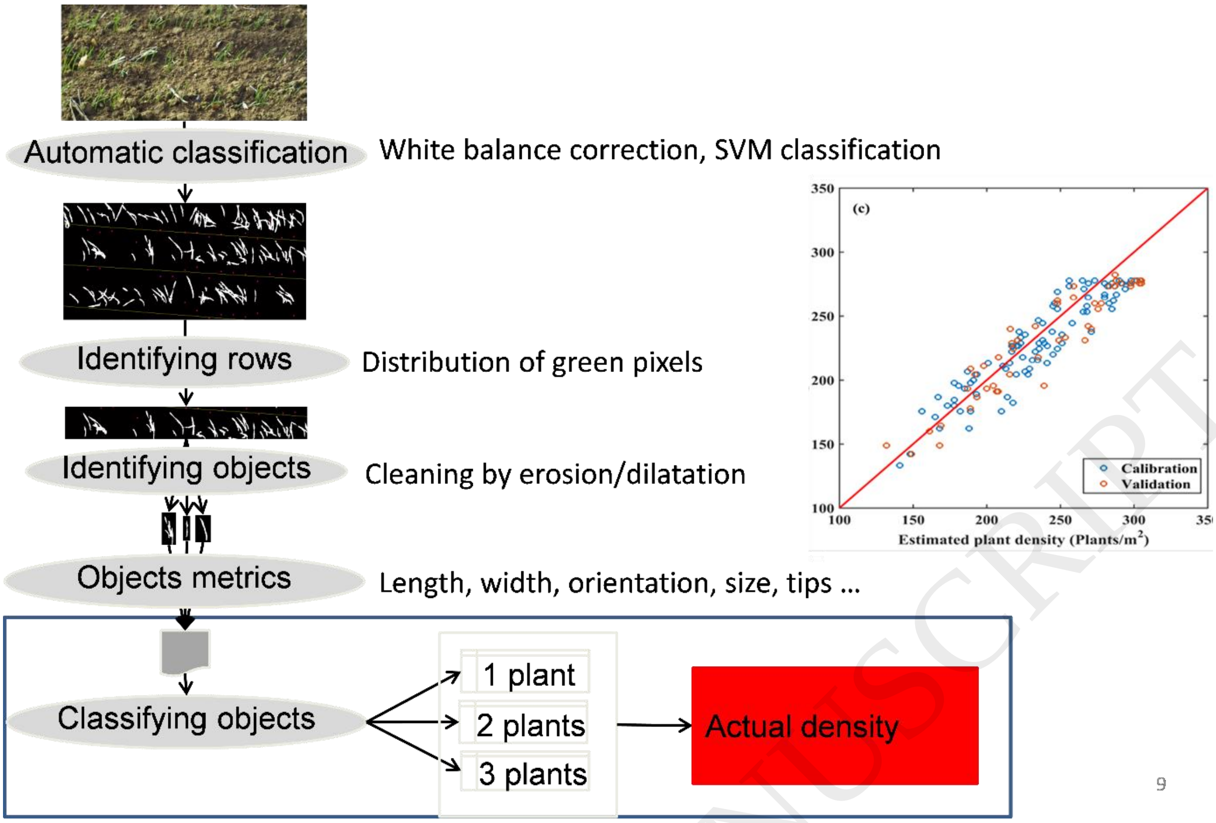

Figure 1. Identification of young wheat plants to count plant density per unit area. After objects are isolated and sized from rows, the data are processed to predict intersecting objects and estimate their number (Liu et al., 2017).

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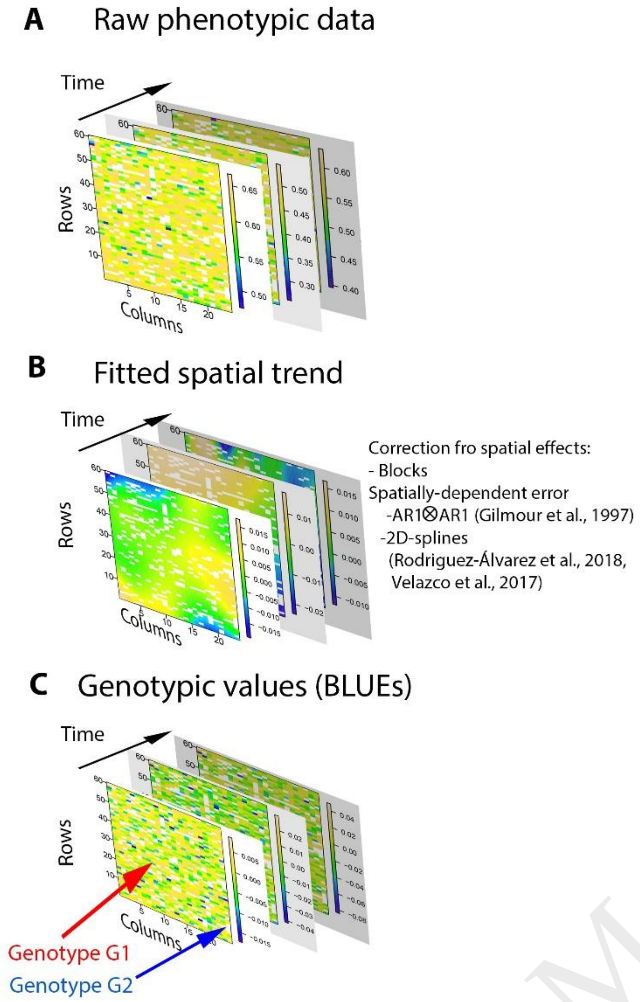
van Eeuwijk, F., Bustos-Korts, Millet, Boer, Kruijer, Thompson, A., Malosetti, Iwata, H., Quiroz, R., Kuppe, C., Muller, Blazakis, K. N., Yu, K., Tardieu, F., Chapman, S. (2019). Modelling strategies for assessing and increasing the effectiveness of new phenotyping techniques in plant breeding. Plant Science, 282, 23-39. . DOI : 10.1016/j.plantsci.2018.06.018



Correction fro spatial effects:
- Blocks
Spatially-dependent error
-AR1⊗AR1 (Gilmour et al., 1997)
-2D-splines
(Rodriguez-Álvarez et al., 2018,
Velazco et al., 2017)

Figure 2. Raw plot data (A) are adjusted for experimental design factors and spatial variation (B). The results are adjusted genotypic means (best linear unbiased estimators, BLUES) or predictions (best linear unbiased predictors, BLUPS) per time point and environment (C).

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breeding. Plant Science, 282, 23-39. . DOI : 10.1016/j.plantsci.2018.06.018

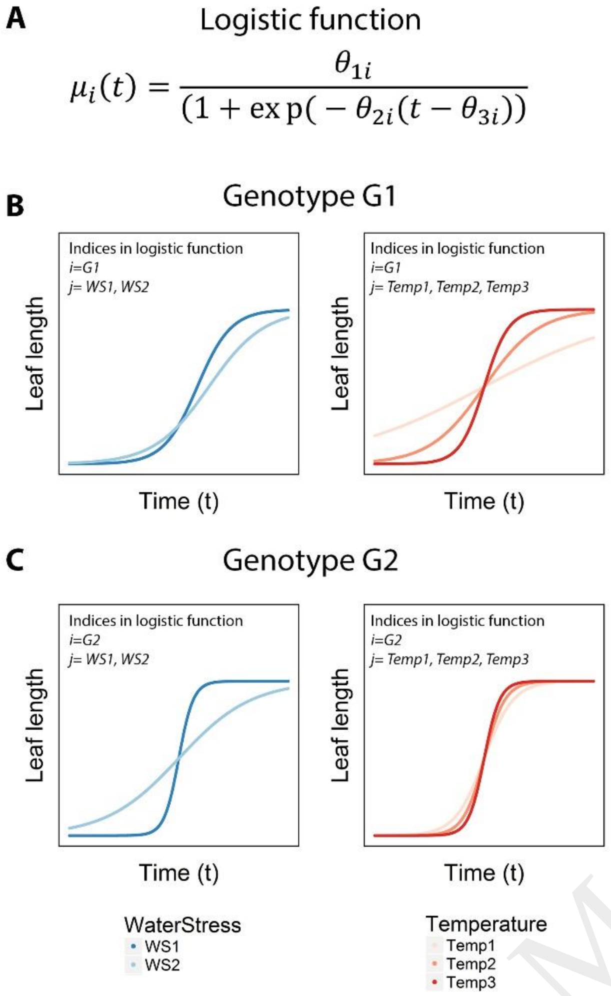

Figure 3. Modelling the dynamics of phenotypic traits. Spatially adjusted genotypic means are modelled in their dependence on time. A logistic curve is fitted and genotype specific parameters describing the dynamics are extracted. (A) Model formulation for logistic curve. (B) Logistic curves as fitted for a genotype G1 on the dynamics of leaf length under two water stress conditions (WS1, WS1) and three temperature stress conditions (Temp1, Temp2, Temp3). (C) as (B) for a genotype G2. Genotype G1 in (B) shows a low sensitivity to water stress and a high sensitivity to temperature stress, whereas G2 in (C) shows a high sensitivity to water stress and a low sensitivity to temperature stress.

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breeding. Plant Science, 282, 23-39. . DOI : 10.1016/j.plantsci.2018.06.018

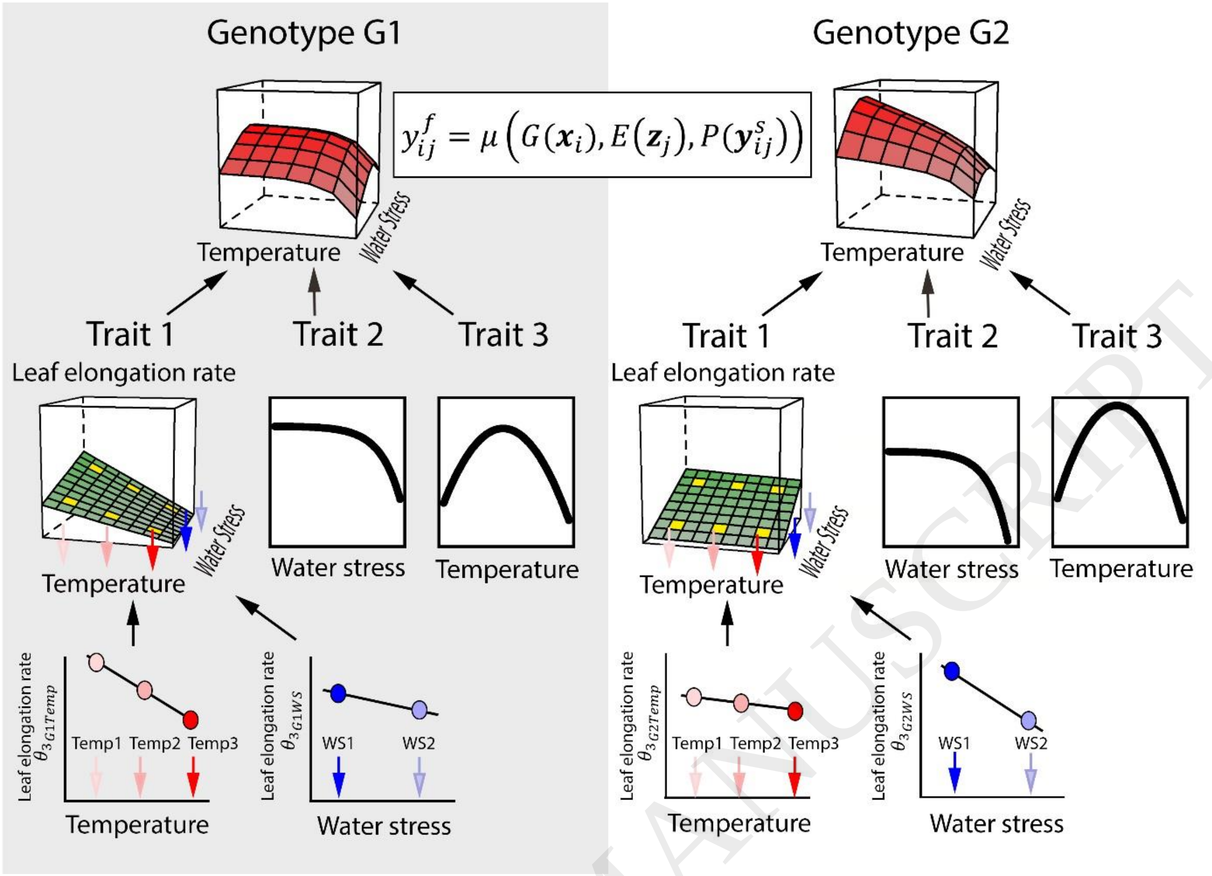

Figure 4. Genotype specific parameters expressing dynamics of leaf length on time as extracted across different environmental conditions, see Fig. 3, are modelled in relation to water and temperature stress characterizations. For leaf elongation rate (trait 1), a two dimensional a response surface is fitted. For other higher order traits (trait 2 and 3) one dimensional reaction norms are fitted as these traits depend in a simpler way on the environmental conditions. In the fitted response surface for leaf elongation rate the yellow points indicate conditions that were sampled in experiments. The higher order traits 1, 2 and 3 together determine a response surface for yield, the target trait. The prediction model for yield has trait 1, 2 and 3 as inputs as well as water and stress temperature characterizations.

Comment citer ce document :
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Quiroz, R., Kuppe, C., Muller, Blazakis, K. N., Yu, K., Tardieu, F., Chapman, S. (2019). Modelling
strategies for assessing and increasing the effectiveness of new phenotyping techniques in plant
breeding. Plant Science, 282, 23-39. , DOI : 10.1016/j.plantsci.2018.06.018

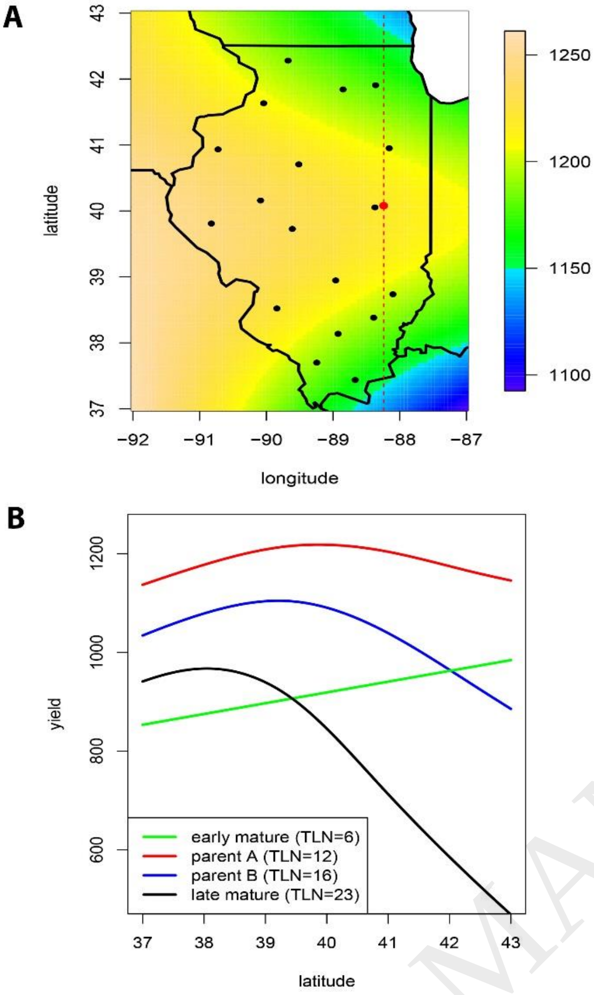


Figure 5. A response surface and four response curves for yield in maize. (A) The response surface for a parent of a bi-parental cross obtained from crop growth simulations using inputs from 19 weather station locations in Illinois, with a heritability of 0.85 per location. (B) For the longitude indicated by the dotted vertical red line in (A) four genotypes are compared for their dependence of yield on latitude; the two parents of a bi-parental cross, plus two offspring lines showing extreme values for the trait total leaf number (TLN).

Table 1. The modelling process that converts raw data into strongly model dependent predictions, thereby adding value to data over successive cycles of modelling. Dimensions of input data decrease because data are replaced by integrative parameters that become increasingly model dependent.

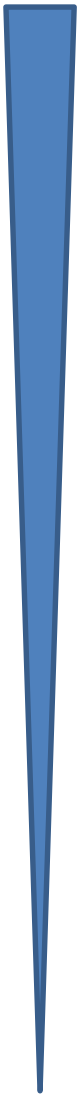
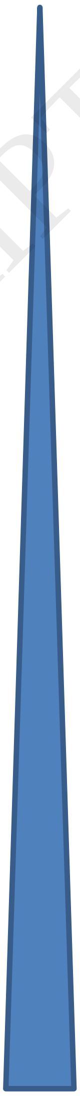
Size input data	**Modelling step**	**Input**	**Model / strategy**	**Output**	**Model dependence output**
	Feature extraction	Multiple pixels/wavelengths for each plot, genotype, time point and environment (low level traits)	Segmentation Organ Tracking Indices (e.g. NDVI) Machine learning	Trait value for each plot, genotype, time point and environment	
	Correcting for design factors and spatial trends	Trait value for each plot, genotype, time point and environment	Mixed models: - AR⊗ AR - SpATS	Adjusted trait value for each genotype, time point and environment	
	Dynamical modelling	Trait value for each genotype, time point and environment	Standard mathematical functions (Logistic, Gompertz) Repeated measures Splines Crop growth models	Genotype specific parameters for each environment (intermediate level traits)	
	Modelling dependence on environmental gradients	Genotype specific parameters for each environment	Standard mathematical functions Splines Crop growth models	Genotypic sensitivities to environmental covariables (higher level traits)	
	Target trait prediction	Higher order traits and environmental characterizations	Mixed models (multi-trait, factorial regression) Crop growth models	Genotype specific yield predictions per environment	

Table 2. Correlated response framework for high precision and whole-plant platforms to predict phenotypes in the field.

Platform		Field	Ref
QTLs of maximum leaf elongation rate	*Co-location*	QTLs of anthesis-silking interval in WW fields	[52]
QTLs of response of leaf elongation rate to WD	*Co-location*	QTLs of anthesis-silking interval in WD fields	
This suggested that common genetic mechanisms are shared between the growth of reproductive organs in the field and leaf growth on the platform			
QTLs for maximum leaf elongation rate	*Co-location*	QTLs involved in the growth of shoots, roots, reproductive organs	[81, 82]
Sensitivity of maize leaf growth to soil water deficit	*Correlation*	Sensitivity of maize grain number to soil water deficit around flowering time	[83]
Genotypic sensitivity of leaf elongation to evaporative demand and of leaf width to intercepted radiation	*Prediction equation with genotype-specific parameters*	Predict individual leaf area in a network of field	[57]
Allelic effects underlying leaf width and length	*Correlation*	Allelic effects underlying leaf width and length	
Although there was G×E between platform and field experiments, the correlated QTL effects would still allow to use platform data to improve selection for leaf area in field conditions.			
Biomass, plant leaf area, length of leaf 2 and 3, leaf breadth	*Correlation and indirect selection*	Biomass	[84]
Illustrates the importance of jointly considering the magnitude of genetic correlations between traits measured on the platforms and those in the field and trait heritability to assess the potential of traits to aid selection for early biomass in the field			