BURLEIGH DODDS SERIES IN AGRICULTURAL SCIENCE

Digital phenotyping and genotype-to-phenotype (G2P) models to predict complex traits in cereal crops

Nicolas Virlet, Rothamsted Research, UK; Danilo H. Lyra, Biometrics and Breeding Research, BASF, Belgium; and Malcolm J. Hawkesford, Rothamsted Research, UK

burleigh dodds
SCIENCE PUBLISHING

Digital phenotyping and genotype-to-phenotype (G2P) models to predict complex traits in cereal crops

Nicolas Virlet, Rothamsted Research, UK; Danilo H. Lyra, Biometrics and Breeding Research, BASF, Belgium; and Malcolm J. Hawkesford, Rothamsted Research, UK

1 Introduction

With the development of Breeding 4.0, new genotyping and phenotyping tools are needed to help the breeding process to increase the productivity of genotypes (Van Eeuwijk et al., 2019, Wallace et al., 2018). This includes a trend to integrate multiple layers of genomics, high-throughput plant phenotyping (HTPP), and large-scale envirotyping to improve the prediction of complex traits (Crossa et al., 2021, Cooper et al., 2014). Whole genome-enabled prediction, referred to as genomic prediction (GP) or genomic selection (GS), is the main approach to integrate these new tools into breeding programs for supporting the delivery of high- and sustainable-yielding cultivars. The main goal of GS is to predict complex traits based on marker information, increasing the precision of selection by generating a genomic estimated breeding value for candidates. Therefore, GS is potentially superior to phenotypic selection for increasing genetic gains per unit time and shortening the length of the breeding cycle (Crossa et al., 2017). Recently, the requirements of breeders are increasingly shifting towards accommodating HTPP data and environmental information into the multi-environment trial analysis (Araus et al., 2018). However, it is

http://dx.doi.org/10.19103/AS.2022.0102.12

uncertain whether the increasing number of phenotypes measured and the depth of information from the new phenotyping platforms will improve the prediction of quantitative traits.

Improvements in yield have been achieved mainly by evaluating grain yield as the sole selection criterion. However, grain yield in cereals is an integrative trait resulting from the genetic ability of a plant to grow, to capture resources, and to transfer them into the grain in a specific environment. Determination of grain yield involves multiple processes, and it is therefore under multi-gene control with complex interactions with the environment. Reynolds and Langridge (2016) suggested that to accelerate yield improvement, physiological traits need to be considered for breeding in addition to the advanced genomics methods (Reynolds et al., 2012). Furthermore, since a comprehensive genetic basis explaining cultivar-level differences in performance does not yet exist for any crop, physiological breeding currently relies heavily on phenomics.

Digital phenotyping tools enable rapid screening of populations in field conditions in a non-invasive and non-destructive approach. These tools make use of remote sensing and close-range technologies (from airplane to handheld device) for screening experimental trials with hundreds or thousands of plots in a fast, non-invasive, and non-destructive way (Araus et al., 2018). Digital phenotyping enables repeat measurements over time and thus provides valuable dynamic information on crop growth as well as crop physiology and phenology, to enable an understanding of the whole life-cycle growth performance of the genetic materials in relation to the end product, that is grain yield. In addition, conducting experiments at multiple locations should help to deliver optimal final products targeting specific environments with optimal yield and performance for farmers. However, while a wealth of information is now available from digital phenotyping, not everything is necessarily needed or even relevant for the breeding community. One important aspect to consider is the cost and the throughput of the technologies being deployed for breeding trials. Reynolds et al. (2012) emphasized that breeders are interested in reducing the size of their test populations to achieve the required genotype at a reasonable probability and cost, even if the methods might be seen as imperfect from a physiological and theoretical point of view.

Digital phenotyping involving the application of remote sensing technologies and methods at spatially close proximal scales enables access to the different components of plant growth with unprecedented accuracy (in terms of temporal, spatial, and spectral resolution). Quantifying the morphological, phenological, and physiological traits at plot scale is now possible even if some approaches still require refinement to replace traditional approaches. The use of optical sensors offers the possibility to assess biomass, nitrogen, and chlorophyll estimation along the plant development cycle, as well as physiological parameters linked to photosynthesis and light use efficiency (LUE) of the crop. Thermal infrared technology measuring leaf and canopy temperature provides information on plant water transpiration status and water use. Lidar technology gives access to plant stature and morphology. Visible imaging, using simple camera technology, offers the greatest versatility, providing high pixel resolution and recording information akin to the human eye. This is extremely valuable as traditionally breeders rely tremendously on visual observation, the 'breeder's eye'.

High-throughput plant phenotyping records numerous traits with high spatiotemporal resolution at a level far beyond what humans can assimilate. As a result, a new method of selecting phenotypes has recently been proposed, known as 'phenomic selection' (Rincent et al., 2018). In this approach, data such as hyperspectral information are used the same way as molecular markers to make inferences about relatedness. In other words, phenotypic variables (referred to as secondary traits) replace genetic information in a traditional GP approach. Integration of both types of information (genetic plus phenomic) as predictors in genotype-to-phenotype (G2P) models has been used to improve the predictive ability for yield in wheat (Krause et al., 2019). To that end, the complexity of the new HTPP data raises many questions about how to efficiently integrate genetic and non-genetic components to improve the accuracy of prediction for complex traits.

Applications of HTPP data for predictive G2P models may be grouped into three categories. The first strategy uses the phenotypic data generated from the platforms as the target phenotype (Lyra et al., 2020, Watanabe et al., 2017). The second strategy uses thousands of reflectance data points (hyperspectral bands or derived vegetation indices (VIs)), captured at many stages of crop development as secondary phenotypes (genotype-specific covariables), with G2P models to improve the prediction of primary (target) traits, that is grain yield (Rutkoski et al., 2016, Sun et al., 2017). A third strategy is modelling plant growth from longitudinal traits (e.g., light interception, biomass accumulation, canopy height), allowing the selection of high-yielding cultivars at the early stages of development (Moreira et al., 2020). Several authors have applied different statistical models to handle this data complexity, including multivariate analysis (Rutkoski et al., 2016, Sun et al., 2017), factorial regression (Van Eeuwijk et al., 2019), functional regression (Montesinos-Lopez et al., 2017b), multi-kernel regression (Krause et al., 2019), deep learning (Cuevas et al., 2019), regularized selection indices (Lopez-Cruz et al., 2020), mega-scale linear mixed model (MegaLMM) (Runcie et al., 2021), and crop growth models (Van Eeuwijk et al., 2019). Furthermore, with the recent developments of precision envirotyping platforms, the integration of new phenotypic and envirotypic information will become a new standard.

Envirotyping is the process of collecting environmental factors (e.g. soil and climate information) in multi-environment trials (MET), intending to characterize the variation of the phenotypic performance of genotypes over, for example environmental gradients (envirotype) (Cooper et al., 2014, Xu, 2016). Another promising concept that could be applied in crop breeding for a more optimized variety selection is 'enviromics', which is the integration of envirotypes with multiple enviromic markers which correspond to environmental variables that may interact with the genetic background (Resende et al., 2021). Envirotyping information has been used to explore envirotype-to-phenotype dynamics and has been incorporated in G2P models to improve the prediction of complex traits (Costa-Neto et al., 2020, 2021a, b, Millet et al., 2019, Porker et al., 2020).

In this chapter, recent literature on incorporating new phenotyping data into predictive G2P models is explored, along with an introduction to the use of envirotyping information. The chapter is presented in two sections. First, the main 'traits' that are currently used and/or should be useful for breeding are introduced. Second, the most common statistical methods used to integrate markers, environmental information, and HTPP data are described.

2 Digital phenotyping as a tool to support breeding programs

Yield is considered a primary trait and is the goal in most breeding programs. For decades, breeding has been focused only on selecting genetic material based on the yield itself at harvest. However, as mentioned in the study by Van Eeuwijk et al. (2019), secondary phenotypes have proved useful as a covariate in prediction models for yield. These secondary phenotypes are defined as basic or intermediate traits (Bustos-Korts et al., 2019). The basic traits correspond to response mechanism/sensitivities to environmental conditions (e.g., sensitivity to photoperiod, water uptake capacity, radiation use efficiency), whilst the intermediate traits result from the integration of several processes over time (e.g. biomass accumulation, flowering time, grain number).

The introduction of secondary traits in prediction models is called physiological breeding (Reynolds and Langridge, 2016). However, the application may be difficult to implement depending on the secondary phenotypes considered. For example, measuring height or scoring for heading or anthesis time is straightforward (despite the fact it is time-consuming), while other phenotypes such as biomass or photosynthesis are more constraining in terms of requiring destructive measurement or demands to collect data at a large scale in a short amount of time. Pask et al. (2012) summarized most of the secondary phenotypes used for breeding as well as the practical methods to collect them. The authors also brought to light some of the remote sensing methods applied at the plot scale, for example using spectroradiometers and thermal infrared sensors, as non-destructive and non-invasive technologies to produce proxies of biomass and transpiration traits, respectively. Although a vast amount of data are now available from the multiple technologies for phenotyping, such as visual, multi-/hyperspectral imaging, thermal infrared, and fluorescence sensors, as well as lidar technologies, not all this information will be relevant for breeders. Digital phenotyping must balance the time of acquisition with the relevance of the proxies and the cost to deploy the technologies.

In this section, we will review the secondary phenotypes measured by high-throughput digital phenotyping tools that are potentially useful for breeding. The secondary phenotypes will be considered in terms of the level of integration and complexity regarding their use as single/multi-indirect traits for yield prediction, covariates for yield prediction, or for integrating over time using growth curves to access new parameters summarizing growth events.

2.1 Simple secondary traits

This section summarizes secondary phenotypes considered as simple variables. In this case, 'simple' means that the variable is the output from a sensor and is not the result of the combination of different metrics or sensors. The secondary phenotypes are sub-divided according to the morphological, physiological, and phenological classification of the traits (Violle et al., 2007).

2.1.1 Morphological traits

Morphological traits such as height and canopy cover are the most straightforward variables to collect using either lidar technologies and/or visible cameras (Red-Green-Blue (RGB)). Height can be easily calculated not only from different lidar systems (Deery et al., 2014, Friedli et al., 2016, Virlet et al., 2016) but also from the structure from motion (SfM) principle when RGB cameras are coupled with an appropriate vector, such as unmanned aerial vehicles (UAV) or tractor-based systems (Holman et al., 2016, Jay et al., 2015). The output of these two approaches is called a point cloud, with each point having *x*, *y*, and *z* coordinates. Height is the easiest parameter derived from the point cloud. Recent studies have shown capabilities to estimate the volume of the canopy, the above-ground biomass (AGB), the leaf area index (LAI), or the stem diameter by processing the point clouds using voxelization (Che et al., 2020, Hosoi et al., 2013, Jimenez-Berni et al., 2018, Salas Fernandez et al., 2017, Xiao et al., 2020).

With sufficient spatial resolution, processing the point cloud enables access to other morphological parameters such as the leaf area and angle (Mantilla-Perez and Salas Fernandez, 2017), as well as the volume of the reproductive organs in cereal crops. It is also possible to extract the fraction vegetation cover (FVC) from the point clouds as in the study by Duan et al. (2016). However, FVC is generally computed from RGB images as the ratio of crop green pixel to the total number of pixels contained in the region of interest. Numerous approaches have been developed to segment the green plant pixel from the background as the ambient illumination is a limiting factor for the efficiency of the segmentation (Casadesús et al., 2007, Guo et al., 2013, Hamuda et al., 2016, Sadeghi-Tehran et al., 2017a). Those methods range from simple threshold approaches to deep learning methods overcoming the illumination issues by training the algorithm with a wide range of illumination conditions. There are multiple applications of monitoring FVC such as enabling quantification of canopy development from emergence to maturity (Borra-Serrano et al., 2020, Sadeghi-Tehran et al., 2017a, Varela et al., 2021).

In recent years, there has been a growing interest in using RGB images to quantify the number of ears/panicles for the major grain crops (Duan et al., 2015, Fernandez-Gallego et al., 2018, Lu et al., 2017, Xiong et al., 2017, Chandra et al., 2020, Ghosal et al., 2019, Liu et al., 2020, Madec et al., 2019, Sadeghi-Tehran et al., 2019, Velumani et al., 2020, Zhou et al., 2019). Many of these approaches rely on machine learning methods and require the acquisition of solid training data sets to encompass the various stages of maturation of the reproductive organs and the genetic variation. To facilitate such data set acquisition, a group of researchers from nine different institutions across seven countries and three continents developed the Global Wheat Head Detection data set that can be used to benchmark methods proposed in the computer vision community (David et al., 2020).

2.1.2 Physiological traits

Digital phenotyping also enables the measurement of physiological traits related to carbon and nitrogen metabolism. Physiological traits are mainly assessed using the spectral properties of the plant, whether in the optical domain or in the thermal infrared. Multi- and hyperspectral technologies (signal point or utilizing imaging systems) are used to derive spectral reflectance indices (SRIs), which are mainly related to biomass accumulation and component traits (light interception and light/radiation use efficiency). SRIs are obtained by the arithmetic combination of two or more wavelengths designed to highlight a particular property of vegetation. Each SRI is designed to accentuate a particular vegetation property (https://www.l3harrisgeospatial.com/docs/vegetationindices.html).

More than 100 indices have been developed over the past 50 years. Most of the indices developed are related to the biomass accumulation and the light interception such as the normalized differences vegetation index (NDVI) and the developed derivatives to overcome NDVI limitations (Corti et al., 2018, Cabrera-Bosquet et al., 2011, Gutierrez et al., 2012, Haboudane et al., 2004, Yue et al., 2017). Chlorophyll and nitrogen leaf/canopy content as well as other pigments have been extensively investigated over recent decades using vegetation reflectance properties (Berger et al., 2020, Blackburn, 2007, Boegh et al., 2002, Camino et al., 2018a, Cammarano et al., 2014, Fitzgerald et al., 2010, Gitelson and Solovchenko, 2018, Jay et al., 2015). Post-harvest traits related to nitrogen have been also explored extensively in the literature (Erdle et al., 2013, Frels et al., 2018, Pavuluri et al., 2015, Prey et al., 2020, 2019, Prey and Schmidhalter, 2020, 2019). The above-mentioned agronomical traits reflect the process of biomass accumulation, which can be monitored and assessed using different VIs such as NDVI and NDVI-like indices. However, those indices do not report short-term variation that might occur with changes in ambient conditions (Dobrowski et al., 2005). Among the SRIs, the photochemical/physiological reflectance index (PRI), a normalized reflectance index that uses the 531 nm and 570 nm wavelengths, is generally used as a direct method to assess LUE over short periods (Gamon et al., 2016). PRI has been shown to negatively correlate with non-photochemical quenching (NPQ) and the de-epoxidation state of the xanthophyll cycle (Evain et al., 2004, Peguero-Pina et al., 2008, Porcar-Castell et al., 2012, Rascher et al., 2007) and positively correlate with steady-state fluorescence, F', and the photosystem II (PSII) operating efficiency (F_q'/F_m') under differing irrigation regimes in controlled or natural environmental conditions (Evain et al., 2004, Peguero-Pina et al., 2008). The use of active sensors such as the laser-induced fluorescence transient should be useful to assess photosynthetic dynamics of the crop and replace gas-exchange measurements. However, this technology still needs refinement to be applied practically on a large scale (Wyber et al., 2017, 2018).

The canopy water status may be investigated using SRIs of specific wavelengths sensitive to water content. The most used of these indices are the water band index and normalized water band indices computed from the wavelengths from the 850–970 nm range (Prasad et al., 2007). However, as shown in Winterhalter et al. (2011), other SRIs have been investigated using various wavelengths in the visible-near infrared domain and wavelengths of the shortwave infrared domain. In addition to the canopy water content, canopy transpiration may be assessed using thermal infrared technologies (Jones et al., 2009), which measure the canopy temperature and its variation due to the control of stomatal opening/closure regulating water loss in response to changes in environmental conditions (Gonzalez-Dugo et al., 2014, Kelly et al., 2019, Maes and Steppe, 2012, Munns et al., 2010).

2.1.3 Phenological traits

Crop phenology is usually scored by using Zadoks, Feekes-Large, or the Haun systems. The remote sensing community has been using VIs to estimate the stage of development of various crops using variations in the VIs during growth (Duncan et al., 2015, Piao et al., 2019, Yamasaki et al., 2017). Recent advances in the phenotyping community allowing collection of images at a closer range to the crops have enabled an unprecedented spatial resolution. The use of RGB cameras, coupled with appropriate algorithms, has enabled detection and quantification of some of the important growth stages such as heading and flowering stages in cereal crops.

The dynamic of ears per image may be used to estimate heading dates (Velumani et al., 2020, Wang et al., 2019). Flowering information has been collected in field conditions for various annual and perennial crops such as *Lesquerella*, apple tree, grapevine, rice, wheat, and cotton (Aquino et al., 2015, Guo et al., 2015, Hocevar et al., 2014, Sadeghi-Tehran et al., 2017b, Thorp and Dierig, 2011, Xu et al., 2018). Different approaches have been used for the flower segmentation using threshold-based algorithms (Hocevar et al., 2014, Thorp and Dierig, 2011), for segmentation and quantification using mathematical morphology and pyramidal algorithm (Aquino et al., 2015), for identification of flowering within RGB images using k-means clustering and support vector machine (SVM) (Guo et al., 2015, Sadeghi-Tehran et al., 2017b), and for identification of flowers in three-dimensional (3D) images from aerial pictures using convolutional neural networks (Xu et al., 2018).

The senescence period has also been investigated using RGB, multi-, and hyperspectral sensors. The temporal data of the senescence enable to derive parameters such as the onset, midpoint, and senescence duration, and the topic will be detailed in Section 2.3 (Anderegg et al., 2020, Borra-Serrano et al., 2020, Christopher et al., 2014, Kipp et al., 2014, Montazeaud et al., 2016).

2.2 Multi-sensor secondary traits modelling

To increase the efficiency of agronomic trait prediction (e.g. biomass and physiological traits), many approaches may be used such as (i) arithmetic combination of secondary traits to try to mimic as much as possible the agronomic trait, (ii) multi-linear/non-linear regression model to select the secondary phenotypes enabling better prediction, and (iii) multivariate analysis which summarizes secondary phenotypes information to predict the agronomic traits of interest. In this Section 2.2, only statistical methods used to predict traits without including genomic information are described.

2.2.1 Arithmetic combination of secondary phenotypes

AGB has been predicted using lidar outputs such as height and volume as well as using spectral VIs and FVC. The accuracy of the predictions varies depending on the crop, the type of trial, treatment, and stage of development. Height itself is not an indicator of biomass. The use of SRIs as a biomass predictor, as well as the FVC derived from the RGB camera, is often limited by the excess (saturating) density of the cover, and height itself might not be sufficient enough as a biomass indicator. It has been shown that the combination of SRI or FVC (or both) with height improves biomass prediction. Yue et al. (2017) showed that the incorporation of the height data by multiplication or division of the eight VIs tested improved the biomass prediction in all cases. Maimaitijiang and Sidike (2019) developed a canopy volume index based on the parameters extracted from the crop height model from the orthomosaic image obtained by UAV and combine them with different SRIs to improve the biomass prediction with success. Another approach was taken by Jin et al. (2019) to predict biomass by estimating the volume of the plot. The authors combined height at anthesis time when it is considered to be at its maximum, the post-harvest stem diameter, and the number extracted from RGB images capturing the residual stems standing straight after harvest. Lu et al. (2021) also used a combination of VI and height measurement to estimate the canopy nitrogen content (CNC). They showed that the combination of height, VI, and FVC increased the CNC prediction.

SRIs have been used extensively to determine the canopy nitrogen (N) status in various crops. However, as mentioned by Fitzgerald et al. (2010), measuring the N status by SRI was found to be challenging across the season, as the ground coverage and the canopy structure are both changing along with crop growth, as well as there being an N dilution effect. The canopy chlorophyll content index (CCCI) has been developed to differentiate N from water stress in irrigated cotton and separate the confounding effects of canopy density (Barnes et al., 2000, Clarke et al., 2001, Rodriguez et al., 2006). Fitzgerald et al. (2010) have developed a proxy of canopy nutrition index (CNI, also called nutrition nitrogen index), allowing the monitoring of crop N status at different growth stages without being affected by the N dilution effect. The CNI is built on the relationship between dry biomass and the % N of the vegetation. Based on the same principle, the CCCI, a planar domain VI measuring plant biophysical parameters in a mixed soil/plant pixel, can be built by analysing the relationship between one chlorophyll and one biomass-related SRIs plotted in a two-dimensional (2D) space (Clarke et al., 2001, Pancorbo et al., 2021). Another index, the water deficit index (WDI) has been developed in the 1990s to overcome the confounding N and water stress effect on the SRI. The WDI is also a planar domain index: it is based on the relationship between a VI such as the NDVI and the variable $T_c - T_a$ from a thermal infrared sensor and by building 2D spaces, for the estimation of the evapotranspiration of the crops with less effect on the canopy density is possible (Moran et al., 1994, Pancorbo et al., 2021, Virlet et al., 2014).

2.2.2 Multi-linear/non-linear regression

In Section 2.2.1, most studies generally focused on single regression analysis based on a simple or a complex index to estimate the trait of interest. However, the single regression approaches might not be sufficient to estimate integrative traits such as biomass and grain yield in cereals. Here, different approaches to integrate parameters using multiple regression analysis (linear or non-linear) are reviewed. The first part covers research works predicting traits based on a single date of data collection using multiple traits, and the second section covers studies with data collection on multiple days, irrespective of whether the date was used as an independent variable in the models.

Multi-linear regression has been applied to estimate grain yield on maize, barley, and soft red wheat (Gracia-Romero et al., 2017, Kefauver et al., 2017, Pavuluri et al., 2015). On maize and barely, the best model for improving grain yield prediction from UAV imaging was a combination of two to five indices derived from RGB and/or multispectral imaging (Gracia-Romero et al., 2017, Kefauver et al., 2017). At the ground level, Pavuluri et al. (2015) showed models with three SRIs gave the best predictions for grain yield. On sorghum, Li et al. (2018) used simple and multiple exponential regression analyses to estimate fresh and dry biomass. In this case, a simple exponential regression model based on canopy height gave in most of the cases the best biomass prediction, with some improvements of the prediction by combining VIs. Vargas et al. (2019) used the Lasso algorithm and found that the best prediction for AGB in peas was a combination of VIs, FVC, and canopy volume. In the study by Santini et al. (2019), a combination of VIs and thermal infrared data gave the best prediction for the stem volume of adult trees of *Pinus halepensis*.

Multiple regression has also been applied to nutrient content prediction. Gracia-Romero et al. (2017) used this approach to predict phosphorus (P) content in maize and improve P content prediction compared to simple regression analysis. However, the model prediction was still low. Pavuluri et al. (2015) had more success estimating grain N uptake, yield, and protein nitrogen use efficiency using models built from data collected at different growth stages (stem elongation, booting, heading, and grain filling). The predictions were better by combining the 2 years of measurement for each growth stage.

Bendig et al. (2015) looked at biomass monitoring prediction in barley based on a combination of plant height and VIs using data collected prior and post-heading date. Models based on single and multiple exponential or linear regressions were tested using either the full data set or only the pre-heading data set. Cross-validation showed that the combination of VIs with plant height performed better than using the VIs alone, whatever the use of multiple linear or non-linear regression. In a different approach, Hoyos-Villegas et al. (2014) combined canopy height, FVC, AGB, photosynthesis, and rate of growth collected at 13 time points into multiple regression models to predict grain yield, AGB, photosynthesis rate, and rate of growth. The approach taken by the authors provided interesting model predictions for each of the parameters and showed that multi-sensor data produce highly successful predictions. The main drawback was the upscaling feasibility to large populations for breeding purposes due to the amount of data to collect, especially for the gas exchange.

Magney et al. (2016) used NDVI data and the parameters from the growth and senescence curves (growth rate and duration of NDVI for tillering, stem elongation, heading, and maturation) to predict grain yield, total biomass, protein content, and grain N yield using multi-linear regression models. The best results were obtained by the models using two or three phenological stages. This study also showed that using NDVI-derived phenological metrics from the early season (tillering and stem extension) substantially improved early prediction of yield and biomass, as compared to daily NDVI data, whereas protein and grain N were primarily driven by metrics associated with the reproductive development of the crop (heading and ripening). More recently, Buchaillot et al. (2019) used multiple regression analysis to predict grain yield in maize based on agronomic data coupled with (i) field sensors, (ii) ground imagery, and (iii) UAV imagery. Most of the models improved the grain yield prediction using four to nine parameters. This study also showed that the simple use of the date of anthesis, the duration from anthesis to the silking stage, the chlorophyll index given by the SPAD-502 at the vegetative and reproductive stage gave the best prediction for grain yield prediction ($r^2 = 0.61$). The model using UAV image data showed promising results ($r^2 = 0.60$) but used nine parameters instead of the four used in the previously mentioned model.

Camino et al. (2018b) used multiple regression analysis to assess the contribution of sun-induced fluorescence (SIF) indices for nitrogen prediction in wheat. The performance of the built models with and without SIF was compared with the performance of models built with plant traits estimated by the PROSPECT-SAILH model inversion and with standard approaches based on single SRIs. The use of SIF indices increased the performance of the models based on the output of the inversion models ($r^2 = 0.68$–0.77 without SIF, $r^2 = 0.92$–0.93 with SIF) and also outperformed the prediction for the chlorophyll content by the narrow-band indices ($r^2 = 0.25$–0.57).

2.2.3 Partial least square regression

Partial least square regression (PLSR), a multivariate analysis, has been proved useful for dealing with large numbers of parameters and volumes of data. The use of PLSR in plant phenotyping is increasing and shows promising results to estimate and predict different plant parameters. During the last decade, it has been used to estimate grain yield on barley, maize, and wheat (Barmeier and Schmidhalter, 2017, Elsayed et al., 2018, 2017, 2015, Garriga et al., 2017, Rischbeck et al., 2016, Weber et al., 2012), biomass at tillering and anthesis time on barley, maize, and wheat (El-Hendawy et al., 2019a, Elsayed et al., 2018, Montes et al., 2011), leaf nitrogen and chlorophyll content (Ecarnot et al., 2013, Silva-Perez et al., 2018, Vigneau et al., 2011), canopy water status on barley and wheat (El-Hendawy et al., 2019a, b, Elsayed et al., 2015, 2017), physiological and photosynthesis parameters on cotton, blueberry, tobacco (Fu et al., 2019, 2020, Lobos et al., 2019, Meacham-Hensold et al., 2020, Silva-Perez et al., 2018, Thorp et al., 2015). Most of those studies are using the reflectance data as input for the PLSR. However, some authors have been using PLSR with SRIs directly. Elsayed et al. (2015) used SRIs from different sensors to estimate grain yield. The performance of the PLSR model improved grain yield prediction compared to the single regression model. El-Hendawy et al. (2019a) and El-Hendawy et al. (2019b) built a PLSR model based on SRIs and a selection of the most influential wavelengths. While in the El-Hendawy et al. (2019a) study, both approaches gave similar results, the El-Hendawy et al. (2019b) study showed the PLSR model with higher values of r^2 and lower values of the root mean squared error (RMSE) between observed and predicted values of the measured parameters was the model based on SRIs. Similarly, Fu et al. (2020) compared the performance of the PLSR model based on reflectance data and based on SRIs to estimate two photosynthetic parameters (V_{cmax} and J_{max}). For V_{cmax}, the PLSR model based on SRIs gave better prediction than the model based on the wavelength, while for J_{max}, both approaches gave similar predictions.

PLSR has also been used to integrate variables from different sensors. Montes et al. (2011) used this method to predict early biomass in maize based on height and reflectance data, while Rischbeck et al. (2016) used the method to predict grain yield in barley. Elsayed et al. (2017) used PLSR with different parameters to predict grain yield on wheat. Three PLSR models were built, one based on selected SRIs, one data fusion model based on SRIs and thermal infrared data, and one based on SRIs, thermal infrared data as well as relative water content and canopy water content. In the three last studies, the use of data fusion for PLSR improved the prediction showing the strong potential of the PLSR in plant phenotyping to integrate data from different sensors and cameras.

Some authors have compared the PLSR model to other approaches such as machine learning algorithms, multi-linear regression models, or even to the predicted parameters from the inversion radiative transfer model PROSAIL. In the study by Lobos et al. (2019), the PLSR model performed better than the multi-linear regression model to estimate fluorescence parameters in blueberry based on reflectance data, while in the study by El-Hendawy et al. (2019b), the two approaches gave similar results for yield prediction. Garriga et al. (2017) showed that for most of the traits and conditions tested, the estimations provided by the ridge regression and modified SVM were the same or better than those provided by the SRIs. They also found that among the classification methods, the PLS-discriminant analysis showed the best performance, and unlike the SRI and regression models, most traits were relatively well classified within a specific hydric condition. In the study by Montes et al. (2011), the SVM regression model to estimate biomass at the early stage performed slightly better than the PLSR. Fu et al. (2019) developed a framework combining six machine learning algorithms, including artificial neural network (ANN), SVM, least absolute shrinkage and selection operator, random forest (RF), Gaussian process and PLSR to optimize high-throughput analysis of the two photosynthetic variables, V_{cmax} and J_{max}, based on reflectance data. The PLSR model was the second-best model with r^2 and RMSE close to the best model. Thorp et al. (2015) used PLSR to estimate four phenotypes: leaf water content (C_w), specific leaf mass (C_m), leaf chlorophyll a and b content (C_{ab}), and LAI. The results showed the PSLR model was the most robust to estimate the four investigated parameters compared to linear regression, based on SRIs and the PROSAIL model inversion.

2.3 Integrative secondary traits

Different vectors (platforms) have been used to look at plant growth parameters (canopy height, FVC, and SRIs) such as handheld devices or telescopic poles (Anderegg et al., 2020, Cairns et al., 2012, Christopher et al., 2014, Grieder et al., 2015, Montazeaud et al., 2016, Velumani et al., 2020), tractor-based systems (Comar et al., 2012, Kipp et al., 2014), ground platforms (Aasen et al., 2020, Beauchêne et al., 2019, Kronenberg et al., 2017), or UAV systems (Borra-Serrano et al., 2020, Burkart et al., 2018, Han et al., 2018, Holman et al., 2019, Holman et al., 2016, Varela et al., 2021). A number of these studies have collected time-series data to visually identify (i) the beginning of stem elongation period using canopy height data (Holman et al., 2016), (ii) growth stages on barley based on the growth profile (Burkart et al., 2018), (iii) rapid growth expansion and senescence dates and durations on soybean (Aasen et al., 2020), and (iv) growth pattern among maize breeding material (Han et al., 2018).

Fitted curves maximize the use of time series data, quantifying and summarizing the different curve phases corresponding to the stage of the crop development: slow and rapid canopy development, a plateau, and the senescence phase. Fitted curve parameters enable the comparison of the growth and senescence pattern of multiple genetic materials for genetic studies.

Grieder et al. (2015) used spline functions to smooth the FVC data and compute daily relative growth rate (RGR) to look at the influence of the temperature on early growth data for 29 random lines from wheat germplasm. Varela et al. (2021) also used spline fitting curves on FVC, height, and SRIs data. The author aimed to predict AGB on sorghum using the daily data and their corresponding RGR derived from the spline fitting using an RF algorithm and to understand the relationships between growth dynamics, temporal resolution, and end-of-season AGB in 869 diverse accessions of a highly productive photoperiod sensitive sorghum.

Cairns et al. (2012) used NDVI time series data collected over a growing season of a large set of tropical and subtropical maize inbred lines and single cross hybrids to look at their grain performance. NDVI data were used to compute the area under the curve (AUC) as an integrative indicator of growth and senescence patterns. The AUC was divided into sections corresponding to the different stages of development to investigate the link with grain yield. Comar et al. (2012) used a bi-linear model for investigating the SRIs time series to derive integrative parameters to compare the six wheat varieties growing with different nitrogen levels and planted at different densities. More recently, Borra-Serrano et al. (2020) used a sigmoidal model (Gompertz) and Beta functions to fit FVC and canopy height data. The authors derived parameters including maximum absolute growth rate, early vigour, maximum height, and senescence for a collection of soybean genotypes and were integrated into multi-linear regression model to estimate seed yield.

Some studies have only focused on the senescence period. Christopher et al. (2014), Kipp et al. (2014), and Montazeaud et al. (2016) used NDVI and other spectral data to model the dynamics of the senescence to identify stay-green phenotype using logistic, PLSR, and linear models, respectively. From the fitted curves, parameters such as the onset and mid-point of senescence and the senescence rate have been used to characterize the stay-green phenotype. Anderegg et al. (2020) have investigated different SRIs and modelling approaches to fit the data collected during the senescence period. PLS and cubist regressions have been used on the SRIs, and the derived parameters were assessed by prediction of the grain protein content and grain yield.

The last few years have seen an increase in interest to quantify the number of reproductive organs in cereal crops, as mentioned earlier. Wang et al. (2019) and Velumani et al. (2020) have been using a series of daily RGB images to quantify the number of ears. The authors fitted a logistic curve on the ears data and extracted the inflection point corresponding at half of the total ears to estimate the heading date.

3 Genotype-to-phenotyping (G2P) models: integrating data from phenomics and envirotyping in predictive breeding

3.1 Implementing complex G2P models in breeding programs

It is well known that increasing productivity largely depends on genotype (G) and environment (E). With the newly developed technologies, the G component can now be accessed through multi-omics layers (Scossa et al., 2021), the phenotype (P) component can be precisely measured using HTPP tools (Araus et al., 2018), and the E factors can be evaluated using envirotyping techniques (Xu, 2016). In this section, how to integrate these new phenotyping data into G2P models to improve the prediction of complex traits is discussed. The utilization of HTPP data for genetic dissection (gene/trait discovery) of quantitative traits has been discussed previously (Moreira et al., 2020, Zhang et al., 2021, Mir et al., 2019, Brown et al., 2014, Li and Sillanpää, 2015).

G2P models are considered here as different types of statistical models (e.g., linear, mixed, factorial regression, crop growth) that allow the identification of genetic and environmental factors driving phenotypic variation (Van Eeuwijk et al., 2019, Cooper et al., 2021). G2P models have a wide range of applications in breeding, mainly exploiting the genotype × environment interactions (GEI). Environmental effects and GEI are estimated through METs by evaluating genotypes in many locations and years. Traditionally, breeders have been using the final trait value for selection, which is the cumulative effect of many factors including genotype, environment, and interactions among them. Consequently, a simple linear model can be used to untangle the phenotypic variance quantified as $V_P = V_G + V_E + V_{GE} + V_\varepsilon$, where V_G stands for genotypic variance, V_E for environmental variance, V_{GE} for GEI variance, and $V\varepsilon$ represents the random residual. Note that there are many strategies to handle GEI and the most common approaches are the mixed models, the additive main effects and multiplicative interaction models, the genotype plus genotype-by-environment models, the analysis of variances, and the stability measures (Van Eeuwijk et al., 2016, Malosetti et al., 2013).

Recently, the term 'envirotyping' has been introduced in the context of GEI, and its integration with the new genotyping and phenotyping tools will help support breeding programs speeding up the development of high-yielding cultivars (Cooper et al., 2014, Van Eeuwijk et al., 2019). Envirotyping refers to the process of characterizing environmental factors such as climate, soil, biotic, and crop management (Xu, 2016). Precise characterization of E factors provides the key component for refining field experiments, reducing environmental variance, and thus increasing heritability estimation. Environment-related data have been applied in predictive G2P models resulting in improvements in predictive ability (Pérez-Rodríguez et al., 2015, De Los Campos et al., 2020). For example, Jarquín et al. (2014) and Pérez-Rodríguez et al. (2015) used 68 and 76 environmental covariates in wheat and cotton, respectively. New interest has been going towards 'enviromics' for the exploration of key genetic components linked to environmental factors or development stages (Crossa et al., 2021, Resende et al., 2021). Another hot topic is the establishment of a four-dimensional (4D) profile with G–P–E information incorporated with time series (Xu, 2016), but this process has to be integrated with the new phenotyping data in breeding pipelines.

In recent years, HTPP tools have been used extensively in crop trials generating large amounts of data with high spatial and temporal resolution (Mir et al., 2019, Rebetzke et al., 2019). Many approaches (discussed in Section 2) already have high potential to be integrated into the routine of breeding pipelines such as (i) estimating NDVI to characterize biomass accumulation and canopy greenness in the phenological stages (Rebetzke et al., 2016), (ii) identifying flowering time and the number of spikes in wheat using sequential images (Sadeghi-Tehran et al., 2017b, 2019), (iii) using canopy temperature to identify drought-tolerant genotypes, and (iv) quantification of the severity of infection (Yu et al., 2018). The primary goal in breeding programs is the improvement of yield (commonly referred to as target or primary trait), but characterizing secondary phenotypes could be of great value in selecting yield as they are genetically correlated. Secondary traits can be characterized as intermediate (biomass, flowering time, grain number) or basic (sensitivity to photoperiod, water uptake capacity, radiation use efficiency) phenotypes. Similarly, hundreds of hyperspectral data can be used as secondary traits for predicting yield (Fig. 1). However, it is not clear which secondary traits should be prioritized and how they can be integrated into G2P models (Van Eeuwijk et al., 2019). Furthermore, additional costs for phenotyping secondary traits may not necessarily translate into the improved predictive ability for the primary trait (Bustos-Korts et al., 2019).

Despite grain yield being the primary trait of interest, breeders might also be interested in using other phenotypes collected through phenotyping tools such as canopy height and FVC, to use in combination with secondary traits such as hyperspectral data (Fig. 1). In this case, indirect selection and selection index are two common methods used when seeking improvements of yield in a target population of environments. In indirect selection, a primary trait $\boldsymbol{y}$ is selected indirectly by selecting for another genetically correlated trait $\boldsymbol{x}$ (Fischer and Rebetzke, 2018) that can be quantified using HTPP, for example using spectral reflectance traits to select materials with high yield (Lozada et al., 2020, Kyratzis et al., 2017). In the selection index (SI) context, a primary trait $\boldsymbol{y}$ is selected based on an index calculated from a set of $\boldsymbol{t}$ secondary traits. A linear index is built as follows:

$$I = \sum_{j=1}^{t} \boldsymbol{b}_j \boldsymbol{t}_j ,$$

where $\boldsymbol{b}_j$ and $\boldsymbol{t}_j$ are the weight and phenotypic value of the trait, respectively. The weight represents the relative importance of each trait. Optimization of SI applying hyperspectral data to reduce overfitting and sub-optimal accuracy of indirect selection has been proposed in the recent literature (Lopez-Cruz et al., 2020).

The development of robust G2P frameworks that can accommodate these high-dimensional secondary traits together with genomic and environmental

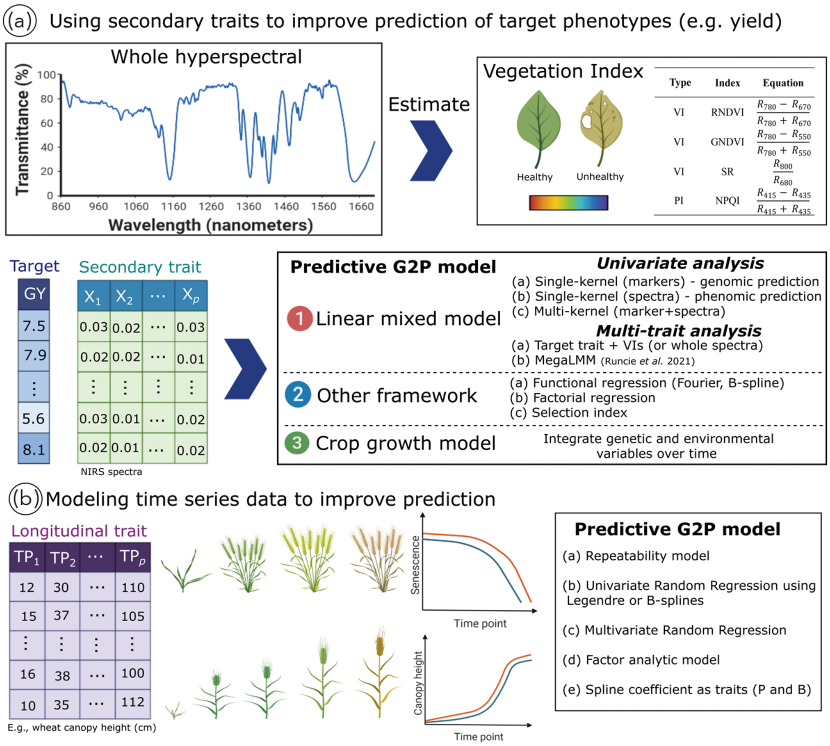

Figure 1 Schematic representation of the integration of HTPP data into genotype-to-phenotype (G2P) predictive models in crop breeding. (a) The first approach is to integrate secondary traits into G2P models to improve the prediction of target or primary phenotypes, that is, grain yield (GY). Secondary phenotypes are represented by whole hyperspectral reflectance data (e.g. near-infrared reflectance spectroscopy) and vegetation (VI) and pigmented (PI) indices. Secondary traits could be incorporated (1) in a linear mixed model (LMM) using hyperspectral data as predictors (single kernel) in an approach called *phenomic prediction* or by using a multivariate linear mixed model (MvLMM), (2) using other frameworks as functional and factorial regression, and (3) by using crop growth models. (b) The second approach is to explore G2P models for longitudinal traits to capture plant functioning at different stages of crop development. The most common predictive G2P models used for such an approach are traditional MvLMM (with specific variance–covariance) and random regression model. TP, time point; MegaLMM, mega-scale linear mixed model.

data is required and has been discussed in recent reviews (Van Eeuwijk et al., 2019, Morota et al., 2019). Primarily, this includes (i) extraction and characterization of HTPP secondary traits and environmental data, (ii) robust experimental design management (e.g. correction for spatial factors), (iii) dynamic modelling (e.g. time point (TP) and environment), and (iv) target trait prediction (using robust approaches as mixed and crop growth models). For a more detailed description of this workflow, see the study by Van Eeuwijk et al. (2019). Briefly, images are pre-processed (alignment, calibration, and segmentation) to extract informative data. This step can be laborious and time-consuming as large amounts of information will be reduced to a small number of variables relevant for phenotypic and genomic prediction. In the second stage, adjustment of genotypic means including spatial variation correction is required. Analyses can be performed per TP (also referred to as time series, longitudinal, and repeated measurements) using a mixed-model approach including first-order auto-regressive structure or 2D P-spline basis to row and column directions. In the third scenario, genotypic means are treated as unique observations and modelled in the function of time (in case the target trait is longitudinal). Parametric (logistic, Gompertz, and exponential growth functions) and spline (P and B) models are used to capture the dynamics of traits, for example, canopy height, AGB, leaf area. Lastly, after estimating genotype-specific parameters, we need to expand this approach to multiple environments. Therefore, a function integrating both factors can effectively adjust for temporal and environmental gradients (Chenu et al., 2009, Cooper et al., 2021).

In summary, G2P models can predict target traits from genotype-specific and environmental inputs. In the future, more measurements using field phenotyping tools in multiple environments will be available; therefore, G2P models must be fine-tuned to incorporate secondary phenotyping information in a breeding pipeline in an efficient way.

3.2 Combining HTPP data into predictive G2P models

The integration of HTPP and genomic data has been a current reality in plant breeding programs (Araus et al., 2018). Many adjustments in standard G2P models have been made to account for the complexity of secondary traits in GS approaches to improve the selection efficiency of the target trait (Table 1). The most used method in whole-genome regression models is the genomic best linear unbiased prediction (GBLUP), which utilizes a genomic relationship matrix to estimate the genetic merit of an individual (Morota and Gianola, 2014). The matrix defines the covariance between individuals based on observed similarity at the genomic level, rather than on expected similarity based on pedigree. Therefore, integrating HTPP data into genomic selection schemes can be classified into two common statistical methods: univariate and multivariate approaches.

3.2.1 Univariate predictive G2P models

The univariate model focuses on predicting one primary trait collected either using manual phenotyping (grain yield) or high-throughput platforms (e.g. canopy height, NDVI, senescence). Several studies used traits collected using UAV as target traits in GP studies, reducing the labour cost compared to traditional measurements (Watanabe et al., 2017). In a mixed-model perspective, GP can be performed with these mentioned traits using a single- or multi-kernel derived from molecular markers and/or traits derived from image data as described in Section 2. The type of hyperspectral data (whole spectra vs. SRIs) and feature selection (e.g., based on heritability) which should be used in G2P models have been discussed (van Eeuwijk et al., 2019, Tardieu et al., 2017). When using only genetic variants (or different layers like gene expression) to predict the genetic values, it is referred to as *genomic prediction*. Alternatively, *phenomic selection or phenomic prediction* is referred to when using only spectral data or any other data collected through digital phenotyping (Rincent et al., 2018).

Phenomic selection was first introduced by Rincent et al. (2018) using only secondary traits such as near-infrared spectroscopy (NIRs), in the same way as genomic regressors (genomic kernel), allowing predictions of untested wheat and poplar (*Populus nigra* L.) genotypes. The authors observed higher predictive ability compared to a single genomic kernel. Lane et al. (2020) further explored this approach predicting grain yield in maize genotypes using NIR spectra as kernel and observed promising results. In practical terms, phenomic selection might be capturing the phenotypic relationship between individuals from a biological composition basis (Rincent et al., 2018). The reflectance spectrum is a result of numerous wavelengths capturing chemical bonds in the analysed tissue. Interpretation of phenomic prediction results must be done with caution as they do not directly model the genetic component of correlations between primary and secondary traits (Runcie et al., 2021).

Suppose we have three scenarios of predictive G2P models from a mixed-model perspective (ignoring environment-specific information and TP variables) as follows:

$$\hat{\boldsymbol{y}} = \boldsymbol{X}\beta + \boldsymbol{Z_g g} + \varepsilon \left(\text{single-kernel genomic prediction}\right) \tag{1}$$

$$\hat{\boldsymbol{y}} = \boldsymbol{X}\beta + \boldsymbol{Z_t T} + \varepsilon \left(\text{single-kernel phenomic prediction}\right) \tag{2}$$

$$\hat{\boldsymbol{y}} = \boldsymbol{X}\beta + \boldsymbol{Z_g g} + \boldsymbol{Z_t T} + \varepsilon \left(\text{multi-kernelprediction}\right) \tag{3}$$

where $\hat{\boldsymbol{y}}$ is a vector of phenotypic values, $\boldsymbol{\beta}$ is a vector of fixed effects, $\boldsymbol{g}$ is a vector of random additive genetic effects of markers, $\boldsymbol{t}$ is a vector of random secondary trait (e.g., whole hyperspectral, NIR) effects, and $\boldsymbol{\varepsilon}$ is a vector of random residuals. The incidence matrices for $\boldsymbol{\beta}$, $\boldsymbol{g}$, and $\boldsymbol{t}$ are $\boldsymbol{X}$, $\boldsymbol{Z_g}$, and $\boldsymbol{Z_t}$, respectively. The random effects are independent and normally distributed $\boldsymbol{g} \sim N\left(0, \sigma_g^2 \boldsymbol{G_g}\right)$, $\boldsymbol{t} \sim N\left(0, \sigma_t^2 \boldsymbol{G_t}\right)$, and $\varepsilon \sim N\left(0, \sigma_\varepsilon^2 \boldsymbol{I}\right)$, where $\boldsymbol{I}$ was the identity matrix. $\boldsymbol{G_g}$ is a kernel or relationship matrix (covariance matrix describing genomic similarities between pairs of genotypes) using $\boldsymbol{G_g} = \boldsymbol{WW}'/m$, where $\boldsymbol{W}$ is a $n \times m$ matrix of scaled and centred markers from n individuals and m

Table 1 Summary of publications using predictive G2P model incorporating HTPP secondary traits

Goal	Crop	Target trait	Secondary trait	No TP	No spectra/ band	G2P model	Reference
Incorporation of secondary traits to improve prediction of target traits	Wheat	Grain yield	CT, GNDVI, RNDVI	12	–	Single- and multi-trait	Rutkoski et al. (2016)
	Wheat	Grain yield	CT, GNDVI, RNDVI	12	–	Simple repeatability, multi-trait, random regression	Sun et al. (2017)
	Maize	Grain yield	Six spectral VI	5	62	Three single-trait models	Aguate et al. (2017)
	Wheat	19 end-use quality traits	NMR, NIR	1	–	Single-trait, multi-trait	Hayes et al. (2017)
	Wheat	Grain yield	Eight spectral VI, whole hyperspectral	9	250	Seven models including one functional regression	Montesinos-Lopez et al. (2017b)
	Wheat	Heading date, grain yield	NIRS	1	1050[a]	Single kernel using markers or NIRS	Rincent et al. (2018)
	Poplar	Height, circumference, bud flush, bud set	NIRS	1	2001[b]	Single kernel using markers or NIRS	Rincent et al. (2018)
	Wheat	Grain yield	CT, NDVI	4	–	Single- and multi-trait	Crain et al. (2018)
	Soybean	Grain yield, days to maturity	CC	58	-	Nine models exploring interactions	Jarquin et al. (2018)
	Wheat	Grain yield	Whole hyperspectral	13 (2013/2014) 14 (2014/2015)	62	Single and multi-kernel using markers and/or hyperspectral	Krause et al. (2019)

				8 (2015/2016) 14 (2016/2017)			
	Wheat	Grain yield	GNDVI	2–4	–	IBCF approach	Juliana et al. (2019)
	Wheat	Grain yield	NIR	1	1059	Three models including one deep kernel	Cuevas et al. (2019)
	Sugarcane	Fibre and sucrose content	NIR	1	3112	Single- and multi-kernel using markers and/or NIR	Gonçalves et al. (2021)
	Maize	Grain yield	NIRS	1	3076	PLSR, single kernel, functional regression	Lane et al. (2020)
	Wheat	Grain yield	Whole hyperspectral	9	250	Regularized selection indices	Lopez-Cruz et al. (2020)
	Wheat	Grain yield	Whole hyperspectral	14 (2014/2015)	62	MegaLMM	Runcie et al. (2021)
Improve prediction for longitudinal traits	Rice	Projected shoot area	–	20	–	Single-trait, random regression	Campbell et al. (2018)
	Rice	Projected shoot area	–	20	–	Random regression with Legendre polynomials and B-splines	Momen et al. (2019)
	Rice	Projected shoot area	–	20	–	Multi-trait random regression	Baba et al. (2020)
	Wheat	Canopy height	–	26	–	Factor analytic and B-splines	Lyra et al. (2020)

GNDVI and RNDVI, green and red normalized difference vegetation index; CT, canopy temperature; VI, vegetative index; NIR or NIRS, near-infrared reflectance spectroscopy; NMR, nuclear magnetic resonance; CC, canopy coverage; IBCF, item-based collaborative filtering; PLSR, partial least square regression; LMM, linear mixed model; TP, time point; G2P, genotype to phenotype.

[a] NIR spectra obtained on wheat grains.

[b] NIR spectra obtained on poplar wood.

is the total number of markers. $\boldsymbol{G_t}$ is a kernel or covariance matrix describing similarities based on secondary trait information between pairs of genotypes using $\boldsymbol{G_t} = \boldsymbol{TT}'/s$, where $\boldsymbol{T}$ is a $n \times s$ matrix of scaled and centred secondary traits from n individuals and s is the total number of secondary traits.

Several studies have integrated HTPP data in predictive models using the multi-kernel approach mentioned above and expanded further on the integration of GEI and envirotyping (Montesinos-Lopez et al., 2017b, Aguate et al., 2017, Rutkoski et al., 2016, Krause et al., 2019, Gonçalves et al., 2021). For example, Aguate et al. (2017) incorporated wavelengths into a GP model in maize hybrids showing that using wavelength as predictors increased predictive ability compared to VIs. Montesinos-Lopez et al. (2017b) compared the full and a subset of bands when predicting grain yield on wheat concluding that using all wavelengths resulted in higher predictive ability. Recently, Krause et al. (2019) used a multi-kernel GBLUP approach combining marker, pedigree, and hyperspectral reflectance kernels and observed the highest predictive ability compared to single kernels when predicting genotypes. Cuevas et al. (2019) applied a non-linear arc-cosine kernel (deep learning artificial neural networks) in wheat data set demonstrating promising results.

3.2.2 Multivariate predictive G2P models

The multivariate approach focuses on predicting multiple traits as response variables using single kernel from molecular markers. Therefore, phenotypes can be a combination of the targeted trait (mainly yield) and the correlated secondary traits (usually VIs). This approach is expected to improve predictive ability relative to single trait by enabling information to be shared among correlated traits, particularly for traits showing low heritability. Initial implementation of such analyses was published by Rutkoski et al. (2016) followed by Sun et al. (2017) and Crain et al. (2018). These three publications used canopy temperature and NDVI as secondary traits to improve the predictive ability of grain yield in wheat. Rutkoski et al. (2016) showed that the integration of both types of secondary traits into single-kernel GBLUP model increased the predictive ability by 70% compared to the univariate model. Sun et al. (2017) showed that the incorporation of secondary traits in both training and testing sets in a multivariate model yielded the best results in terms of predictive ability. Hayes et al. (2017) observed improvements in predictive ability when incorporating NIR and nuclear magnetic resonance spectra as secondary traits, in a predictive multi-trait framework in wheat. Crain et al. (2018) included grain yield, canopy temperature, and VI measurements in a multi-trait model showing a slight increase (7% gains) in predictive ability when compared to the single-trait model.

Direct implementation of thousands of hyperspectral spectra in a traditional G2P multivariate model would be computationally demanding. Several authors have used feature selection to identify those traits that are relevant (Crain et al., 2018, Rutkoski et al., 2016, Sun et al., 2017). Other authors have replaced the multivariate method with a direct regression on the secondary phenotype data, for example using secondary traits (wavelengths or environmental input) as functional covariates in functional regression (Montesinos-Lopez et al., 2017a, b) and factorial regression (van Eeuwijk et al., 2018) models. A review on functional regression analysis using HTPP data has been written by Montesinos-Lopez et al. (2018). Alternative methods have also been proposed to handle efficiently this high complexity data such as the 'item-based collaborative filtering' (IBCF) (Juliana et al., 2019) and regularized selection indices (Lopez-Cruz et al., 2020). For example, the IBCF approach can be effectively applied in scenarios where trait correlations with the primary target (grain yield) are moderate to high (Juliana et al., 2019).

While these methods mentioned above (e.g. functional regression) are powerful alternatives to the traditional multi-trait model, they do not explicitly account for the high-dimensional genetic correlations between traits. To overcome this issue, Runcie et al. (2021) proposed a multivariate linear mixed model (MegaLMM) taking advantage of the factor-analytic approach. They used the original data set from Krause et al. (2019) and observed higher predictive ability when using MegaLMM compared to the multi-kernel (genomic + phenomic) approach. According to the authors, by directly modelling the genetic covariance between the hyperspectral reflectance traits, MegaLMM should be more efficient, mainly when secondary traits and the target (focal) traits are measured on the same plants.

3.2.3 Predictive G2P models using longitudinal (time-series) traits

Measuring plant development has become feasible with the advancements of HTPP in recent years. A 4D profile can be built based on the genotype, phenotype, and envirotype (3D profile) while the fourth involves the developmental stages (temporal data) (Xu, 2016). For example, collecting time-series data enables the comparison between the canopy height of different accessions at the same growth stage in sorghum (Watanabe et al., 2017) and also allows the selection of high-yielding cultivars at an early plant developmental stage (Sun et al., 2017). Analysing G2P models from different TPs collected in the same environment is straightforward, but it is more difficult when measurements are made across environments. Also, Lyra et al. (2020) pointed out the importance of sampling data in later stages of growth development to capture more genetic variance. Therefore, many G2P frameworks have been adapted to incorporate information from new phenotyping and envirotyping data across developmental stages. A review on using longitudinal data from HTPP in predictive G2P models has been discussed by Moreira et al. (2020).

For longitudinal data, a simple univariate mixed model can be fitted at each TP for traits like FVC, canopy height, senescence, and biomass accumulation. However, to capture the covariance between TPs, a multivariate approach can be used allowing each TP to have a unique variance and covariance between TPs. Other common methods used to model longitudinal data more flexibly are random regression and factorial regression (Baba et al., 2020, Campbell et al., 2018, Momen et al., 2019). Random regression model (RRM) (Schaeffer, 2016, Schaeffer, 2004) is used to estimate covariance functions and to model the shape/trajectory of observations taken over time. This trajectory (covariance across TPs) can be modelled using Legendre polynomials and splines. Sun et al. (2017) applied an RRM using a cubic smoothing spline in wheat aiming to capture the trait development (canopy temperature and NDVI) during the growth stages across multiple environments. Campbell et al. (2018) observed improvements of predictive ability using RRM using Legendre polynomials to model shoot growth trajectories in rice when compared to single-time prediction. Lyra et al. (2020) also observed higher predictive ability compared to single TP using B-spline basis coefficients as phenotypes after adjusting the values using a factor analytic model in 26 TPs for canopy height in wheat.

4 Conclusion

In this chapter, the current methods accessible for monitoring crop canopy development and nutrition, for predicting grain yield and yield components, as well as the various approaches available for integrating data from phenomics and envirotyping in predictive breeding, have been reviewed. Whilst much has been achieved in the last decade, digital phenotyping as a tool to support breeding programs is still in its infancy. A limitation has been the application of digital phenotyping into the breeding process. The temporal and spatial resolution required to look at a trait of interest is likely to be different at earlier or the later stages of the selection programs, requiring tools to scan hundreds to thousands of genetic materials or fined-tuned tools for detailed analysis of the performance of the targeted traits on a sub-sample of a population. Such considerations define the cost–benefit of the technology deployed. Further limitations are the ability to deploy such technologies at different locations and the coordination of the data acquisition in multi-environment studies. Finally, the level of data integration to develop efficient pipelines to integrate digital phenotyping data into G2P models still requires further development. None of these points should be insurmountable with appropriate investment. The last decade has seen an exponential increase in terms of initiatives and studies around digital phenotyping applications to breeding, which should lead to significant breakthroughs in the next decade.

5 Acknowledgements

Rothamsted Research receives grant-aided support from the Biotechnology and Biological Sciences Research Council (BBSRC) through the Designing Future Wheat programme [BB/P016855/1].

6 Where to look for further information

The following articles provide a good overview of the subject:

- Crossa, J., Perez-Rodriguez, P., Cuevas, J., Montesinos-Lopez, O., Jarquin, D., de los Campos, G., Burgueno, J., Gonzalez-Camacho, J. M., Perez-Elizalde, S., Beyene, Y., Dreisigacker, S., Singh, R., Zhang, X. C., Gowda, M., Roorkiwal, M., Rutkoski, J. and Varshney, R. K. 2017. Genomic selection in plant breeding: methods, models, and perspectives. *Trends in Plant Science* 22, 961–975.
- Pask, A. J. D., Pietragalla, J., Mullan, D. M. and Reynolds, MP. (Eds.) 2012. *Physiological Breeding II: A Field Guide to Wheat Phenotyping*. Mexico, D.F.: CIMMYT.
- van Eeuwijk, F. A., Bustos-Korts, D., Millet, E. J., Boer, M. P., Kruijer, W., Thompson, A., Malosetti, M., Iwata, H., Quiroz, R., Kuppe, C., Muller, O., Blazakis, K. N., Yug, K., Tardieu, F. and Chapman, S. C. 2018. Modelling strategies for assessing and increasing the effectiveness of new phenotyping techniques in plant breeding. *Plant Science*. doi: 10.1016/j.plantsci.2018.06.018.
- Reynolds, M. and Langridge, P. 2016. Physiological breeding. *Current Opinion in Plant Biology* 31, 162–171.

Further information about infrastructure and initiatives about phenotyping:

- IPPN (International Plant Phenotyping Network) is an association representing the major plant phenotyping centers and providing relevant information about plant phenotyping: www.plant-phenotyping.org/IPPN_home.
- EMPHASIS is a project aiming to address the limitations of the current phenotyping to fully exploit the genetic and genomic resources available for crop improvement in changing climate: https://emphasis.plant-phenotyping.eu.

Database for spectral reflectance indices:

- L3 Harris Geospatial documentation center is regrouping a vast database of spectral indices: www.l3harrisgeospatial.com/docs/vegetationindices.html.

7 Abbreviations

AGB	Above-ground biomass
ANN	Artificial neural network
AUC	Area under the curve
C_{ab}	Leaf chlorophyll a and b content
CCCI	Canopy chlorophyll content index
C_m	Specific leaf mass
CNC	Canopy nitrogen content
CNI	Canopy nutrition index
CT	Canopy temperature
C_w	Leaf water content
F'	Steady-state fluorescence
F_q'/F_m'	Photosystem II operating efficiency
FVC	Fraction vegetation cover
G	Genotype
G2P	Genotype to phenotype
GBLUP	Genomic best linear unbiased prediction
GEBV	Genomic estimated breeding value
GEI	Genotype by environment interaction
GP	Genomic Prediction
GP	Gaussian process
GS	Genomic selection
HTPP	High-throughput plant phenotyping
IBCF	Item-based collaborative filtering
LAI	Leaf area index
LUE	Light use efficiency
MegaLMM	Mega-scale linear mixed model
MET	Multi-environment trials
N	Nitrogen
NDVI	Normalized difference vegetation index
NIRs	Near-infrared spectroscopy
NPQ	Non-photochemical quenching
P	Phenotype
PLSR	Partial least square regression
PRI	Photochemical/physiological reflectance index
PSII	Photosystem 2
RF	Random Forest
RGB	Red-green-blue
RMM	Random regression model
SfM	Structure from motion
SI	Selection index

Published by Burleigh Dodds Science Publishing Limited, 2022.

SIF	Sun-induced fluorescence
SRI	Spectral reflectance index
SVM	Support vector machine
$T_c - T_a$	Canopy minus air temperature
TP	Time point
UAV	Unmanned aerial vehicle
VE	Environmental variance
V_ε	Random residual variance
V_{GE}	GEI variance
VI	Vegetation index
VP	Phenotypic variance
WDI	Water deficit index

8 References

Aasen, H., Kirchgessner, N., Walter, A. and Liebisch, F. 2020. PhenoCams for field phenotyping: using very high temporal resolution digital repeated photography to investigate interactions of growth, phenology, and harvest traits. *Frontiers in Plant Science* 11, 593.

Aguate, F. M., Trachsel, S., Perez, L. G., Burgueno, J., Crossa, J., Balzarini, M., Gouache, D., Bogard, M. and De Los Campos, G. 2017. Use of hyperspectral image data outperforms vegetation indices in prediction of maize yield. *Crop Science* 57(5), 2517–2524.

Anderegg, J., Yu, K., Aasen, H., Walter, A., Liebisch, F. and Hund, A. 2020. Spectral vegetation indices to track senescence dynamics in diverse wheat germplasm. *Frontiers in Plant Science* 10, 1749.

Aquino, A., Millan, B., Gutierrez, S. and Tardaguila, J. 2015. Grapevine flower estimation by applying artificial vision techniques on images with uncontrolled scene and multi-model analysis. *Computers and Electronics in Agriculture* 119, 92–104.

Araus, J. L., Kefauver, S. C., Zaman-Allah, M., Olsen, M. S. and Cairns, J. E. 2018. Translating high-throughput phenotyping into genetic gain. *Trends in Plant Science* 23(5), 451–466.

Baba, T., Momen, M., Campbell, M. T., Walia, H. and Morota, G. 2020. Multi-trait random regression models increase genomic prediction accuracy for a temporal physiological trait derived from high-throughput phenotyping. *PLoS ONE* 15(2), e0228118.

Barmeier, G. and Schmidhalter, U. 2017. High-throughput field phenotyping of leaves, leaf sheaths, culms and ears of spring barley cultivars at anthesis and dough ripeness. *Frontiers in Plant Science* 8, 1920.

Barnes, E. M., Clarke, T. R., Richards, S. E., Colaizzi, P. D., Haberland, J., Kostrzewski, M., Waller, P., Choi, C., Riley, E. and Thompson, T. 2000. Coincident detection of crop water stress, nitrogen status and canopy density using ground based multispectral data. Proceedings of the 5th International Conference on Precision Agriculture and Other Resource Management July 16-19, 2000, Bloomington, MN USA, 15 p. Madison, WI: Precision Agriculture Center, University of Minnesota, ASA-CSSA-SSSA, c2000.

Beauchêne, K., Leroy, F., Fournier, A., Huet, C., Bonnefoy, M., Lorgeou, J., De Solan, B., Piquemal, B., Thomas, S. and Cohan, J. P. 2019. Management and characterization of abiotic stress via PhénoField®, a high-throughput field phenotyping platform. *Frontiers in Plant Science* 10, 904.

Bendig, J., Yu, K., Aasen, H., Bolten, A., Bennertz, S., Broscheit, J., Gnyp, M. L. and Bareth, G. 2015. Combining UAV-based plant height from crop surface models, visible, and near infrared vegetation indices for biomass monitoring in barley. *International Journal of Applied Earth Observation and Geoinformation* 39, 79–87.

Berger, K., Verrelst, J., Féret, J.-B., Hank, T., Wocher, M., Mauser, W. and Camps-Valls, G. 2020. Retrieval of aboveground crop nitrogen content with a hybrid machine learning method. *International Journal of Applied Earth Observation and Geoinformation* 92, 102174.

Blackburn, G. A. 2007. Hyperspectral remote sensing of plant pigments. *Journal of Experimental Botany* 58(4), 855–867.

Boegh, E., Soegaard, H., Broge, N., Hasager, C. B., Jensen, N. O., Schelde, K. and Thomsen, A. 2002. Airborne multispectral data for quantifying leaf area index, nitrogen concentration, and photosynthetic efficiency in agriculture. *Remote Sensing of Environment* 81(2–3), 179–193.

Borra-Serrano, I., De Swaef, T., Quataert, P., Aper, J., Saleem, A., Saeys, W., Somers, B., Roldán-Ruiz, I. and Lootens, P. 2020. Closing the phenotyping gap: high resolution UAV time series for soybean growth analysis provides objective data from field trials. *Remote Sensing* 12(10), 1644.

Brown, T. B., Cheng, R., Sirault, X. R., Rungrat, T., Murray, K. D., Trtilek, M., Furbank, R. T., Badger, M., Pogson, B. J. and Borevitz, J. O. 2014. TraitCapture: genomic and environment modelling of plant phenomic data. *Current Opinion in Plant Biology* 18, 73–79.

Buchaillot, M. L., Gracia-Romero, A., Vergara-Diaz, O., Zaman-Allah, M. A., Tarekegne, A., Cairns, J. E., Prasanna, B. M., Araus, J. L. and Kefauver, S. C. 2019. Evaluating maize genotype performance under low nitrogen conditions using RGB UAV phenotyping techniques. *Sensors* 19(8), 1815.

Burkart, A., Hecht, V. L., Kraska, T. and Rascher, U. 2018. Phenological analysis of unmanned aerial vehicle based time series of barley imagery with high temporal resolution. *Precision Agriculture* 19(1), 134–146.

Bustos-Korts, D., Boer, M. P., Malosetti, M., Chapman, S., Chenu, K., Zheng, B. and Van Eeuwijk, F. A. 2019. Combining crop growth modeling and statistical genetic modeling to evaluate phenotyping strategies. *Frontiers in Plant Science* 10, 1491.

Cabrera-Bosquet, L., Molero, G., Stellacci, A., Bort, J., Nogués, S. and Araus, J. 2011. NDVI as a potential tool for predicting biomass, plant nitrogen content and growth in wheat genotypes subjected to different water and nitrogen conditions. *Cereal Research Communications* 39(1), 147–159.

Cairns, J. E., Sanchez, C., Vargas, M., Ordonez, R. and Araus, J. L. 2012. Dissecting maize productivity: ideotypes associated with grain yield under drought stress and well-watered conditions. *Journal of Integrative Plant Biology* 54(12), 1007–1020.

Camino, C., Gonzalez-Dugo, V., Hernandez, P., Sillero, J. C. and Zarco-Tejada, P. J. 2018a. Improved nitrogen retrievals with airborne-derived fluorescence and plant traits quantified from VNIR-SWIR hyperspectral imagery in the context of precision agriculture. *International Journal of Applied Earth Observation and Geoinformation* 70, 105–117.

Camino, C., Zarco-Tejada, P. J. and Gonzalez-Dugo, V. 2018b. Effects of heterogeneity within tree crowns on airborne-quantified SIF and the CWSI as indicators of water stress in the context of precision agriculture. *Remote Sensing* 10(4), 604.

Cammarano, D., Fitzgerald, G. J., Casa, R. and Basso, B. 2014. Assessing the robustness of vegetation indices to estimate wheat N in Mediterranean environments. *Remote Sensing* 6(4), 2827–2844.

Campbell, M., Walia, H. and Morota, M. 2018. Utilizing random regression models for genomic prediction of a longitudinal trait derived from high-throughput phenotyping. *The Plant Journal* 2, 1–11.

Casadesús, J., Kaya, Y., Bort, J., Nachit, M. M., Araus, J. L., Amor, S., Ferrazzano, G., Maalouf, F., Maccaferri, M., Martos, V., Ouabbou, H. and Villegas, D. 2007. Using vegetation indices derived from conventional digital cameras as selection criteria for wheat breeding in water-limited environments. *Annals of Applied Biology* 150(2), 227–236.

Chandra, A. L., Desai, S. V., Balasubramanian, V. N., Ninomiya, S. and Guo, W. 2020. Active learning with point supervision for cost-effective panicle detection in cereal crops. *Plant Methods* 16, 34.

Che, Y., Wang, Q., Xie, Z., Zhou, L., Li, S., Hui, F., Wang, X., Li, B. and Ma, Y. 2020. Estimation of maize plant height and leaf area index dynamics using an unmanned aerial vehicle with oblique and nadir photography. *Annals of Botany* 126(4), 765–773.

Chenu, K., Chapman, S. C., Tardieu, F., Mclean, G., Welcker, C. and Hammer, G. L. 2009. Simulating the yield impacts of organ-level quantitative trait loci associated with drought response in maize: a "gene-to-phenotype" modeling approach. *Genetics* 183(4), 1507–1523.

Christopher, J. T., Veyradier, M., Borrell, A. K., Harvey, G., Fletcher, S. and Chenu, K. 2014. Phenotyping novel stay-green traits to capture genetic variation in senescence dynamics. *Functional Plant Biology* 41(11), 1035–1048.

Clarke, T. R., Moran, M. S., Barnes, E. M., Pinter, P. J. and Qi, J. 2001. Planar domain indices: a method for measuring a quality of a single component in two-component pixels. IGARSS 2001. Scanning the Present and Resolving the Future. Proceedings. IEEE 2001 International Geoscience and Remote Sensing Symposium (Cat. No.01CH37217), 9–13 July 2001. 1279–1281.

Comar, A., Burger, P., De Solan, B., Baret, F. D. R., Daumard, F. and Hanocq, J. O. 2012. A semi-automatic system for high throughput phenotyping wheat cultivars in-field conditions: description and first results. *Functional Plant Biology* 39(11), 914–924.

Cooper, M., Messina, C. D., Podlich, D., Totir, L. R., Baumgarten, A., Hausmann, N. J., Wright, D. and Graham, G. 2014. Predicting the future of plant breeding: complementing empirical evaluation with genetic prediction. *Crop and Pasture Science* 65(4), 311–336.

Cooper, M., Powell, O., Voss-Fels, K. P., Messina, C. D., Gho, C., Podlich, D. W., Technow, F., Chapman, S. C., Beveridge, C. A., Ortiz-Barrientos, D. and Hammer, G. L. 2021. Modelling selection response in plant-breeding programs using crop models as mechanistic gene-to-phenotype (CGM-G2P) multi-trait link functions. *In Silico Plants* 3(1), diaa016.

Corti, M., Cavalli, D., Cabassi, G., Marino Gallina, P. and Bechini, L. 2018. Does remote and proximal optical sensing successfully estimate maize variables? A review. *European Journal of Agronomy* 99, 37–50.

Costa-Neto, G., Fritsche-Neto, R. and Crossa, J. 2021a. Nonlinear kernels, dominance, and envirotyping data increase the accuracy of genome-based prediction in multi-environment trials. *Heredity* 126(1), 92–106.

Costa-Neto, G., Galli, G., Carvalho, H. F., Crossa, J. and Fritsche-Neto, R. 2021b. EnvRtype: a software to interplay enviromics and quantitative genomics in agriculture. *G3* 11(4), jkab040.

Costa-Neto, G. M. F., Júnior, O. P. M., Heinemann, A. B., De Castro, A. P. and Duarte, J. B. 2020. A novel GIS-based tool to reveal spatial trends in reaction norm: upland rice case study. *Euphytica* 216, 1–16.

Crain, J., Mondal, S., Rutkoski, J., Singh, R. P. and Poland, J. 2018. Combining high-throughput phenotyping and genomic information to increase prediction and selection accuracy in wheat breeding. *Plant Genome* 11(1), 1–14.

Crossa, J., Fritsche-Neto, R., Montesinos-Lopez, O. A., Costa-Neto, G., Dreisigacker, S., Montesinos-Lopez, A. and Bentley, A. R. 2021. The modern plant breeding triangle: optimizing the use of genomics, phenomics, and enviromics data. *Frontiers in Plant Science* 12, 651480.

Crossa, J., Perez-Rodriguez, P., Cuevas, J., Montesinos-Lopez, O., Jarquin, D., De Los Campos, G., Burgueno, J., Gonzalez-Camacho, J. M., Perez-Elizalde, S., Beyene, Y., Dreisigacker, S., Singh, R., Zhang, X. C., Gowda, M., Roorkiwal, M., Rutkoski, J. and Varshney, R. K. 2017. Genomic selection in plant breeding: methods, models, and perspectives. *Trends in Plant Science* 22(11), 961–975.

Cuevas, J., Montesinos-López, O., Juliana, P., Guzmán, C., Pérez-Rodríguez, P., González-Bucio, J., Burgueño, J., Montesinos-López, A. and Crossa, J. 2019. Deep Kernel for genomic and near infrared predictions in multi-environment breeding trials. *G3* 9(9), 2913–2924.

David, E., Madec, S., Sadeghi-Tehran, P., Aasen, H., Zheng, B., Liu, S., Kirchgessner, N., Ishikawa, G., Nagasawa, K., Badhon, M. A., Pozniak, C., De Solan, B., Hund, A., Chapman, S. C., Baret, F., Stavness, I. and Guo, W. 2020. Global Wheat Head Detection (GWHD) dataset: a large and diverse dataset of high resolution RGB labelled images to develop and benchmark wheat head detection methods. *Plant Phenomics* 2020, 3521852.

De Los Campos, G., Pérez-Rodríguez, P., Bogard, M., Gouache, D. and Crossa, J. 2020. A data-driven simulation platform to predict cultivars' performances under uncertain weather conditions. *Nature Communications* 11(1), 4876.

Deery, D., Jimenez-Berni, J., Jones, H., Sirault, X. and Furbank, R. 2014. Proximal remote sensing buggies and potential applications for field-based phenotyping. *Agronomy* 4(3), 349–379.

Dobrowski, S. Z., Pushnik, J. C., Zarco-Tejada, P. J. and Ustin, S. L. 2005. Simple reflectance indices track heat and water stress-induced changes in steady-state chlorophyll fluorescence at the canopy scale. *Remote Sensing of Environment* 97(3), 403–414.

Duan, L., Huang, C., Chen, G., Xiong, L., Liu, Q. and Yang, W. 2015. Determination of rice panicle numbers during heading by multi-angle imaging. *The Crop Journal* 3(3), 211–219.

Duan, T., Zheng, B., Guo, W., Ninomiya, S., Guo, Y. and Chapman, S. C. 2016. Comparison of ground cover estimates from experiment plots in cotton, sorghum and sugarcane based on images and Ortho-mosaics captured by UAV. *Functional Plant Biology* 44(1), 169–183.

Duncan, J. M. A., Dash, J. and Atkinsonz, P. M. 2015. The potential of satellite-observed crop phenology to enhance yield gap assessments in smallholder landscapes. *Frontiers in Environmental Science* 3, 56. doi: 10.3389/fenvs.2015.00056.

Ecarnot, M., Compan, F. and Roumet, P. 2013. Assessing leaf nitrogen content and leaf mass per unit area of wheat in the field throughout plant cycle with a portable spectrometer. *Field Crops Research* 140, 44–50.

El-Hendawy, S. E., Al-Suhaibani, N. A., Elsayed, S., Hassan, W. M., Dewir, Y. H., Refay, Y. and Abdella, K. A. 2019a. Potential of the existing and novel spectral reflectance indices for estimating the leaf water status and grain yield of spring wheat exposed to different irrigation rates. *Agricultural Water Management* 217, 356 –373.

El-Hendawy, S. E., Alotaibi, M., Al-Suhaibani, N., Al-Gaadi, K., Hassan, W., Dewir, Y. H., Emam, M. A. E., Elsayed, S. and Schmidhalter, U. 2019b. Comparative performance of spectral reflectance indices and multivariate modeling for assessing agronomic parameters in advanced spring wheat lines under two contrasting irrigation regimes. *Frontiers in Plant Science* 10, 1537.

Elsayed, S., Barmeier, G. and Schmidhalter, U. 2018. Passive reflectance sensing and digital image analysis allows for assessing the biomass and nitrogen status of wheat in early and late tillering stages. *Frontiers in Plant Science* 9, 1478.

Elsayed, S., Elhoweity, M., Ibrahim, H. H., Dewir, Y. H., Migdadi, H. M. and Schmidhalter, U. 2017. Thermal imaging and passive reflectance sensing to estimate the water status and grain yield of wheat under different irrigation regimes. *Agricultural Water Management* 189, 98–110.

Elsayed, S., Rischbeck, P. and Schmidhalter, U. 2015. Comparing the performance of active and passive reflectance sensors to assess the normalized relative canopy temperature and grain yield of drought-stressed barley cultivars. *Field Crops Research* 177, 148–160.

Erdle, K., Mistele, B. and Schmidhalter, U. 2013. Spectral high-throughput assessments of phenotypic differences in biomass and nitrogen partitioning during grain filling of wheat under high yielding Western European conditions. *Field Crops Research* 141, 16–26.

Evain, S., Flexas, J. and Moya, I. 2004. A new instrument for passive remote sensing: 2. Measurement of leaf and canopy reflectance changes at 531 nm and their relationship with photosynthesis and chlorophyll fluorescence. *Remote Sensing of Environment* 91(2), 175–185.

Fernandez-Gallego, J. A., Kefauver, S. C., Gutierrez, N. A., Nieto-Taladriz, M. T. and Araus, J. L. 2018. Wheat ear counting in-field conditions: high throughput and low-cost approach using RGB images. *Plant Methods* 14, 22.

Fischer, R. A. and Rebetzke, G. J. 2018. Indirect selection for potential yield in early-generation, spaced plantings of wheat and other small-grain cereals: a review. *Crop and Pasture Science* 69(5), 439–459.

Fitzgerald, G., Rodriguez, D. and O'Leary, G. 2010. Measuring and predicting canopy nitrogen nutrition in wheat using a spectral index-the canopy chlorophyll content index (CCCI). *Field Crops Research* 116(3), 318–324.

Frels, K., Guttieri, M., Joyce, B., Leavitt, B. and Baenziger, P. S. 2018. Evaluating canopy spectral reflectance vegetation indices to estimate nitrogen use traits in hard winter wheat. *Field Crops Research* 217, 82–92.

Friedli, M., Kirchgessner, N., Grieder, C., Liebisch, F., Mannale, M. and Walter, A. 2016. Terrestrial 3D laser scanning to track the increase in canopy height of both monocot and dicot crop species under field conditions. *Plant Methods* 12, 9.

Fu, P., Meacham-Hensold, K., Guan, K. and Bernacchi, C. J. 2019. Hyperspectral leaf reflectance as proxy for photosynthetic capacities: an ensemble approach based on multiple machine learning algorithms. *Frontiers in Plant Science* 10, 730.

Fu, P., Meacham-Hensold, K., Guan, K., Wu, J. and Bernacchi, C. 2020. Estimating photosynthetic traits from reflectance spectra: a synthesis of spectral indices, numerical inversion, and partial least square regression. *Plant, Cell and Environment* 43(5), 1241–1258.

Gamon, J. A., Huemmrich, K. F., Wong, C. Y. S., Ensminger, I., Garrity, S., Hollinger, D. Y., Noormets, A. and Peñuelas, J. 2016. A remotely sensed pigment index reveals photosynthetic phenology in evergreen conifers. *Proceedings of the National Academy of Sciences of the United States of America* 113(46), 13087–13092.

Garriga, M., Romero-Bravo, S., Estrada, F., Escobar, A., Matus, I. A., Del Pozo, A., Astudillo, C. A. and Lobos, G. A. 2017. Assessing wheat traits by spectral reflectance: do we really need to focus on predicted trait-values or directly identify the Elite Genotypes Group? *Frontiers in Plant Science* 8, 280.

Ghosal, S., Zheng, B., Chapman, S. C., Potgieter, A. B., Jordan, D. R., Wang, X., Singh, A. K., Singh, A., Hirafuji, M., Ninomiya, S., Ganapathysubramanian, B., Sarkar, S. and Guo, W. 2019. A weakly supervised deep learning framework for sorghum head detection and counting. *Plant Phenomics* 2019, 1525874.

Gitelson, A. and Solovchenko, A. 2018. Non-invasive quantification of foliar pigments: possibilities and limitations of reflectance- and absorbance-based approaches. *Journal of Photochemistry and Photobiology. B, Biology* 178, 537–544.

Gonçalves, M. T. V., Morota, G., Costa, P. M. A., Vidigal, P. M. P., Barbosa, M. H. P. and Peternelli, L. A. 2021. Near-infrared spectroscopy outperforms genomics for predicting sugarcane feedstock quality traits. *PLoS ONE* 16(3), e0236853.

Gonzalez-Dugo, V., Zarco-Tejada, P. J. and Fereres, E. 2014. Applicability and limitations of using the crop water stress index as an indicator of water deficits in citrus orchards. *Agricultural and Forest Meteorology* 198–199, 94–104.

Gracia-Romero, A., Kefauver, S. C., Vergara-Diaz, O., Zaman-Allah, M. A., Prasanna, B. M., Cairns, J. E. and Araus, J. L. 2017. Comparative performance of ground vs. aerially assessed RGB and multispectral indices for early-growth evaluation of maize performance under phosphorus fertilization. *Frontiers in Plant Science* 8, 2004.

Grieder, C., Hund, A. and Walter, A. 2015. Image based phenotyping during winter: a powerful tool to assess wheat genetic variation in growth response to temperature. *Functional Plant Biology* 42(4), 387–396.

Guo, W., Fukatsu, T. and Ninomiya, S. 2015. Automated characterization of flowering dynamics in rice using field-acquired time-series RGB images. *Plant Methods* 11, 7.

Guo, W., Rage, U. K. and Ninomiya, S. 2013. Illumination invariant segmentation of vegetation for time series wheat images based on decision tree model. *Computers and Electronics in Agriculture* 96, 58–66.

Gutierrez, M., Norton, R., Thorp, K. R. and Wang, G. 2012. Association of spectral reflectance indices with plant growth and lint yield in upland cotton. *Crop Science* 52(2), 849–857.

Haboudane, D., Miller, J. R., Pattey, E., Zarco-Tejada, P. J. and Strachan, I. B. 2004. Hyperspectral vegetation indices and novel algorithms for predicting green LAI of crop canopies: modeling and validation in the context of precision agriculture. *Remote Sensing of Environment* 90(3), 337–352.

Hamuda, E., Glavin, M. and Jones, E. 2016. A survey of image processing techniques for plant extraction and segmentation in the field. *Computers and Electronics in Agriculture* 125, 184–199.

Han, L., Yang, G. J., Yang, H., Xu, B., Li, Z. H. and Yang, X. D. 2018. Clustering field-based maize phenotyping of plant-height growth and canopy spectral dynamics using a UAV remote-sensing approach. *Frontiers in Plant Science* 9, 1638.

Hayes, B. J., Panozzo, J., Walker, C. K., Choy, A. L., Kant, S., Wong, D., Tibbits, J., Daetwyler, H. D., Rochfort, S., Hayden, M. J. and Spangenberg, G. C. 2017. Accelerating wheat breeding for end-use quality with multi-trait genomic predictions incorporating near infrared and nuclear magnetic resonance-derived phenotypes. *TAG. Theoretical and Applied Genetics. Theoretische und Angewandte Genetik* 130(12), 2505–2519.

Hocevar, M., Sirok, B., Godesa, T. and Stopar, M. 2014. Flowering estimation in apple orchards by image analysis. *Precision Agriculture* 15(4), 466–478.

Holman, F. H., Riche, A. B., Castle, M., Wooster, M. J. and Hawkesford, M. J. 2019. Radiometric calibration of 'commercial off the shelf' cameras for UAV-based high-resolution temporal crop phenotyping of reflectance and NDVI. *Remote Sensing* 11(14), 1657.

Holman, F. H., Riche, A. B., Michalski, A., Castle, M., Wooster, M. J. and Hawkesford, M. J. 2016. High throughput field phenotyping of wheat plant height and growth rate in field plot trials using UAV based remote sensing. *Remote Sensing* 8(12), 23.

Hosoi, F., Nakai, Y. and Omasa, K. 2013. 3-D voxel-based solid modeling of a broad-leaved tree for accurate volume estimation using portable scanning lidar. *ISPRS Journal of Photogrammetry and Remote Sensing* 82, 41–48.

Hoyos-Villegas, V., Houx, J. H., Singh, S. K. and Fritschi, F. B. 2014. Ground-based digital imaging as a tool to assess soybean growth and yield. *Crop Science* 54(4), 1756–1768.

Jarquín, D., Crossa, J., Lacaze, X., Du Cheyron, P., Daucourt, J., Lorgeou, J., Piraux, F., Guerreiro, L., Pérez, P., Calus, M., Burgueño, J. and de los Campos, G. 2014. A reaction norm model for genomic selection using high-dimensional genomic and environmental data. *TAG. Theoretical and Applied Genetics. Theoretische und Angewandte Genetik* 127(3), 595–607.

Jarquín, D., Howard, R., Xavier, A., Das Choudhury, S. 2018. Increasing predictive ability by modeling interactions between environments, genotype and canopy coverage image data for soybeans. *Agronomy* 8, 51. https://doi.org/10.3390/agronomy8040051.

Jay, S., Rabatel, G., Hadoux, X., Moura, D. and Gorretta, N. 2015. In-field crop row phenotyping from 3D modeling performed using structure from motion. *Computers and Electronics in Agriculture* 110, 70–77.

Jimenez-Berni, J. A., Deery, D. M., Rozas-Larraondo, P., Condon, A. T. G., Rebetzke, G. J., James, R. A., Bovill, W. D., Furbank, R. T. and Sirault, X. R. R. 2018. High throughput determination of plant height, ground cover, and above-ground biomass in wheat with LiDAR. *Frontiers in Plant Science* 9, 237.

Jin, X., Madec, S., Dutartre, D., De Solan, B., Comar, A. and Baret, F. 2019. High-throughput measurements of stem characteristics to estimate ear density and above-ground biomass. *Plant Phenomics* 2019, 4820305.

Jones, H. G., Serraj, R., Loveys, B. R., Xiong, L. Z., Wheaton, A. and Price, A. H. 2009. Thermal infrared imaging of crop canopies for the remote diagnosis and quantification of plant responses to water stress in the field. *Functional Plant Biology* 36(11), 978–989.

Juliana, P., Montesinos-Lopez, O. A., Crossa, J., Mondal, S., Gonzalez Perez, L., Poland, J., Huerta-Espino, J., Crespo-Herrera, L., Govindan, V., Dreisigacker, S., Shrestha, S., Perez-Rodriguez, P., Pinto Espinosa, F. and Singh, R. P. 2019. Integrating genomic-enabled prediction and high-throughput phenotyping in breeding for climate-resilient bread wheat. *TAG. Theoretical and Applied Genetics. Theoretische und Angewandte Genetik* 132(1), 177–194.

Kefauver, S. C., Vicente, R., Vergara-Díaz, O., Fernandez-Gallego, J. A., Kerfal, S., Lopez, A., Melichar, J. P. E., Serret Molins, M. D. and Araus, J. L. 2017. Comparative UAV and field phenotyping to assess yield and nitrogen use efficiency in hybrid and conventional barley. *Frontiers in Plant Science* 8, 1733.

Kelly, J., Kljun, N., Olsson, P.-O., Mihai, L., Liljeblad, B., Weslien, P., Klemedtsson, L. and Eklundh, L. 2019. Challenges and best practices for deriving temperature data from an uncalibrated UAV thermal infrared camera. *Remote Sensing* 11(5), 567. https://doi.org/10.3390/rs11050567.

Kipp, S., Mistele, B. and Schmidhalter, U. 2014. Identification of stay-green and early senescence phenotypes in high-yielding winter wheat, and their relationship to grain yield and grain protein concentration using high-throughput phenotyping techniques. *Functional Plant Biology* 41(3), 227–235.

Krause, M. R., González-Pérez, L., Crossa, J., Pérez-Rodríguez, P., Montesinos-López, O., Singh, R. P., Dreisigacker, S., Poland, J., Rutkoski, J., Sorrells, M., Gore, M. A. and Mondal, S. 2019. Hyperspectral reflectance-derived relationship matrices for genomic prediction of grain yield in wheat. *G3* 9(4), 1231–1247.

Kronenberg, L., Yu, K., Walter, A. and Hund, A. 2017. Monitoring the dynamics of wheat stem elongation: genotypes differ at critical stages. *Euphytica* 213(7), 157.

Kyratzis, A. C., Skarlatos, D. P., Menexes, G. C., Vamvakousis, V. F. and Katsiotis, A. 2017. Assessment of vegetation indices derived by UAV imagery for durum wheat phenotyping under a water limited and heat stressed Mediterranean environment. *Frontiers in Plant Science* 8, 1114.

Lane, H. M., Murray, S. C., MontesinosLópez, O. A., MontesinosLópez, A., Crossa, J., Rooney, D. K., Barrero-Farfan, I. D., De La Fuente, G. N. and Morgan, C. L. S. 2020. Phenomic selection and prediction of maize grain yield from near-infrared reflectance spectroscopy of kernels. *The Plant Phenome Journal* 3(1), e20002.

Li, J., Shi, Y., Veeranampalayam-Sivakumar, A. N. and Schachtman, D. P. 2018. Elucidating sorghum biomass, nitrogen and chlorophyll contents With spectral and morphological traits derived From unmanned aircraft system. *Frontiers in Plant Science* 9, 1406.

Li, Z. and Sillanpää, M. J. 2015. Dynamic quantitative trait locus analysis of plant phenomic data. *Trends in Plant Science* 20(12), 822–833.

Liu, Y., Cen, C., Che, Y., Ke, R., Ma, Y. and Ma, Y. 2020. Detection of maize tassels from UAV RGB imagery with faster R-CNN. *Remote Sensing* 12(2), 338.

Lobos, G., Escobar-Opazo, A., Estrada, F., Romero, S., Garriga, M., Del Pozo, A., Poblete-Echeverría, C., Gonzalez-Talice, J., González-Martinez, L. and Caligari, P. 2019. Spectral reflectance modeling by wavelength selection: studying the scope for blueberry physiological breeding under contrasting water supply and heat conditions. *Remote Sensing* 11(3), 329. https://doi.org/10.3390/rs11030329.

Lopez-Cruz, M., Olson, E., Rovere, G., Crossa, J., Dreisigacker, S., Mondal, S., Singh, R. and De Los Campos, G. 2020. Regularized selection indices for breeding value prediction using hyper-spectral image data. *Scientific Reports* 10, 1.

Lozada, D. N., Godoy, J. V., Ward, B. P. and Carter, A. H. 2020. Genomic prediction and indirect selection for grain yield in US Pacific Northwest winter wheat using spectral reflectance indices from high-throughput phenotyping. *International Journal of Molecular Sciences* 21(1), 165.

Lu, H., Cao, Z., Xiao, Y., Zhuang, B. and Shen, C. 2017. TasselNet: counting maize tassels in the wild via local counts regression network. *Plant Methods* 13, 79.

Lu, J. S., Cheng, D. L., Geng, C. M., Zhang, Z. T., Xiang, Y. Z. and Hu, T. T. 2021. Combining plant height, canopy coverage and vegetation index from UAV-based RGB images to estimate leaf nitrogen concentration of summer maize. *Biosystems Engineering* 202, 42–54.

Lyra, D. H., Virlet, N., Sadeghi-Tehran, P., Hassall, K. L., Wingen, L. U., Orford, S., Griffiths, S., Hawkesford, M. J. and Slavov, G. T. 2020. Functional QTL mapping and genomic prediction of canopy height in wheat measured using a robotic field phenotyping platform. *Journal of Experimental Botany* 71(6), 1885–1898.

Madec, S., Jin, X. L., Lu, H., De Solan, B., Liu, S. Y., Duyme, F., Heritier, E. and Baret, F. 2019. Ear density estimation from high resolution RGB imagery using deep learning technique. *Agricultural and Forest Meteorology* 264, 225–234.

Maes, W. H. and Steppe, K. 2012. Estimating evapotranspiration and drought stress with ground-based thermal remote sensing in agriculture: a review. *Journal of Experimental Botany* 63(13), 4671–4712.

Magney, T. S., Eitel, J. U. H., Huggins, D. R. and Vierling, L. A. 2016. Proximal NDVI derived phenology improves in-season predictions of wheat quantity and quality. *Agricultural and Forest Meteorology* 217, 46–60.

Maimaitijiang, M. and Sidike, P. 2019. Vegetation Index Weighted Canopy Volume Model (CVMVI) for soybean biomass estimation from Unmanned Aerial System-based RGB imagery. *ISPRS Journal of Photogrammetry and Remote Sensing* 151, 27–41.

Malosetti, M., Ribaut, J. M. and Van Eeuwijk, F. A. 2013. The statistical analysis of multi-environment data: modeling genotype-by-environment interaction and its genetic basis. *Frontiers in Physiology* 4, 44.

Mantilla-Perez, M. B. and Salas Fernandez, M. G. 2017. Differential manipulation of leaf angle throughout the canopy: current status and prospects. *Journal of Experimental Botany* 68(21–22), 5699–5717.

Meacham-Hensold, K., Fu, P., Wu, J., Serbin, S., Montes, C. M., Ainsworth, E., Guan, K., Dracup, E., Pederson, T., Driever, S. and Bernacchi, C. 2020. Plot-level rapid screening for photosynthetic parameters using proximal hyperspectral imaging. *Journal of Experimental Botany* 71(7), 2312–2328.

Millet, E. J., Kruijer, W., Coupel-Ledru, A., Prado, S. A., Cabrera-Bosquet, L., Lacube, S., Charcosset, A., Welcker, C., Van Eeuwijk, F. and Tardieu, F. 2019. Genomic prediction of maize yield across European environmental conditions. *Nature Genetics* 51(6), 952–956.

Mir, R. R., Reynolds, M., Pinto, F., Khan, M. A. and Bhat, M. A. 2019. High-throughput phenotyping for crop improvement in the genomics era. *Plant Science* 282, 60–72.

Momen, M., Campbell, M. T., Walia, H. and Morota, G. 2019. Predicting longitudinal traits derived from high-throughput phenomics in contrasting environments using genomic Legendre polynomials and B-splines. *G3* 9(10), 3369–3380.

Montazeaud, G., Karatogma, H., Ozturk, I., Roumet, P., Ecarnot, M., Crossa, J., Ozer, E., Ozdemir, F. and Lopes, M. S. 2016. Predicting wheat maturity and stay-green parameters by modeling spectral reflectance measurements and their contribution to grain yield under rainfed conditions. *Field Crops Research* 196, 191–198.

Montes, J. M., Technow, F., Dhillon, B. S., Mauch, F. and Melchinger, A. E. 2011. High-throughput non-destructive biomass determination during early plant development in maize under field conditions. *Field Crops Research* 121(2), 268–273.

Montesinos-Lopez, A., Montesinos-Lopez, O. A., Cuevas, J., Mata-Lopez, W. A., Burgueno, J., Mondal, S., Huerta, J., Singh, R., Autrique, E., Gonzalez-Perez, L. and Crossa, J. 2017a. Genomic Bayesian functional regression models with interactions for predicting wheat grain yield using hyper-spectral image data. *Plant Methods* 13, 62.

Montesinos-Lopez, A., Montesinos-Lopez, O. A., De Los Campos, G., Crossa, J., Burgueno, J. and Luna-Vazquez, F. J. 2018. Bayesian functional regression as an alternative statistical analysis of high-throughput phenotyping data of modern agriculture. *Plant Methods* 14, 46.

Montesinos-Lopez, O. A., Montesinos-Lopez, A., Crossa, J., De Los Campos, G., Alvarado, G., Suchismita, M., Rutkoski, J., Gonzalez-Perez, L. and Burgueno, J. 2017b. Predicting grain yield using canopy hyperspectral reflectance in wheat breeding data. *Plant Methods* 13, 4.

Moran, M. S., Clarke, T. R., Inoue, Y. and Vidal, A. 1994. Estimating crop water-deficit using the relation between surface-air temperature and spectral vegetation index. *Remote Sensing of Environment* 49(3), 246–263.

Moreira, F. F., Oliveira, H. R., Volenec, J. J., Rainey, K. M. and Brito, L. F. 2020. Integrating high-throughput phenotyping and statistical genomic methods to genetically improve longitudinal traits in crops. *Frontiers in Plant Science* 11, 681.

Morota, G. and Gianola, D. 2014. Kernel-based whole-genome prediction of complex traits: a review. *Frontiers in Genetics* 5, 363.

Morota, G., Jarquin, D., Campbell, M. T. and Iwata, H. 2019. Statistical methods for the quantitative genetic analysis of high-throughput phenotyping data. arXiv preprint arXiv:1904.12341. https://arxiv.org/abs/1904.12341.

Munns, R., James, R. A., Sirault, X. R. R., Furbank, R. T. and Jones, H. G. 2010. New phenotyping methods for screening wheat and barley for beneficial responses to water deficit. *Journal of Experimental Botany* 61(13), 3499–3507.

Pancorbo, J. L., Camino, C., Alonso-Ayuso, M., Raya-Sereno, M. D., Gonzalez-Fernandez, I., Gabriel, J. L., Zarco-Tejada, P. J. and Quemada, M. 2021. Simultaneous assessment of nitrogen and water status in winter wheat using hyperspectral and thermal sensors. *European Journal of Agronomy* 127, 126287.

Pask, A., Pietragalla, J., Mullan, D. and Reynolds, M. P. 2012. *Physiological Breeding II: A Field Guide to Wheat Phenotyping*. Mexico, D.F.: CIMMYT.

Pavuluri, K., Chim, B. K., Griffey, C. A., Reiter, M. S., Balota, M. and Thomason, W. E. 2015. Canopy spectral reflectance can predict grain nitrogen use efficiency in soft red winter wheat. *Precision Agriculture* 16(4), 405–424.

Peguero-Pina, J. J., Morales, F., Flexas, J., Gil-Pelegrín, E. and Moya, I. 2008. Photochemistry, remotely sensed physiological reflectance index and de-epoxidation state of the xanthophyll cycle in Quercus coccifera under intense drought. *Oecologia* 156(1), 1–11.

Pérez-Rodríguez, P., Crossa, J., Bondalapati, K., De Meyer, G., Pita, F. and Campos, Gdl 2015. A pedigree-based reaction norm model for prediction of cotton yield in multienvironment trials. *Crop Science* 55(3), 1143–1151.

Piao, S. L., Liu, Q., Chen, A. P., Janssens, I. A., Fu, Y. S., Dai, J. H., Liu, L. L., Lian, X., Shen, M. G. and Zhu, X. L. 2019. Plant phenology and global climate change: current progresses and challenges. *Global Change Biology* 25(6), 1922–1940.

Porcar-Castell, A., Garcia-Plazaola, J. I., Nichol, C. J., Kolari, P., Olascoaga, B., Kuusinen, N., Fernández-Marín, B., Pulkkinen, M., Juurola, E. and Nikinmaa, E. 2012. Physiology of the seasonal relationship between the photochemical reflectance index and photosynthetic light use efficiency. *Oecologia* 170(2), 313–323.

Porker, K., Coventry, S., Fettell, N., Cozzolino, D. and Eglinton, J. 2020. Using a novel PLS approach for envirotyping of barley phenology and adaptation. *Field Crops Research* 246, 107697.

Prasad, B., Carver, B. F., Stone, M. L., Babar, M. A., Raun, W. R. and Klatt, A. R. 2007. Genetic analysis of indirect selection for winter wheat grain yield using spectral reflectance indices. *Crop Science* 47(4), 1416–1425.

Prey, L., Hu, Y. and Schmidhalter, U. 2020. High-throughput field phenotyping traits of grain yield formation and nitrogen use efficiency: optimizing the selection of vegetation indices and growth stages. *Frontiers in Plant Science* 10, 1672.

Prey, L., Kipp, S., Hu, Y. and Schmidhalter, U. 2019. Nitrogen use efficiency and carbon traits of high-yielding european hybrid vs. line winter wheat cultivars: potentials and limitations. *Frontiers in Plant Science* 9, 1988.

Prey, L. and Schmidhalter, U. 2019. Temporal and spectral optimization of vegetation indices for estimating grain nitrogen uptake and late-seasonal nitrogen traits in wheat. *Sensors* 19(21), 27.

Prey, L. and Schmidhalter, U. 2020. Deep phenotyping of yield-related traits in wheat. *Agronomy* 10(4), 603.

Rascher, U., Nichol, C. J., Small, C. and Hendricks, L. 2007. Monitoring spatio-temporal dynamics of photosynthesis with a portable hyperspectral imaging system. *Photogrammetric Engineering and Remote Sensing* 73(1), 45–56.

Rebetzke, G. J., Jimenez-Berni, J., Fischer, R. A., Deery, D. M. and Smith, D. J. 2019. Review: high-throughput phenotyping to enhance the use of crop genetic resources. *Plant Science* 282, 40–48.

Rebetzke, G. J., Jimenez-Berni, J. A., Bovill, W. D., Deery, D. M. and James, R. A. 2016. High-throughput phenotyping technologies allow accurate selection of stay-green. *Journal of Experimental Botany* 67(17), 4919–4924.

Resende, R. T., Piepho, H.-P., Rosa, G. J., Silva-Junior, O. B., e Silva, F. F., De Resende, M. D. V. and Grattapaglia, D. 2021. Enviromics in breeding: applications and perspectives on envirotypic-assisted selection. *Theoretical and Applied Genetics* 134, 95–112.

Reynolds, M., Foulkes, J., Furbank, R., Griffiths, S., King, J., Murchie, E., Parry, M. and Slafer, G. 2012. Achieving yield gains in wheat. *Plant, Cell and Environment* 35(10), 1799–1823.

Reynolds, M. and Langridge, P. 2016. Physiological breeding. *Current Opinion in Plant Biology* 31, 162–171.

Rincent, R., Charpentier, J. P., Faivre-Rampant, P., Paux, E., Le Gouis, J., Bastien, C. and Segura, V. 2018. Phenomic selection is a low-cost and high-throughput method based on indirect predictions: proof of concept on wheat and poplar. *G3* 8(12), 3961–3972.

Rischbeck, P., Elsayed, S., Mistele, B., Barmeier, G., Heil, K. and Schmidhalter, U. 2016. Data fusion of spectral, thermal and canopy height parameters for improved yield prediction of drought stressed spring barley. *European Journal of Agronomy* 78, 44–59.

Rodriguez, D., Fitzgerald, G. J., Belford, R. and Christensen, L. K. 2006. Detection of nitrogen deficiency in wheat from spectral reflectance indices and basic crop eco-physiological concepts. *Australian Journal of Agricultural Research* 57(7), 781–789.

Runcie, D. E., Qu, J., Cheng, H. and Crawford, L. 2021. MegaLMM: mega-scale linear mixed models for genomic predictions with thousands of traits. *Genome Biology* 22(1), 213.

Rutkoski, J., Poland, J., Mondal, S., Autrique, E., Perez, L. G., Crossa, J., Reynolds, M. and Singh, R. 2016. Canopy temperature and vegetation indices from high-throughput phenotyping improve accuracy of pedigree and genomic selection for grain yield in wheat. *G3* 6(9), 2799–2808.

Sadeghi-Tehran, P., Virlet, N., Sabermanesh, K. and Hawkesford, M. J. 2017a. Multi-feature machine learning model for automatic segmentation of green fractional vegetation cover for high-throughput field phenotyping. Plant Methods, 13(1): 103.

Sadeghi-Tehran, P., Sabermanesh, K., Virlet, N. and Hawkesford, M. J. 2017b. Automated method to determine two critical growth stages of wheat: heading and flowering. *Frontiers in Plant Science* 8, 252.

Sadeghi-Tehran, P., Virlet, N., Ampe, E. M., Reyns, P. and Hawkesford, M. J. 2019. DeepCount: in-field automatic quantification of wheat spikes using simple linear iterative clustering and deep convolutional neural networks. *Frontiers in Plant Science* 10, 1176.

Salas Fernandez, M. G., Bao, Y., Tang, L. and Schnable, P. S. 2017. A high-throughput, field-based phenotyping technology for tall biomass crops. *Plant Physiology* 174(4), 2008–2022.

Santini, F., Kefauver, S. C., Resco De Dios, V., Araus, J. L. and Voltas, J. 2019. Using unmanned aerial vehicle-based multispectral, RGB and thermal imagery for phenotyping of forest genetic trials: a case study in *Pinus halepensis*. *Annals of Applied Biology* 174(2), 262–276.

Schaeffer, L. 2016. Random regression models. http://animalbiosciences.uoguelph.ca/~lrs/BOOKS/rrmbook.pdf.

Schaeffer, L. R. 2004. Application of random regression models in animal breeding. *Livestock Production Science* 86(1–3), 35–45.

Scossa, F., Alseekh, S. and Fernie, A. R. 2021. Integrating multi-omics data for crop improvement. *Journal of Plant Physiology* 257, 153352.

Silva-Perez, V., Molero, G., Serbin, S. P., Condon, A. G., Reynolds, M. P., Furbank, R. T. and Evans, J. R. 2018. Hyperspectral reflectance as a tool to measure biochemical and physiological traits in wheat. *Journal of Experimental Botany* 69(3), 483–496.

Sun, J., Rutkoski, J. E., Poland, J. A., Crossa, J., Jannink, J. L. and Sorrells, M. E. 2017. Multitrait, random regression, or simple repeatability model in high-throughput phenotyping data improve genomic prediction for wheat grain yield. *Plant Genome* 10(2), 1–12.

Tardieu, F., Cabrera-Bosquet, L., Pridmore, T. and Bennett, M. 2017. Plant phenomics, from sensors to knowledge. *Current Biology* 27(15), R770–R783.

Thorp, K. R. and Dierig, D. A. 2011. Color image segmentation approach to monitor flowering in *Lesquerella*. *Industrial Crops and Products* 34(1), 1150–1159.

Thorp, K. R., Gore, M. A., Andrade-Sanchez, P., Carmo-Silva, A. E., Welch, S. M., White, J. W. and French, A. N. 2015. Proximal hyperspectral sensing and data analysis approaches for field-based plant phenomics. *Computers and Electronics in Agriculture* 118, 225–236.

Van Eeuwijk, F. A., Bustos-Korts, D., Millet, E. J., Boer, M. P., Kruijer, W., Thompson, A., Malosetti, M., Iwata, H., Quiroz, R., Kuppe, C., Muller, O., Blazakis, K. N., Yu, K., Tardieu, F. and Chapman, S. C. 2019. Modelling strategies for assessing and increasing the effectiveness of new phenotyping techniques in plant breeding. *Plant Science* 282, 23–39.

Van Eeuwijk, F. A., Bustos-Korts, D. V. and Malosetti, M. 2016. What should students in plant breeding know about the statistical aspects of genotype×environment interactions? *Crop Science* 56(5), 2119–2140.

Varela, S., Pederson, T., Bernacchi, C. J. and Leakey, A. D. B. 2021. Understanding growth dynamics and yield prediction of sorghum using high temporal resolution UAV imagery time series and machine learning. *Remote Sensing* 13(9), 17.

Vargas, J. J. Q., Zhang, C. Y., Smitchger, J. A., McGee, R. J. and Sankaran, S. 2019. Phenotyping of plant biomass and performance traits using remote sensing techniques in pea (*Pisum sativum*, L.). *Sensors* 19, 23.

Velumani, K., Madec, S., De Solan, B., Lopez-Lozano, R., Gillet, J., Labrosse, J., Jezequel, S., Comar, A. and Baret, F. 2020. An automatic method based on daily in situ images and deep learning to date wheat heading stage. *Field Crops Research* 252, 107793.

Vigneau, N., Ecarnot, M., Rabatel, G. and Roumet, P. 2011. Potential of field hyperspectral imaging as a non destructive method to assess leaf nitrogen content in wheat. *Field Crops Research* 122(1), 25–31.

Violle, C., Navas, M. L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. and Garnier, E. 2007. Let the concept of trait be functional! *Oikos* 116(5), 882–892.

Virlet, N., Lebourgeois, V., Martinez, S., Costes, E., Labbe, S. and Regnard, J. L. 2014. Stress indicators based on airborne thermal imagery for field phenotyping a heterogeneous tree population for response to water constraints. *Journal of Experimental Botany* 65(18), 5429–5442.

Virlet, N., Sabermanesh, K., Sadeghi-Tehran, P. and Hawkesford, M. J. 2016. Field Scanalyzer: an automated robotic field phenotyping platform for detailed crop monitoring. *Functional Plant Biology* 44(1), 143–153.

Wallace, J. G., Rodgers-Melnick, E. and Buckler, E. S. 2018. On the road to breeding 4.0: unraveling the good, the bad, and the boring of crop quantitative genomics. *Annual Review of Genetics* 52, 421–444.

Wang, X., Xuan, H., Evers, B., Shrestha, S., Pless, R. and Poland, J. 2019. High-throughput phenotyping with deep learning gives insight into the genetic architecture of flowering time in wheat. *GigaScience* 8(11), giz120, https://doi.org/10.1093/gigascience/giz120.

Watanabe, K., Guo, W., Arai, K., Takanashi, H., Kajiya-Kanegae, H., Kobayashi, M., Yano, K., Tokunaga, T., Fujiwara, T., Tsutsumi, N. and Iwata, H. 2017. High-throughput phenotyping of sorghum plant height using an unmanned aerial vehicle and its application to genomic prediction modelling. *Frontiers in Plant Science* 8, 421.

Weber, V. S., Araus, J. L., Cairns, J. E., Sanchez, C., Melchinger, A. E. and Orsini, E. 2012. Prediction of grain yield using reflectance spectra of canopy and leaves in maize plants grown under different water regimes. *Field Crops Research* 128, 82–90.

Winterhalter, L., Mistele, B., Jampatong, S. and Schmidhalter, U. 2011. High throughput phenotyping of canopy water mass and canopy temperature in well-watered and drought stressed tropical maize hybrids in the vegetative stage. *European Journal of Agronomy* 35(1), 22–32.

Wyber, R., Malenovský, Z., Ashcroft, M., Osmond, B. and Robinson, S. 2017. Do daily and seasonal trends in leaf solar induced fluorescence reflect changes in photosynthesis, growth or light exposure? *Remote Sensing* 9(6), 604.

Wyber, R., Osmond, B., Ashcroft, M. B., Malenovsky, Z. and Robinson, S. A. 2018. Remote monitoring of dynamic canopy photosynthesis with high time resolution light-induced fluorescence transients. *Tree Physiology* 38(9), 1302–1318.

Xiao, S., Chai, H., Shao, K., Shen, M., Wang, Q., Wang, R., Sui, Y. and Ma, Y. 2020. Image-based dynamic quantification of aboveground structure of sugar beet in field. *Remote Sensing* 12(2), 269.

Xiong, X., Duan, L., Liu, L., Tu, H., Yang, P., Wu, D., Chen, G., Xiong, L., Yang, W. and Liu, Q. 2017. Panicle-SEG: a robust image segmentation method for rice panicles in the field based on deep learning and superpixel optimization. *Plant Methods* 13, 104.

Xu, R., Li, C., Paterson, A. H., Jiang, Y., Sun, S. and Robertson, J. S. 2018. Aerial images and convolutional neural network for cotton bloom detection. *Frontiers in Plant Science* 8, 2235.

Xu, Y. 2016. Envirotyping for deciphering environmental impacts on crop plants. *TAG. Theoretical and Applied Genetics. Theoretische und Angewandte Genetik* 129(4), 653–673.

Yamasaki, E., Altermatt, F., Cavender-Bares, J., Schuman, M. C., Zuppinger-Dingley, D., Garonna, I., Schneider, F. D., Guillen-Escriba, C., Van Moorsel, S. J., Hahl, T., Schmid, B., Schaepman-Strub, G., Schaepman, M. E. and Shimizu, K. K. 2017. Genomics meets remote sensing in global change studies: monitoring and predicting phenology, evolution and biodiversity. *Current Opinion in Environmental Sustainability* 29, 177–186.

Yu, K., Anderegg, J., Mikaberidze, A., Karisto, P., Mascher, F., McDonald, B. A., Walter, A. and Hund, A. 2018. Hyperspectral canopy sensing of wheat Septoria tritici blotch disease. *Frontiers in Plant Science* 9, 1195.

Yue, J. B., Yang, G. J., Li, C. C., Li, Z. H., Wang, Y. J., Feng, H. K. and Xu, B. 2017. Estimation of winter wheat above-ground biomass using unmanned aerial vehicle-based snapshot hyperspectral sensor and crop height improved models. *Remote Sensing* 9(7), 708.

Zhang, Z., Chen, C., Rutkoski, J., Schnable, J., Murray, S., Wang, L., Jin, X., Stich, B., Crossa, J. and Hayes, B. 2021. *Harnessing Agronomics Through Genomics and Phenomics in Plant Breeding: A Review*, 2021030519. doi: 10.20944/preprints202103.0519.v1.

Zhou, C. Q., Ye, H. B., Hu, J., Shi, X. Y., Hua, S., Yue, J. B., Xu, Z. F. and Yang, G. J. 2019. Automated counting of rice panicle by applying deep learning model to images from unmanned aerial vehicle platform. *Sensors* 19(14), 16.