REVIEW

Plant Phenomics, From Sensors to Knowledge

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Major improvements in crop yield are needed to keep pace with population growth and climate change. While plant breeding efforts have greatly benefited from advances in genomics, profiling the crop phenome (i.e., the structure and function of plants) associated with allelic variants and environments remains a major technical bottleneck. Here, we review the conceptual and technical challenges facing plant phenomics. We first discuss how, given plants' high levels of morphological plasticity, crop phenomics presents distinct challenges compared with studies in animals. Next, we present strategies for multi-scale phenomics, and describe how major improvements in imaging, sensor technologies and data analysis are now making high-throughput root, shoot, whole-plant and canopy phenomic studies possible. We then suggest that research in this area is entering a new stage of development, in which phenomic pipelines can help researchers transform large numbers of images and sensor data into knowledge, necessitating novel methods of data handling and modelling. Collectively, these innovations are helping drive the selection of the next generation of crops more sustainable and resilient to climate change, and whose benefits promise to scale from physiology to breeding and to deliver real world impact for ongoing global food security efforts.

Introduction

Genetic improvement of crop resilience to abiotic stresses and new pests arising from climate change is imperative to ensure future food security [1,2]. The increasing use of gene editing [3,4] and continued exploitation of natural genetic variability [5,6] provide invaluable opportunities for generating novel alleles and selecting natural sources of genetic variation for crop improvement [2]. This requires analysis of hundreds of lines grown under diverse environmental scenarios. While genotyping has reached this throughput at a relatively low cost through advances in DNA marker assays and sequencing technologies [7], equivalent

33   improvements to generate high-throughput and valuable phenotypic information are urgently
34   needed [8]. This is the object of the field of **(au:ok?)**plant phenomics, which we define here
35   as the suite of tools and methods used for three major goals (**au:ok?)** — capturing
36   information on structure, function and performance of large numbers of plants, together with
37   their environment; analysing, organizing and storing the resulting datasets; and developing
38   models able to disentangle and simulate plant behaviour in a range of scenarios.

39   Over the past decade, plant phenomics has made impressive progress, developing novel
40   sensors and imaging techniques for a wide range of traits, organs and situations [8–10].
41   However, data handling and processing remain major challenges when translating sensor
42   information into knowledge. This Review focuses on that translation. We first discuss the
43   reasons why the challenges differ between plant and animal phenomics, which are largely
44   due to the strong interaction between environmental conditions and plant structure, function
45   and metabolism. We suggest the need for a multi-scale strategy that links physiological
46   mechanisms with plant performance across genotypes and environments from the molecular
47   to field scales, based on a series of novel approaches and techniques. We then discuss the
48   challenges of studying these processes in the naturally fluctuating conditions in the field
49   *versus* controlled environment conditions [11–14]. Finally, we suggest that phenomics is
50   entering a new stage of development, necessitating novel methods for data handling,
51   statistical approaches and modelling to connect and interpret the knowledge generated at
52   different scales.

53   One Genotype, Many Phenotypes in Plants

54   Plant phenomics does not consist of solely associating a genotype to one phenotype in a
55   given condition (e.g., in a controlled environment), but rather in characterizing the plasticity
56   of the plant phenome when exposed to a range of environmental conditions. In contrast to
57   most animals, which essentially retain the same structure regardless of their environment, a
58   plant can form very different architectures depending on environmental conditions. For
59   example, the same variety of *Arabidopsis thaliana* can exhibit a large 30-leaf plant or a small
60   8-leaf plant, after being exposed to either short or long day conditions, respectively (Figure
61   1A,B) [15]. Similarly, water deficit, nitrogen deprivation and low light have major effects on
62   the number and size of plant organs (Figure 1B,C). As a consequence, plant phenomics
63   research dedicates a large amount of effort to the study of variation in organism structure,
64   whereas animal phenomics essentially focuses on metabolism.

65   Plant water status, temperature, fluxes or growth rate vary within minutes. Indeed, unlike
66   mammals and birds, plants are not homoeostatic for temperature and water under rapidly

67 fluctuating environmental conditions. Plants transpire 50–200% of their own weight daily (*vs.*
68 1–2% for humans) [16], while their temperature follows their energy balance, resulting in
69 rapid variations [17]. During a summer day, a plant can be at 11°C with a favorable water
70 status in the early morning, but then experience 36°C and suffer severe water stress six
71 hours later (Figure 1E), triggering spectacular changes in plant morphology (Figure 1D–F).
72 Displacement transducers reveal that, under these conditions, plants exhibit rapid
73 fluctuations in growth [18]. Leaf elongation can occur at a rate of 4 mm per hour at dawn
74 *versus* 0 at 2pm [18]. Hence, although some degree of homeostasis exists at the cellular
75 level [19,20], this is not the case at the organism level. Many molecular events occur during
76 transitions between different environmental conditions [21], so phenomic analysis of non-
77 stable states is essential. The low degree of homeostasis in plants also results in large
78 functional consequences of the spatial variability of conditions a plant is exposed to [17]. For
79 example, root system architecture exhibits large spatial variation reflecting local adaptation
80 to highly heterogeneous soil water content [22,23]. Hence, the analysis of phenotypic
81 datasets needs consistent time course information on environmental conditions as sensed by
82 plants and organs, together with growth and physiology-related processes.

83 Because there is no central 'orchestrator' organ **(au:ok?)** in plants [24], the control of most
84 functions relies on feedback loops involving different organs that exchange information
85 through, for example, hormonal or hydraulic messages [25–27]. Such exchanges of
86 information operate at short-term scales at the cell or organ levels, and translate into long-
87 term plant or canopy behaviours through whole-plant mechanisms that are highly non-linear.
88 Hence, plant phenomics requires analyses at spatial scales ranging from single cell to
89 canopy, and temporal scales ranging from minutes (for metabolism and hydraulics) to
90 months (for yield) (Table1). Modelling is, therefore, an intrinsic part of plant phenomics,
91 aimed at connecting these scales. Indeed, while non-intuitive, feedback mechanisms are
92 predictable using mathematical models [28].

93

Analysing the Plant Phenome Across Spatial and Temporal Scales

95 Given the issues raised above, plant phenomics needs to capture and interpret a multi-
96 dimensional matrix of functional and architectural variables measured at different scales
97 (organ, plant, canopy), developmental stages and environmental scenarios. To address this
98 inherent complexity, researchers have developed three categories of phenotyping platforms
99 that have distinct objectives and employ different approaches and methods (Table 1).

100 ***High-Precision Platforms***

101 These platforms operate at the organ level, most often over short time scales (Table 1).
102 They aim at the identification of physiological mechanisms allowing plants to respond to
103 changes in environmental conditions, leading to the elucidation of their genetic control.

104 Profiling organ growth and architecture is used in high-precision platforms to uncover
105 adaptive mechanisms associated with environmental signals. For example, X-Ray micro
106 computed tomography (µCT; Figure 2A–D) of roots growing in soil macropores revealed the
107 importance of direct contact with soil water to determine where new lateral root branches
108 are positioned (Figure 2E) [23]. This translates into improved water and nutrient uptake
109 (Figure 2F). Similarly, time-lapse 3-D imaging of leaves combined with computational
110 modelling allows identification of where and when tissue expansion and cell division occur
111 [29]. In the case of leaves or sepals, this approach has revealed how new buds with few
112 cells result in reproducible shapes through feedback between patterns of oriented growth
113 and tissue deformation (Figure 3A) [30,31]. Analyzing leaf elongation rate of maize plants
114 with displacement transducers at high temporal resolution (i.e., minutes) in contrasting and
115 fluctuating conditions allowed identification of a novel mechanism of drought adaptation.
116 This mechanism involves regulatory interactions between circadian control of plant hydraulic
117 properties, daily time course of evaporative demand and hydraulic properties of the
118 rhizosphere (i.e., roots and the adjacent soil) [32].

119 The composition of plant tissues and the fluxes of substances (**au:ok?)** through organs can
120 be characterized in 'omics-based' platforms for thousands of plants [33]. For instance
121 Ionomics employs ICP-MS to perform elemental profiling [34]. This has allowed identification
122 of *Arabidopsis* mutants whose leaves have altered elemental composition. Many of these
123 mutants were later shown to be defective for an impermeable barrier in roots, termed the
124 Casparian strip, that regulates loading of elements into vascular tissues [35]. Metabolomic-
125 based methods profile the compounds involved in major metabolic pathways. This approach
126 has helped discover how different genotypes cope with environmental cues, uncovering the
127 dialogue between the circadian clock and changes in light availability that allow plants to
128 optimize the use of starch reserves [36]. Fluxomics (i.e., *in situ* imaging of the concentration
129 and fluxes of elements [37]) have provided important insights about where, when and how
130 water and nutrients are transferred in the plant [38]. For example, MRI-PET-based imaging
131 has enabled researchers to map carbon flow from leaves to individual roots [39]. Imaging-
132 based phenomic approaches can also be employed for cell-scale profiling studies. For
133 example, eGFP- and FRET-based sensors have proved highly effective for monitoring the

134 spatio-temporal dynamics of hormones and elements like zinc in *Arabidopsis* root cells [40–
135 42] (Figure 3D) and uncover new mechanistic insights into their homeostatic regulation.

136 The examples above highlight how high-precision platforms are effective for discovering new
137 physiological mechanisms, but also for upscaling them from organ to plant level.
138 Nevertheless, at their current stage of development, these platforms cannot analyse the
139 many thousands of plants needed to perform genetic studies across a range of environments
140 over a whole life-cycle timescale. Hence, they are not directly relevant for upscaling
141 mechanisms to predict important traits such as yield (Table 1).

142 **Field Multi-Environment Networks**
143 At the other extreme of plant phenomics, 'field multi-environment networks' (Table 1) are
144 series of field experiments distributed in a geographical region, aimed at uncovering the
145 genetics of yield stability. They probe the genetic control of plant performance in a range of
146 environmental scenarios, without pre-conceived reference to a particular mechanism.

147 The yield of a given genotype often differs between field sites, as does the ranking of
148 genotypes (genotype by environment interactions; GxE) [43,44]. Indeed, the relationship
149 between yield and environmental conditions results from trade-offs between mechanisms
150 that have distinct optima [45]. The relationship between genotype and phenotype therefore
151 needs to be analysed in clusters of microclimatic conditions referred to hereafter as
152 environmental scenarios [46,47]. For example, a network of 29 field experiments across
153 Europe was used to grow a maize diversity panel and identify genomic regions associated
154 with yield (quantitative trait loci, QTLs) under heat or water stresses [48]. Nearly all QTLs
155 had conditional effects, positive, negative or null, depending on environmental scenarios. For
156 instance, an allele at one QTL that controls the biosynthesis of the stress hormone abscisic
157 acid (ABA) was favourable in drought but detrimental in well-watered situations. Hence, a
158 large number (typically 20–40) of experiments needs to be conducted under diverse
159 environmental conditions to explore such allelic effects. Genomic selection (GS) extends the
160 former approach to establish predictions of the best combinations of alleles for yield [49]. GS
161 requires phenotyping of hundred/thousands of genotypes (the 'training population'), in some
162 cases, with the effects of environmental conditions [50]. The best combinations of alleles are
163 then used to select, *in silico*, tens of thousands of plants, thereby avoiding direct
164 phenotyping of these plants [50].

165 **Whole-Plant, Multi-Environment Platforms**

166 Given the complex interactions between QTL and environment and between QTLs [51], the
167 interpretation of results generated by networks of field experiments is most often
168 challenging, making it difficult to relate gene alleles with physiological mechanisms. To
169 achieve this goal, a third category of plant phenomic platforms, 'whole-plant, multi-
170 environment platforms', has been developed. These platforms are highly instrumented
171 greenhouses or fields allowing one to follow and dissect variables such as the growth or
172 transpiration of thousands of plants or small canopies, thereby allowing their genetic analysis
173 (Table 1).

174 Highly automated platforms in greenhouses enable researchers to perform 4-D
175 characterisation of the architecture of shoot, root or canopy systems of hundreds of
176 genotypes (Figure 3B,E; Figure 4A). They allow genetic analyses of traits such as shoot
177 topology, angles, branching and growth rate as a function of environmental conditions [52–
178 56]. More elaborate traits such as the utilisation efficiency of water, light or nutrients can be
179 calculated from these data using functional/structural plant models (Figure 2F; Figure 4J)
180 [57–59]. This is illustrated in Figure 4, in which 4-D imaging of whole plants and the
181 mapping of incident light in a greenhouse makes it possible to disentangle the biomass
182 accumulation of 1000s of plants into well-defined processes, such as the amount of light
183 intercepted by each plant (a function of leaf area and geometry) and the photosynthetic
184 ability of each plant [58]. Crop models can then be used to connect the genetic variability of
185 these processes to yield [60].

186 High-throughput field phenotyping has progressed rapidly in the last five years, based on the
187 use of multi spectral 4-D analyses with sensors mounted on mobile systems such as gantries
188 [61,62], ground vehicles or drones [63,64] (Figure 3C,F). They offer the possibility of
189 estimating the genetic variability of yield, biomass accumulation and underlying processes in
190 a variety of environmental scenarios. For example, canopy temperature provides a proxy for
191 genetic differences in transpiration, which is often due to variation in root system
192 architecture [63,64] (Figure 2F).

193

194 ***Cross-Scale Meta Analyses***
195 Currently, joint analyses of field experiments have been performed across years and sites
196 [43,65]. While cross-scale approaches are also beginning to appear [66], they need to be
197 developed further.

198 No single plant phenomic platform can analyse every scale, throughput or environment. For
199 example, it would be misleading to measure yield in greenhouse experiments, as the amount
200 and spectrum of light available to plants in a greenhouse and the distribution of roots in the
201 soil in pots would make any attempt irrelevant [11]. Reciprocally, phenotyping of thousands
202 of varieties in tens of field experiments is not compatible with costly and labour-intensive
203 methods. A combination of approaches is therefore necessary, which we term 'cross scale
204 meta-analyses'. For instance, the plasticity of yield can be analysed in 'field multi-
205 environment networks'. The underlying genetic variability of trait adaptation can then be
206 analysed in 'whole-plant, multi environment' platforms for the same panels of genotypes,
207 thereby associating QTLs affecting yield in specific environments to allelic variations of traits.
208 The resulting alleles can be tested for their effects on mechanisms of plant adaptation in
209 'high precision' platforms [67]. Such meta analyses are particularly vital in the case of root
210 studies, in which the root architecture or growth can only be analysed in 'high precision' or
211 'whole plant multi environment platforms', whereas only consequences can be observed in
212 the field, for instance through differences in canopy temperature (Figure 3D–F).

Employing Trans-Scale Analyses to Link Sensors with Knowledge

214 Cross-scale meta analyses, as defined above, require consistent methods for recovering data
215 across all platforms, time scales and levels of plant organization (Table 1; Figure 3). We
216 discuss below the major challenges researchers face to achieve this ambitious, yet essential,
217 next step in plant phenomic research.

Environmental Characterization, Sensor Networks

219 In our own experience, the analysis of datasets originating from different experiments and
220 groups faces a lack of consistent environmental information, which makes it impossible to
221 analyse and model the differences in plant behaviour between experiments. To that end,
222 several research consortia have proposed 'minimum environmental datasets' with the
223 necessary environmental variables and protocols for data analysis and modelling at any scale
224 [68,69]. Furthermore, a full environmental characterisation is now being facilitated by rapid
225 progress in sensor technology. Cost-effective sensors can now be placed in wireless
226 networks to characterize the micro-environment of many organs in a plant and many plants
227 in a canopy (Figure 5, arrows 1 and 2). This progressively applies to the characterization of
228 the soil environment by combination of soil sensors with modelling [70]. This local
229 information can be scaled up at whole-platform, field or regional levels using local, UAV or
230 satellite imaging, respectively. This allows efficient mapping of environmental variables,

231 thereby characterizing and capturing the effects of the spatial and temporal variation of
232 growth conditions sensed by individual plants or fields (Table 1).

233 ***Consistent Analysis of Images and Time Series****.*

234 Imaging systems have progressed exponentially in recent years, with a variety of non-
235 invasive and information-rich techniques (e.g., laser microscopy and rangefinders, X-ray
236 µCT, multi- and hyper-spectral cameras, isotope tracing methods). These techniques have
237 recently been reviewed in detail [8,71] and can be used at a variety of scales to support the
238 4-D functional analysis of root or shoot systems, and capture the structure and physiological
239 status of plants (Figure 3). However, imaging devices and protocols perform photography,
240 not phenotyping: traits need to be recovered from raw image data via image analysis (Figure
241 5, arrows 1 and 2). We discuss some of the key issues and solutions below.

242 Many software tools dedicated to image analysis of shoots [72], roots [73,74], canopies
243 [75], leaves [76], seeds [77] and fruit [78] have been developed in recent years. An
244 increasing number of these tools offer realistic and non-invasive 3-D reconstructions of plant
245 organs [79], based on the combination of multi-view stereo [80] and modelling [81,82], or
246 use laser-scanning systems [83,84], time-of-flight sensors [85,86], X-ray [74,87] or magnetic
247 resonance imaging [88]. Because plants are structurally complex and highly variable, a given
248 set of sensor or camera viewpoints at fixed positions cannot provide all the data needed to
249 reconstruct a complete 3-D model of a plant or a canopy. Partial descriptions recovered from
250 an initial set of camera views can be used, by solving a next-best-view problem, to guide a
251 robot to acquire the data needed to complete the model. Indeed, robot-assisted imaging
252 allows a loop to be established between image acquisition, analysis and *de novo* positioning
253 of sensors at the most insightful places in plants [61,83,89]. This opens the way for a
254 dialogue between models, sensors and imaging, enabling high-throughput, high-performance
255 phenotyping of plants or canopies.

256 Interpretation of sensor or camera outputs requires the millions of raw data points to be
257 organized into environmental or phenotypic time courses. This first requires the identification
258 of dubious points due to sensor malfunction or computational errors, inevitable when
259 thousands of sensors are involved, or when thousands of images are automatically
260 processed. Such data cleaning can now be performed based on statistical or machine-
261 learning methods for the large datasets originating from high-throughput platforms [90].

262 ***Data Analysis and Reproducibility Tests***

263 Making reproducible measurements of the same plants or accessions over time and across

264 platforms requires standardized protocols, including camera calibration, careful selection of

265 number and position of viewpoints and the time of day at which images are acquired. This

266 was done with success in a multi-laboratory study using *Arabidopsis thaliana* accessions

267 grown in controlled chambers [91], but requires further attention. A phenotyping platform

268 might give different assessments of the same genotype at two different sites, either because

269 of environmental changes or as the result of variations in the phenotyping process. Image

270 analysis methods in particular need to be both understood [92] and evaluated by comparing

271 their results with pre-obtained ground truth data [93], allowing identification of the limitation

272 of each method [94].

273 The wealth of methods used in phenomics (Figures 3–4) raises the question of how to jointly

274 analyse image and sensor outputs (Figure 5, arrows 3 and 4). Mixed model approaches have

275 progressed rapidly, allowing genetic analysis of datasets involving different sources of

276 information [95,96]. Novel developments allow identification of genotypic means of any

277 variable, from omics to yield, which are isolated from the noise created by the spatial

278 variability in field or platform experiments (Figures 3C,F; Figure 4E), the effect of

279 experimental co-variables (e.g., site, or persons who performed experiments) and

280 environmental variables [97]. These 'best linear unbiased estimates' (BLUEs) are then

281 analysed individually or in multi-trait analyses [98].

282 ***Model-Assisted Phenotyping: Connecting Scales***

283 Models naturally partner with phenotyping (Figure 5, arrow 7). For example, dynamic models

284 offer the possibility of scaling up the effects of a short-term mechanism at the organ scale,

285 identified in 'high-precision platforms', to biomass accumulation after several time steps in

286 'whole-plant, multi environment platforms', or to yield in field networks. Dynamic models are

287 based on the discretization of a process into time steps (e.g., minutes or days). Calculations

288 are iterative, with short-term effects taken into account at each time step (e.g., the effect of

289 light on photosynthesis, with different effects between genotypes), and long-term effects

290 emerging from feedback (e.g., the uptake of water or nutrients by the plant at a given time

291 step reduces their availability for the next time step) [99]. Models have been used in plant

292 phenomics in two ways [60].

293 Firstly, the dissection of a phenotype observed on a given day into the most likely set of

294 mechanisms (model inference; Figure 5, arrows 5,7). For example, the biomass on a given

295 day can be dissected into the amount of light received by the plant, multiplied by the

296 proportion of light intercepted by plants every day, multiplied by the efficiency with which

297 intercepted light is converted into biomass (Figure 4). Similarly, leaf area can be analysed as
298 the result of time courses of leaf growth over time, resulting from environmental conditions
299 and intrinsic traits of the considered genotype [100].

300 Secondly, the prediction of a given phenotype from environmental conditions and
301 hypothetical mechanisms observed in high-precision or whole-plant platforms' (Figure 5,
302 arrow 7). Model prediction operates in the opposite direction compared with dissection, and
303 serves as a test for the proposed mechanisms based on their ability to account for an
304 observed phenotype. The set of mechanisms taken into account are written as equations
305 which result in a phenotype after several time-steps [101].

306 Hence, modelling is an essential tool for phenomics because it helps to develop hypotheses
307 allowing multi-scale interpretations of results obtained in the three types of phenotyping
308 infrastructures presented in Table 1. Reciprocally, multi-scale phenomics represents a major
309 challenge for modelling. Indeed, phenomic technology allows multiple traits that contribute
310 to yield to be measured at high temporal resolution, providing a rich data set against which
311 models can be tested [101]. This avoids compensation of errors associated with each trait
312 underlying yield, a common feature of many current crop models that are parametrized
313 based on yield only [102].

314 ***Tracing and Storing All Steps from Data to Knowledge in Information Systems****.*

315 Phenomic experiments are not directly reproducible because of the variability of
316 environmental conditions. It is essential that any scientist, including those in 30 years, can
317 re-use phenotypic data and reproduce the data-flows presented above to perform meta-
318 analyses of the effects of alleles or mechanisms in a range of environmental conditions. This
319 has led to the definition of new norms named FAIR (findable, accessible, interoperable and
320 reusable) [103], primarily for tracing data, but also protocols, methods and workflows. They
321 involve information systems capable of managing thousands of data points and images
322 captured during an experiment, together with the necessary metadata, parameters and
323 methods of data analysis (Figure 5). Such information systems serve three distinct purposes
324 with different requirements [104–107].

325 The first purpose is for real-time management of the dataflow to optimise data quality. Real-
326 time access to images, environmental conditions and metadata is required when managing
327 the quality of an experiment, in particular for testing (typically every day) the validity of
328 outputs. This may seem trivial in small-scale experiments but it is not when thousands of
329 plants and hundreds of sensors are involved. Protocols [108,109] and management tools

330 [90] have been developed to visualize large volumes of temporal data in real-time, thereby
331 allowing one to detect potentially incorrect sensors and to act accordingly.

332 Secondly, these information systems help organize datasets in such a way that they can be
333 re-analysed by different groups. Data identification and annotation involves organizing
334 outputs in such a way that a scientist not involved in the original experiments can trace the
335 history of plants, re-analyse images with new methods of his/her own and *a posteriori*
336 check the calibration of each sensor in case of inconsistencies, possibly years after that the
337 experiment has been performed.

338

339 This requires protocols describing content and format of phenotypic information [110], and a
340 formalised description of all involved objects (i.e., plants, organs, sensors, phenotyping
341 facilities) using ontologies [111,112]. Such ontologies may seem un-necessary in simple
342 experiments where unique correspondences exist between, for example, each plant and its
343 position in a greenhouse. They become indispensable, however, when plants are
344 transferred from one platform to another during an experiment for better multi-scale
345 characterization. In the same way, sensors are replaced, so calibrations of devices located
346 at a given position change with time. Keeping track of these changes requires open and
347 extensible database schemas based on ontologies and semantics [111]. This also requires
348 keeping track of all operations, including parameters, used in analyses that produce an
349 elaborate result from raw data. Such scientific workflows are being developed [110],
350 thereby allowing any user to perform the same analysis and obtain the same results as
351 those published.

352

353 Finally, these systems help organise data to facilitate genetic analyses. Correspondence
354 between phenotype and genotype requires connection of matrices of genotypic data,
355 consisting of millions of marker data items or genomic sequences, with associated
356 phenotypic data that synthesize time courses or spatial variation into single figures
357 supporting the genetic analyses [113]. Because of the complexity of the information
358 systems reviewed above, and of the need for high calculation power, this is performed in
359 dedicated information systems that are physically distinct from those managing dataflow
360 and object identification. Hence, maintaining consistency of information across multiple
361 information systems will remain a major issue.

362 **The 'Big-Data' Challenge of Plant Phenomics**

363 Big data approaches can enhance phenotyping pipelines. Image analysis methods have
364 typically employed fixed sequences of image processing and measurement processes,
365 crafted by their designers to suit specific procedures. As a result, moving a given tool to a
366 slightly different problem or environment often requires a near-complete rewrite of the
367 software. Recently, deep machine-learning methods, and particularly convolutional neural
368 networks (CNNs) have produced impressive results and been widely adopted in the computer
369 vision community [114,115]. CNNs offer the potential to provide generic solutions to plant
370 image analysis problems [116] and, rather than requiring tuning to their environment,
371 benefit most from access to training data spanning multiple environments. This brings its
372 own challenges — maximum benefit can only be gained from deep-learned tools if large-
373 scale datasets (input images and required outputs) capturing shared problems are made
374 available.

375 In addition, hundreds of experiments with thousands of accessions are carried out each year.
376 The formalized meta-analysis of phenotypic data, allowed by the pipelines reviewed above, is
377 critical to the pathway from sensors to knowledge, and would be a huge source of
378 information if data were open, with all necessary meta-data and environmental conditions
379 included [117]. Indeed, the discussion above suggests that the combination of datasets
380 collected by distinct groups from different phenotyping platforms and fields could result in
381 unprecedented information that may build up year after year. Recent papers present 'proofs
382 of concept' of the meta-analysis of large datasets combining environmental and phenotypic
383 data [118–120], and discuss their role in multi-environment quantitative genetics [121].

384 Finally, combining large-scale environmental characterization with data collected by farmers
385 and advisors in the context of precision agriculture. The sensor networks that are appearing
386 in farmer's fields, multi-layer maps of climate and soil characteristics and progress in remote
387 sensing may soon provide the environmental data necessary to interpret the diversity of yield
388 corresponding to each variety in each field. If large-scale collections of yield and
389 environmental conditions in farmer's fields were organized, association genetics at the level
390 of countries or continents would become possible. This type of approach is already
391 operational in big-data analyses of, for example, human social media behaviour, and its
392 adoption in phenomics is of interest to a range of stakeholders.

Concluding Remarks

394 Plant phenomics research faces a conceptual challenge. To date, researchers have focused
395 on employing and/or developing novel sensors and imaging techniques [8–10]. However,

methodological advances in terms of data acquisition, handling and processing are becoming increasingly important. Indeed, the challenges of translating sensor information into knowledge have been grossly underestimated during the first years of plant phenomics research **(au:ok?).** Facing this challenge involves taking into account the intimate interaction between environmental conditions and plant structure, functions and metabolism, which require environmental characterization to be part of all steps of phenotyping, from data collection to meta-analyses. It also requires the use of both dynamic and statistical models allowing multi-scale analyses across experiments and platforms, which are essential to deal with the plant peculiarities reviewed at the beginning of this paper. Finally, the most recent advances in information technology must be employed to face the big-data challenge associated with multi-image processing, of meta-analysis of heterogeneous data and of the deployment of phenomics beyond the strict world of research. For obvious budget issues, it will not be possible to monitor all temporal and organization scales in every environment, but we believe that the rapid progress in modelling and information systems will allow identification of adequate cocktails of equipment, methods and meta-analyses allowing optimization of resources.

Hence, we propose that phenomics has reached a stage at which the limiting step is the design of methods and approaches allowing one to take into account different temporal and spatial scales and perform meta-analyses for addressing the challenges of plant adaptation to changing environments and underpin secure food security efforts.

431 Figure 1. Illustrations of phenotypic plasticity.

432 *Arabidopsis* plants under low evaporative demand with short (A) or long (B) day, or under
433 high evaporative demand(C) [15]. Note the differences in leaf number and leaf size. (D,E)
434 Maize plants in the morning and early afternoon and time courses of leaf temperature (T,
435 from 11 to 36°C) and leaf water potential (, MPa) during the day. A leaf water potential of
436 0 MPa means free water, whereas -1.5 MPa is close to lethal values in many species. In the
437 lower panel of E, symbols are measurements, lines are an interpolation using a model. In
438 (F), the change in canopy aspect is due to leaf rolling, a symptom of water stress. Panels
439 (D), (F) kindly provided by C. Fournier, INRA LEPSE Montpellier France.

440 Figure 2. Plant root phenotyping pipeline using X-ray micro computed tomography (µCT).

441 (A) µCT scanning system to non-invasively image columns of soil-grown plants (ranging in
442 resolution from 0.5µm–150µm). (B) Example 2-D cross-sectional image generated with µCT
443 scanner showing root material (in red) and the heterogeneous structure of soil (soil and
444 water in grey, air spaces in black). (C) Image analysis software [74] can be used to recover
445 root system of maize from the µCT volume data after segmenting roots from thousands of 2-
446 D image slices, (D) and quantify root system traits, (E) to discover new root responses to
447 environmental signal, like how soil water distribution patterns the positioning of lateral root
448 branches [23], and (F) parameterise models to simulate growth and foraging for natural
449 resources by root systems.

450 Figure 3. Novel imaging techniques at organ scale with high-precision (HP) platforms, at
451 plant scale with whole-plant multi environment platforms and at canopy scale.

452 (A) Heat map denoting areal rates of leaf growth using time-lapse imaging and computer
453 modelling (red to green, rapid to slow growth) [30]. (B) 3-D representation of a maize plant
454 from multiple images, at a throughput of 1000s plants/day. Colors indicate the amount of
455 light received by each pixel of plant. (C) Multi-spectral (NDVI) image of a canopy;
456 increasingly red colors represent increasing leaf area per unit m^2 of soil. (D) Image of an
457 auxin biosensor in the *Arabidopsis* primary root obtained by confocal imaging [122]. (E)
458 Whole-plant root system imaged in a rhizotron at throughput of 1000s plants/day. Inset,
459 zoom on root nodules [53]. (F) Image of a canopy in the thermal infrared; increasingly red
460 colors indicate lower transpiration rate, often linked to an unfavorable root system.
461 Horizontal regions with distinct colors: (i) non-irrigated plot, (ii) irrigated plot. Note in (i) the
462 superposition of spatial patterns with specific effects of genotypes in different plots. Panel B

463   kindly provided by C. Fournier, INRA LEPSE Montpellier France. Panels (C) and (F) kindly

464   provided by F. Baret, INRA CAPTE Avignon France.

465   Figure 4. Light interception, photosynthesis and radiation use efficiency, from images to

466   function. [58]

467   (A) Phenotyping platform (PhenoArch) where 1680 plants can be grown in controlled

468   conditions of soil water status and temperature, imaged and assessed for transpiration rate.

469   Sensors measure light, relative humidity and air and leaf temperature and transpiration. (B)

470   Twelve images per plant are captured every day allowing 3-D reconstruction. (C) Time

471   courses of leaf area and biovolume are calculated in real time. (D) Spatial distribution of

472   incident light. Images are captured every m^2 in the greenhouse, oriented to the vertical.

473   Blue, sky; black, obstacles (lamps, beams, etc.). The path of sunbeams is modelled every

474   day of the year (yellow line). This allows calculation of direct and diffuse light in every

475   position of the greenhouse. (F) Virtual digital plants are placed at their positions in a virtual

476   greenhouse. (G) This allows calculation of light interception by competing plants, in the

477   whole greenhouse. (H) The above steps allow dissection of biomass accumulation into

478   incident light on day i (*PPFD*$_i$), the proportion of light intercepted by plants (   ) and radiation

479   use efficiency (*RUE*$_i$, ratio of biomass production to intercepted light). (i) RUE is presented

480   for three plants in (F), pink, green and black. Bars near the x and y axes represent the

481   amounts of cumulated biomass and intercepted light, the slope of regression lines is RUE. (J)

482   RUE closely correlates with photosynthesis rate in a series of genotypes denoted by different

483   colors. Note that it would be impossible to directly measure gas exchanges for 1680 plants.

484   Figure 5. Flow chart of operations during phenotyping; roles of information systems and

485   modelling.

486   The left panel represents steps from image/sensor to knowledge; the right panel represents

487   the rationale for information systems at each step (green: tools). Red text represents

488   questions at each step. Dark blue arrows and text: modelling tools. Purple arrows:

489   connection between steps. (1) Transforming raw data into time courses for environmental

490   data, fluxes, growth rates etc. (2) Image analysis to transform a series of images into a

491   phenotype. (3) and (4) Data analysis with statistical and modelling tools, reproducibility. (5)

492   Extraction of mechanisms or composite variables encapsulating the genotype x environment

493   interaction, genetic analysis (6) association of yields to environmental scenarios, genetic

494   analysis. (7) Prediction and inference of mechanisms vs scenario-dependent yields using

495   models. (8) Theory, test using meta-analysis and/or new experiments.

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In Brief

In this Review, Tardieu *et al.* discuss the techniques, challenges, and potential of the field of plant phenomics (au:ok?)

Box 1

Glossary of Terms.

Convolutional neural nets (CNNs): CNNs are a variant of traditional artificial neural networks (ANNs), machine-learning methods inspired by biological neuronal systems. Traditional neural nets take a pre-determined set of measurements or features as their input and learn to perform various tasks; classification is by far the most common. CNNs extend scope of ANNs, learning both how to achieve the task and what measurements are needed. CNNs operate over raw sensor data, and learn how to extract the necessary features.

Genome-wide association studies (GWAS): this consists in associating markers in the genome with phenotypes (omic, traits or yield) through a statistical analysis. The values of alleles at one genome position are associated with a quantitative increase or decrease of phenotypic values.

Genotype x environment interaction (GxE) : the ranking of a set of genotypes differs between experiments for every trait or yield. GxE can be extracted from a statistical model, or can be analysed in detail using regressions of the considered trait with environmental variables. GxE is therefore analysed through the variability of slopes of these regressions.

Genomic selection (GS): represents a novel approach to marker-assisted breeding where, rather than attempting to identify individual loci significantly associated with a trait, GS uses all marker data as predictors of performance to deliver more accurate predictions.

Laser scanning systems: A 3-D reconstruction method in which a known pattern of light (a line, grid or array of dots) is projected onto the target object by a laser light source. A camera, often fitted with a filter making the laser pattern easier to detect, views the reflected pattern. 3-D is recovered from differences in the projected and viewed patterns of light.

Magnetic resonance imaging (MRI): MRI is a 3-D imaging modality in which the target sample is placed in a strong magnetic field. Under these conditions some atomic

nuclei, particularly hydrogen nuclei, absorb and emit radio frequency energy. Pulses of radio waves excite the hydrogen atoms, which emit signals that are detected by nearby antenna. The magnetic field allows these signals to be localised, mapping hydrogen atoms and so water.

Multi-view stereo: a 3-D reconstruction technique in which multiple, usually colour, images are taken of a target object from different viewpoints. Features of interest are identified by independent analysis of each, individual image. These features are then matched between images — features are matched if they are considered to depict the same point on the target object. The cameras' viewpoints are obtained by calibration and the 3-D location of each object feature is recovered by triangulation.

Phenotype: here, we mean the profiling of the structures and functions associated with allelic variants, at the scales of cells (omic phenotyping), organs (main plant functions), whole plant (controls of these functions) and canopy (plant performance).

Quantitative trait loci (QTL): QTLs are regions of the genome containing one or more genes, associated to variation with a quantitative trait (phenotype). QTLs are identified by showing a statistical association between polymorphic markers and the measured phenotype.

Unmanned airborne vehicle (UAV): Helicopters, drones or small planes able to fly over a field experiment, carrying a diversity of sensors. Their trajectory is programmed using GPS.

X-ray micro-computed tomography (µCT): X-ray CT produces a 3-D image in which each element (voxel) contains a value proportional to the density of the imaged object. The target object is placed on a rotating stage inside the imaging device. An emitter projects X-rays through the rotating sample to a detector on the other side of the device. The detector records the X-ray energy passing through the object. Density can be estimated from the difference in projected and detected X-ray energy.

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Typical Phenotyping Platforms	*High-precision platforms (cell, anatomy, organ)*	*Whole-plant, multi-environment platforms (field or controlled)*	*Field multi-environment networks*
Level of plant organization	Organ	Plant or canopy	Canopies in a range of environments
Typical methods	Omics, 4-D organ imaging, fluxes	4-D plant/canopy imaging, fluxes, sensors	Yield, sensor network, remote sensing
Typical mechanism	Hydraulics, metabolism, signalling	Light interception, Water transfer, whole-plant signaling	Trades off between processes
Ratio biology/other processes			
Relevance for yield prediction			
Methods for Trans-scale communication	Gene editing, plant simulation → ; ← GWAS, model-assisted dissection		

A Short day
Low ev. demand

B Long day
Low ev. demand

C Long day
High ev. demand

D 8 am

E

Leaf T °C

Ψ MPa

Time of day

F 2 pm

Current Biology
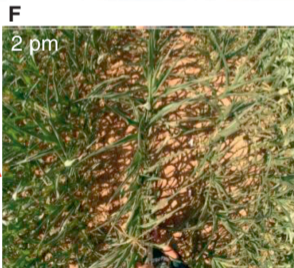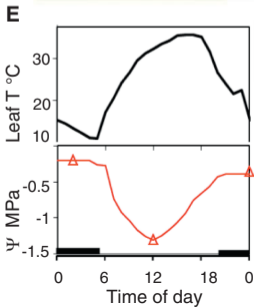
A X-ray CT phenotyping platform
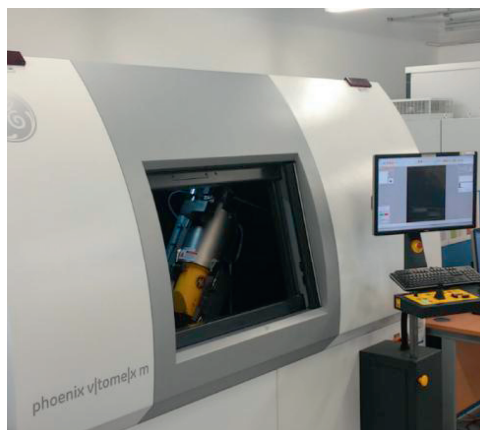
B CT cross-section data
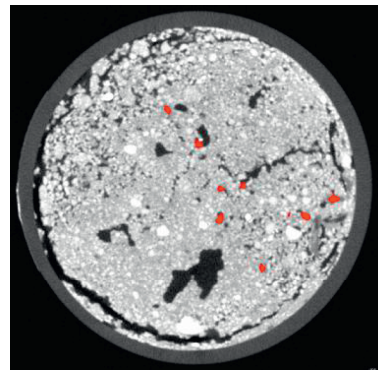
Roots in soil; 25μm resolution
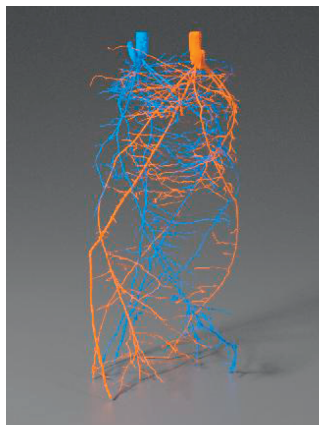
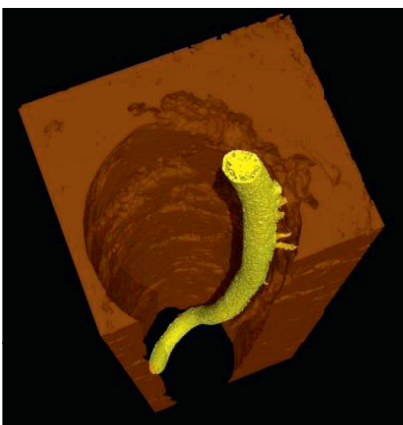**C** Root system recovery

Root system of maize

D Quantification of root traits
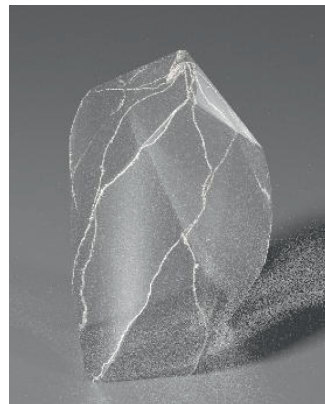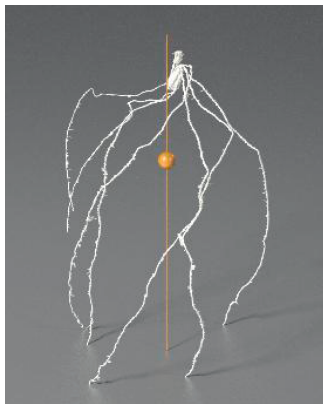
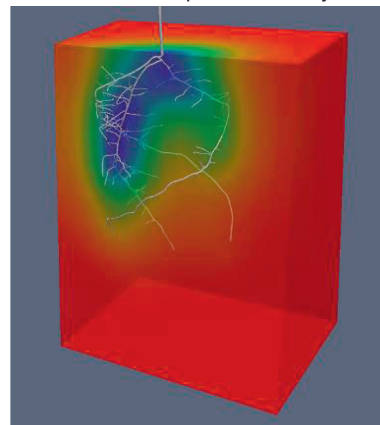Quantification of global and local root system traits for plant phenotyping

E Response to environmental signals

Soil–root and root–root interaction

F Simulate uptake efficiency

CT data embedded in a finite element mesh
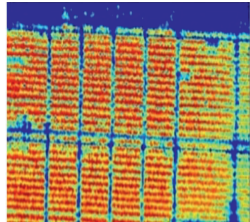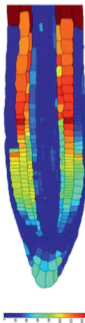
	HP organ	Whole plants	Canopy
Leaf, leaf area	A	B	C
Roots, transpiration	D	E	F

Current Biology

Phenotyping platform

A
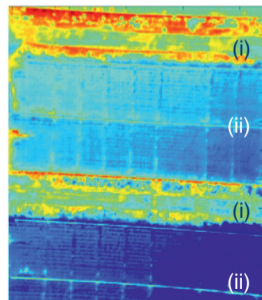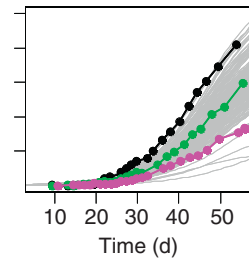
Data aquisition
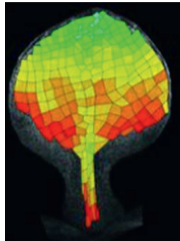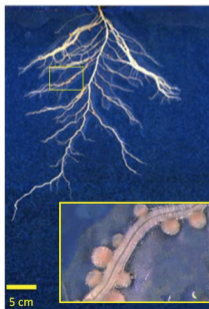
B
Environmental data (sensors)
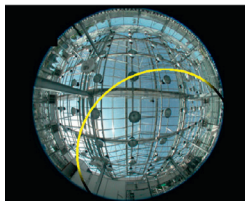Transpiration rates
12 images/plant

C
Leaf area/biovolume
(1000s plants)

Time (d)

Spatial distribution of incident light

3-D plants and light interception

D

E
Y Position
X Position
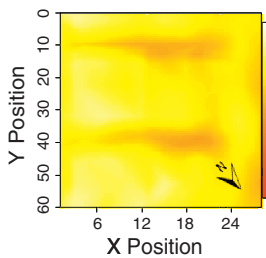
F

G

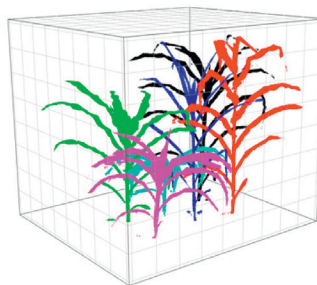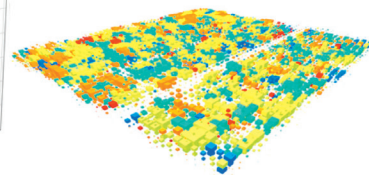Modelling sunbeam trajectories
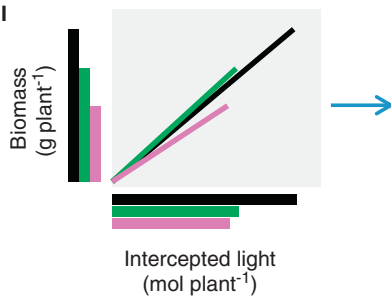
Functional-structural plant model,
distribution in the greenhouse

From radiation-use efficiency to photosynthesis

H
$$Biomass = \sum_{i=1}^{n} PPFD_i \times \varepsilon_i \times RUE_i$$

I
Biomass
(g plant^{-1})

Intercepted light
(mol plant^{-1})

J
RUE (g FW mol^{-1})

$r^2 = 0.54$
$P < 0.001$

Photosynthesis
(μmol m^{-2}s^{-1})

Current Biology

Steps   Information systems

Images, sensors
Which ones? Where?
What to measure? How often?

Trace sensors and plants
(position, timings)
Ontologies

① ②

Time courses:
Environment or
physiological rates
Variables? Time constants?
Correlations?

Visible phenotype
(interpreted image)
Which objects?
Correctly represented?

Trace methods
(calibrations,
parameters)
Workflows

③ ④

Multi-scale analysis of phenotypes
Reproducible?
Spatial/temporal variability?
Compatible with known mechanisms?
Can be ascribed to cues?

Trace rationale
and methods
Workflows

⑤ ⑥

Composite variables
or mechanisms.
Causal polymorphisms

or

Yield per environmental
scenarios.
Causal polymorphisms

Trace variables
Traits and methods
Trait ontologies

Model prediction ⑦
Model inference

Trace models
(equations,
parameters)
Workflows

Theory, novel hypotheses
New meta-analyses or experiments

⑧

Model-assisted dissection

Current Biology