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TraitCapture: genomic and environment modelling of plant phenomic data[☆]

Tim B Brown^{1,5}, Riyan Cheng^{1,5}, Xavier RR Sirault^{2,5},
Tepsuda Rungrat¹, Kevin D Murray¹, Martin Trtilek^{1,2,3,4},
Robert T Furbank², Murray Badger^{1,4}, Barry J Pogson^{1,4} and
Justin O Borevitz¹

Agriculture requires a second green revolution to provide increased food, fodder, fiber, fuel and soil fertility for a growing population while being more resilient to extreme weather on finite land, water, and nutrient resources. Advances in phenomics, genomics and environmental control/sensing can now be used to directly select yield and resilience traits from large collections of germplasm if software can integrate among the technologies. *Traits* could be *Captured* throughout development and across environments from multi-dimensional phenotypes, by applying Genome Wide Association Studies (GWAS) to identify causal genes and background variation and functional structural plant models (FSPMs) to predict plant growth and reproduction in target environments. *TraitCapture* should be applicable to both controlled and field environments and would allow breeders to simulate regional variety trials to pre-select for increased productivity under challenging environments.

Addresses

¹ Division of Plant Sciences, Research School of Biology, Australian National University, Australia

² High Resolution Plant Phenomics Centre, Plant Industry, CSIRO, Australia

³ Photon Systems Instruments, Czech Republic

⁴ ARC Centre of Excellence in Plant Energy Biology, Australia

Corresponding author: Borevitz, Justin O (justin.borevitz@anu.edu.au)

⁵Co-first authors.

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Introduction

Global agricultural demand is expanding rapidly due to increased consumption of food, feed, and fuel by a larger, more affluent population. To meet projected global food

demands in coming decades, global cereal production must increase by 70% by 2050, a net annual increase in productivity of nearly 40% over historic levels, every year for the next 38 years [1]. At the same time, climates are changing globally, shifting growing regions and reducing climate predictability. Models predict even larger changes in critical growing regions [2]. These pressures are leading to increased plantings on marginal lands, displacement of natural ecosystems and intensification of existing agricultural practices. Consequently, a better understanding of how to breed for increased yield and yield stability in the face of shifting climates is of utmost economic and social importance.

Plant physiology research is progressing from detailed studies of a few different genotypes at a time, to high throughput, quantitative, phenomic studies on populations with fully sequenced genomes. These modern techniques provide the potential for plant scientists to identify heritable traits and the complex regulatory networks underlying adaptive phenotypic variation [3,4,5,6]. The current challenges are: first, to weave these new techniques into a package that can be implemented across phenomics platforms on different plant species and second, to bridge the gap between lab and field studies. Quantification of phenotypes combined with genetic analysis allows the identification and prediction of heritable traits. By incorporating growth models that include genetic and environmental variation, phenotypic predictions can be made for different growing regions to pre-select specific genotypes for local field trials.

High throughput phenotyping, phenomics, and environmental control

High throughput phenotyping (HTP) can record time-series data on plant functional traits as well as top down and 3D models of plant growth and development. This comprehensive, multi-dimensional phenotyping allows specific hypotheses about genotypic and/or environmental effects to be tested across hundreds or thousands of plants and then to associate it with whole genome sequence variation. New plant phenomics facilities are opening worldwide (plant-phenotyping.org) and many smaller labs are developing their own systems [7]. Integrating HTP and genome wide association studies (GWAS) [8**] has the potential to revolutionize the rate of trait discovery and vastly improve phenotypic predictions.

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New hardware enables new research

Commercial HTP phenomics platforms such as the TrayScan (psi.cz) can provide image data from standard visible color spectra cameras (RGB), thermal cameras, and fluorescence for hundreds of plants per plants run (Figure 1d). Real-time analysis enhances experimental resolution, for example, image analysis settings can be optimized to improve the genetic association. Furthermore, additional image acquisition can be performed at critical time points to further explore genetic associations while redundant observations can be eliminated, increasing throughput.

For lower cost and continuous phenotyping that incorporates environmental variation, specialized growth chambers can remove weather noise from the field while maintaining appropriate climate signals. For example, we are developing the SpectralPhenoClimatron ('SPC' [9,10**]) to extend standard growth chamber conditions beyond fixed on/off lighting and high/low temperatures. The SP

C can provide diurnal and seasonal control of light color via multi-band LED lights (Heliospectra AB, Göteborg, Sweden) and intensity, temperature and moisture. The SPC chambers also include high resolution time-lapse cameras integrated with automated phenotyping software for real-time developmental analysis. SolarCalc control software [11] allows regional and future climates to be simulated. For field applications it is becoming feasible to set up a large, spatial and temporally distributed sensor networks (phenonet.com [12]) with phenomics capacity

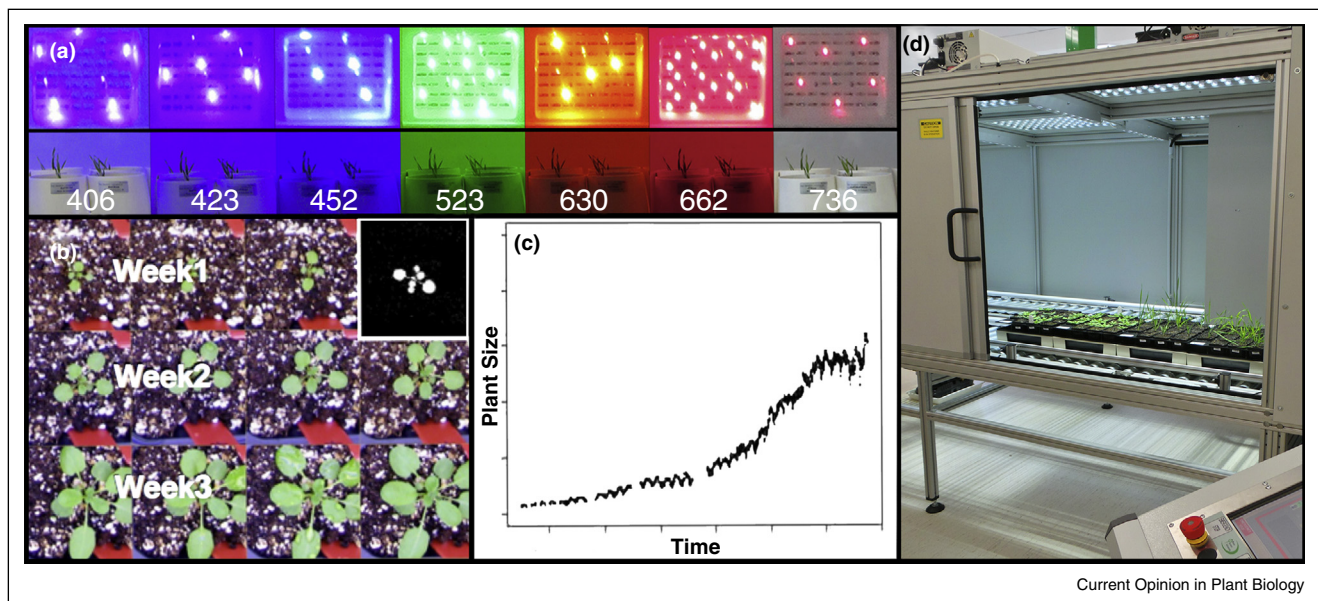
('Phenomobile' [13–15]). Finally, open-source and web-based software allow phenomic data to be remotely processed and easily shared.

Multitrait genome wide association studies

Genome-wide association studies have been a useful tool to study the genetic basis of heritable phenotypes, provide valuable information for gene hunting, understanding of biological processes, and plant and animal breeding. GWAS have become widely adopted for gene mapping in various plant studies such as *Arabidopsis thaliana* [16*], barley [17], maize [19], tomato [20] and rice [21]. GWAS can be computationally challenging, however research efforts have been made to develop computationally efficient algorithms [22–27]; additionally several web tools that simplify GWAS are available (e.g. GWAPP [28] and easyGWAS [29]).

High throughput phenotyping enables the extraction of data for numerous phenotypes [4]. While multiple traits are typically analyzed separately (unitrait analysis), joint analysis of multiple traits (multitrait analysis) has long been advocated in breeding and quantitative trait locus (QTL) mapping. By taking advantages of the residual correlation structure among the traits, multitrait analysis potentially results in a higher statistical power, more accurate estimation and a better control of false positives. It can also formally test biological hypotheses such as pleiotropy and genotype by environment interaction [30–33]. However, application of multitrait analysis is limited for a number of reasons. First, current practice generally

Figure 1



TraitCapture links high throughput phenotyping, GWAS, and functional structural plant modelling. (a) Multi waveband LED lights provide variation in light quality and quantity as input to FPSMs. (b) Plants are imaged to quantify fluorescence and green pixel phenotypes, through time (c) for GWAS analysis. (d) TrayScan high throughput phenotyping provided by our partner PSI.

does not facilitate the biological interpretation of results as the model for multitrait analysis typically assumes the putative QTL is associated with all of the traits. In reality, however, it is very likely that some of the traits are influenced by the QTL whereas the rest are not and therefore it is highly desirable to know which traits are which. Second, one of the main motivations to employ multitrait analysis is to increase statistical power for QTL detection but multitrait analysis is not always more powerful than univariate analysis [30,34]. New statistical methodologies can address these limitations allowing multitrait GWAS to be more useful [35].

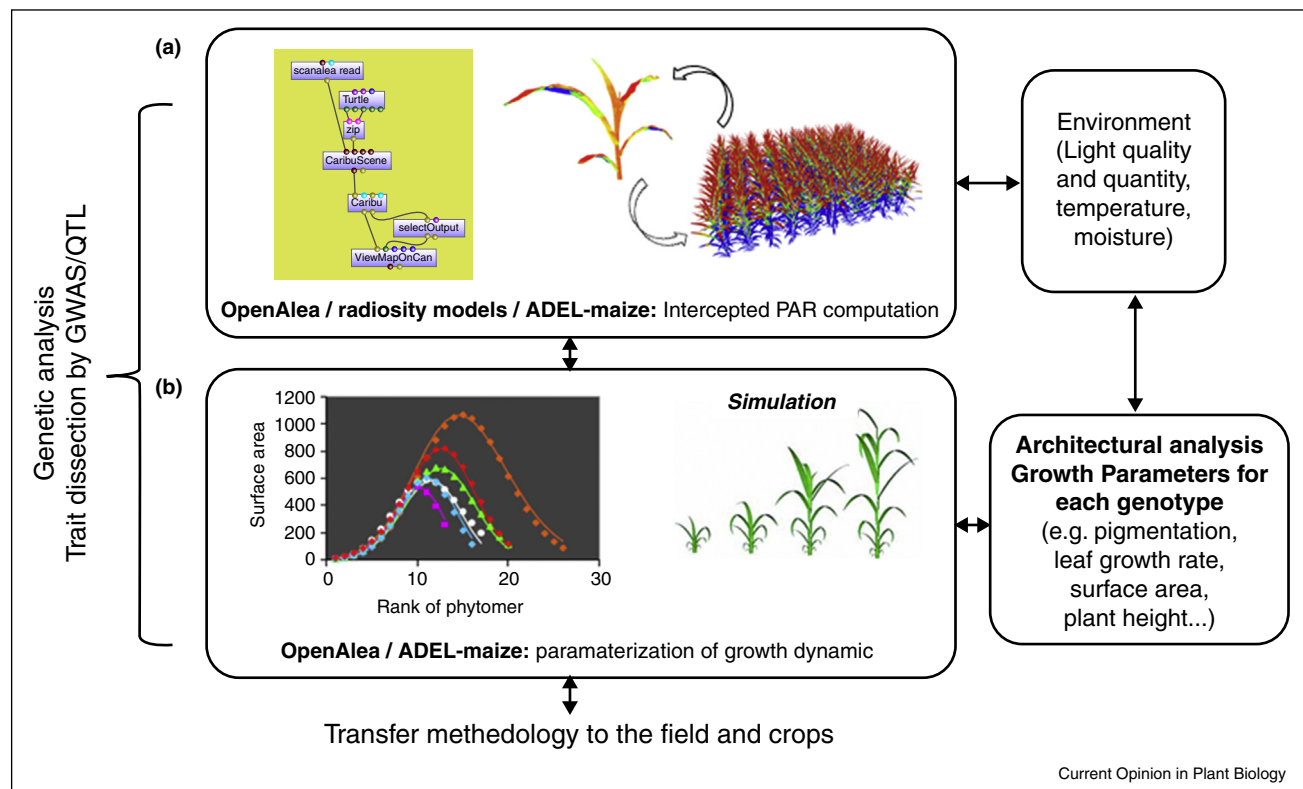
Functional structural plant models

Functional structural plant models (FSPMs, Figure 2) have traditionally been used in an agricultural context to simulate aspects of plant response and growth as governed by physiological processes which are in turn driven by local environmental conditions at the plant organ level [36,37]. These models incorporate 3D developmental modelling and mechanistic physiological models. Including plant 3D architectural information is particularly relevant for photosynthetic growth responses because light quantity and quality inputs vary with the spatial structure of a plant [38]. Although the FSPM approach has given us very sophisticated tools for predicting crop

yield, the often significant impact that plant genetics can have on yield outcomes has yet to be fully integrated into these models. Typically, plant genetic variation is treated as 'noise' in FSPMs because the intent of these models is to understand how a *generalized* plant of a given species will respond under *specific* climatic conditions. By contrast, in lab phenotyping experiments environmental variation is usually considered noise that limits trait discovery and the intent is typically to identify *specific* genotypes and understand how they vary. In the real world of course, environment and genetics interact together to determine a plant's actual phenotypic characteristics in the field (and hence resilience, yield, etc.). It is thus necessary to integrate both the FSPM and the genetics to better predict yield of particular genotypes across typical growing regions.

New work has shown that FSPMs can integrate genetic information from QTL studies [39]. There is potential to streamline this method using controlled but dynamic growing conditions such as those enabled by the SPC which simulates regional seasonal climates [40,10]. The growth and environmental data allows parameterization of FSPMs that include major genetic effects. This would be an important test case before attempting similar studies under field conditions. In addition, advanced GWAS analysis would fit QTL that interact with the

Figure 2



(a) Functional plant models such as OpenAlea [50] incorporate environmental as input along with (b) Structural models that include plant architecture to predict phenotype from environment and genetic variation. Figure adapted from [51].

environment such that degree days would have different effects on growth for different genotypes. Creation of FSPMs that incorporate the effects of genotype and environment would permit the prediction of phenotypes for sets of genetic variants across many environments using only *in silico* approaches. This approach enables ‘virtual plant breeding’ where both potential germplasm and field site/environmental combinations can be evaluated computationally. Such virtual plant breeding would allow one to determine optimal genotypes at existing locations and to predict high yielding genotypes under future climate change scenarios.

Challenges to HTP

Despite ongoing advances in computational and imaging technologies, reliably extracting quantitative traits from time-series imagery of thousands of plants remains a challenge. A typical HTP experiment might involve imaging 900 *Arabidopsis* plants for three weeks in three growth chambers with different growth conditions in each chamber, resulting in a million or more images at the pot level. Image analysis is challenging for many reasons from variations in soil coloration to pots being moved during watering or sampling to effectively managing the huge number of images. Image analysis for phenotyping is a very active area of research and many solutions exist, but most of them require supervised algorithms (e.g. [41]) that do not easily scale to large datasets. HTP of root growth and architecture has been more successful perhaps because it is easier to standardize backgrounds and lighting conditions so they are more amenable to automated [42] or manual image analysis [43]. Although large commercial or federally funded projects have developed large-scale software pipelines for high throughput phenotyping, the community still lacks widely usable open-source tools for HTP of thousands of samples for multiple traits. Consequently there is a need for easy to use, widely used open source tools to identify, map, and predict genetically heritable traits.

High throughput trait capture pipeline

We are working to develop an open-source software pipeline (‘TraitCapture’) that will integrate the approaches described above to facilitate wider application of these techniques. Web-based visualization tools will allow real-time graphing of environment data with associated plant growth in time-lapse. Cloud-enabled GWAS on plant growth variation can be performed during an experiment allowing for real time results. This feedback allows a user to tune the phenotyping and image analysis to improve QTL detection. When QTL are identified, a user can resort plants based on alternative genotype classes to look for pleiotropic effects on growth, development, and physiology. Finally, published results should include links to the datasets and analysis protocols expanding on projects like the Phenomics Ontology Driven Data repository [9,44]. This will allow new and

previously cryptic traits to be identified. Importantly, standardized seed sets, growth protocols, phenotyping and analysis tools, will allow replication of experiments between different labs.

A brief list of experiments enabled by TraitCapture includes:

- Iterative QTL identification and tests of pleiotropy.
- Heritability of potential spectral indices using hyperspectral cameras.
- Spatial and temporal distribution of fluorescent pigments under environmental stress.
- Light and temperature interactions on transpiration using Infrared (IR) cameras.
- Genetic basis of photosynthetic activity and efficiency using chlorophyll fluorescence cameras.
- Integration of 2.5D and 3D quantification of plant growth with stereo imaging [45*].

Pipeline details

Here we present typical pilot experiments to set up and validate components of the pipeline that would subsequently be integrated.

Capture heritable traits

Plant traits are heritable phenotypes detected at unique developmental time points and under specific environments. Thus, several correlated phenotypes may better measure and describe the same pleiotropic plant trait. To optimize detection and characterization of these plant traits a design is needed to quantify and separate the genetic signal from the biological noise that exists among inbred lines. A simple experimental design with replicates of several inbred lines provides a novel solution to this challenge because signal to noise ratio thresholds can be optimized [7]. Real time phenotyping is then performed in standard or dynamic growth chamber conditions using imaging techniques described above. Initial image analysis functions that identify and count plant pixels can quantify relative growth and spectral properties. Whole plant 3D architecture is interpolated using stereoscopy [45*]. At a predetermined time point an environmental stress is applied to alter phenotypes and measure the emergence of heritable differences in response to the stress. The resulting data will contain information about the variation between accessions in the timing and nature of their responses to abiotic stress including the accumulation of photoprotective pigments, ability to maintain leaf water potential, and the ability to alter life strategy by early flowering to avoid stress. Heritability can be analyzed for each of the hundreds of specific phenotype measures at thousands of time points. Subsequently, clustering of time points could identify key developmental stages and the timing of transitions between them. A genetic correlation matrix

among raw phenotypes could be hierarchically clustered into composite traits that can be used for multi-trait mapping [35]. This will guide optimization to iteratively improve trait identification and characterization.

Genetic dissection and prediction using GWAS

The next step is to identify the causal genetic basis of complex traits by phenotyping large sequenced mapping populations (e.g. 1001genomes.org). A diverse subset of lines (300–600) should be selected to increase genetic variation, mapping resolution and to balance population structure [9,46*]. Specific genotype datasets could be preloaded into *TraitCapture* software as is currently done in EasyGWAS and GWAPP. Selecting among multiple phenotypes for multi-trait GWAS is then performed and empirical genome wide thresholds are set by permutations [24,35]. Once major QTL are identified they will be jointly fit with a full model to estimate major QTL and background effects as ‘best linear unbiased predictors’ (*blups*). The *blups* allow phenotypes to be predicted from genotypes which is important for fitting functional structural plant models.

Environmental effects and phenotypic prediction using functional structural plant models

Controlled conditions are ideal for mapping of complex traits, but are limited in their ability to translate genetic effects to the field. To overcome this, dynamic growth chamber conditions can be used to parameterize plant models with environment (radiation, temperature, water, etc.) and known genetic effects [7,39**]. For example, plants can be grown under simulated conditions or in locations spanning the native range limits of a species (e.g. temperate to subtropical and coastal to inland) and could include cyclic drought stress [47]. Specialized phenomics equipment or field level irrigation and remote sensing (e.g. Trayscan or Scanalyzer) can record light, temperature, humidity and soil moisture which are then input values to FSPMs. The models can then be parameterized to allow prediction of phenotypic outcomes for other sets of climate values [48*]. Joint modelling across multiple growing conditions allow fits of the environmental parameter estimates and accuracy can be estimated by cross validation. Lastly, incorporating genetic variation in FSPMs [39**] will allow prediction of phenotypes from genotypes in a range of environments. To improve predictions, deviations between model results and observations can be used as a residual phenotype in GWAS to identify new components and further improve the model [3].

Conclusion

Independently, Granier and Vile [49] in this issue argue for many of the same computational advances as we do here. Multiple skill sets are needed to integrate advanced

imaging equipment, feature detection from image data, genomic analysis of complex traits (GWAS) and FSPMs. Such a pipeline is here described as *TraitCapture* (Figure 1). The data generated by this work will address the gap between controlled conditions and the field by incorporating genetic and environmental effects into functional structural plant models. The biological innovation comes from associating multiple phenotypes as a single trait, or trait locus, gives mechanistic insight into the biological function of the underlying gene and regulatory pathway. Furthermore, a *TraitCapture* system would be open source and incorporate a modular, scalable design to be used by phenomics facilities, smaller labs, and field sites with remote sensing.

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