

Phenotyping and beyond: modelling the relationships between traits

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Plant phenotyping technology has become more advanced with the capacity to measure many morphological and physiological traits on a given individual. With increasing automation, getting access to various traits on a high number of genotypes over time raises the need to develop systems for data storage and analyses, all congregating into plant phenotyping pipelines. In this review, we highlight several studies that illustrate the latest advances in plant multi-trait phenotyping and discuss future needs to ensure the best use of all these quantitative data. We assert that the next challenge is to disentangle how plant traits are embedded in networks of dependencies (and independencies) by modelling the relationships between them and how these are affected by genetics and environment.

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Introduction

With the rapid development of sequencing technologies over recent decades, whole genomes of many plant species are now available and the race towards the functional characterisation of thousands of genes has started [1,2]. Two big concerns often discussed in the literature rapidly arose: the need for automated high-throughput systems to record traits on large numbers of samples (numerous organelles, organs or individuals of large populations of genotypes), and the availability of sets of information about experimental protocols and growing conditions to ensure data reuse and meta-analyses [3,4].

Plant phenotyping, i.e. the process of recording quantitative and qualitative plant traits, is not a new research activity, but it has been the backbone of most studies in

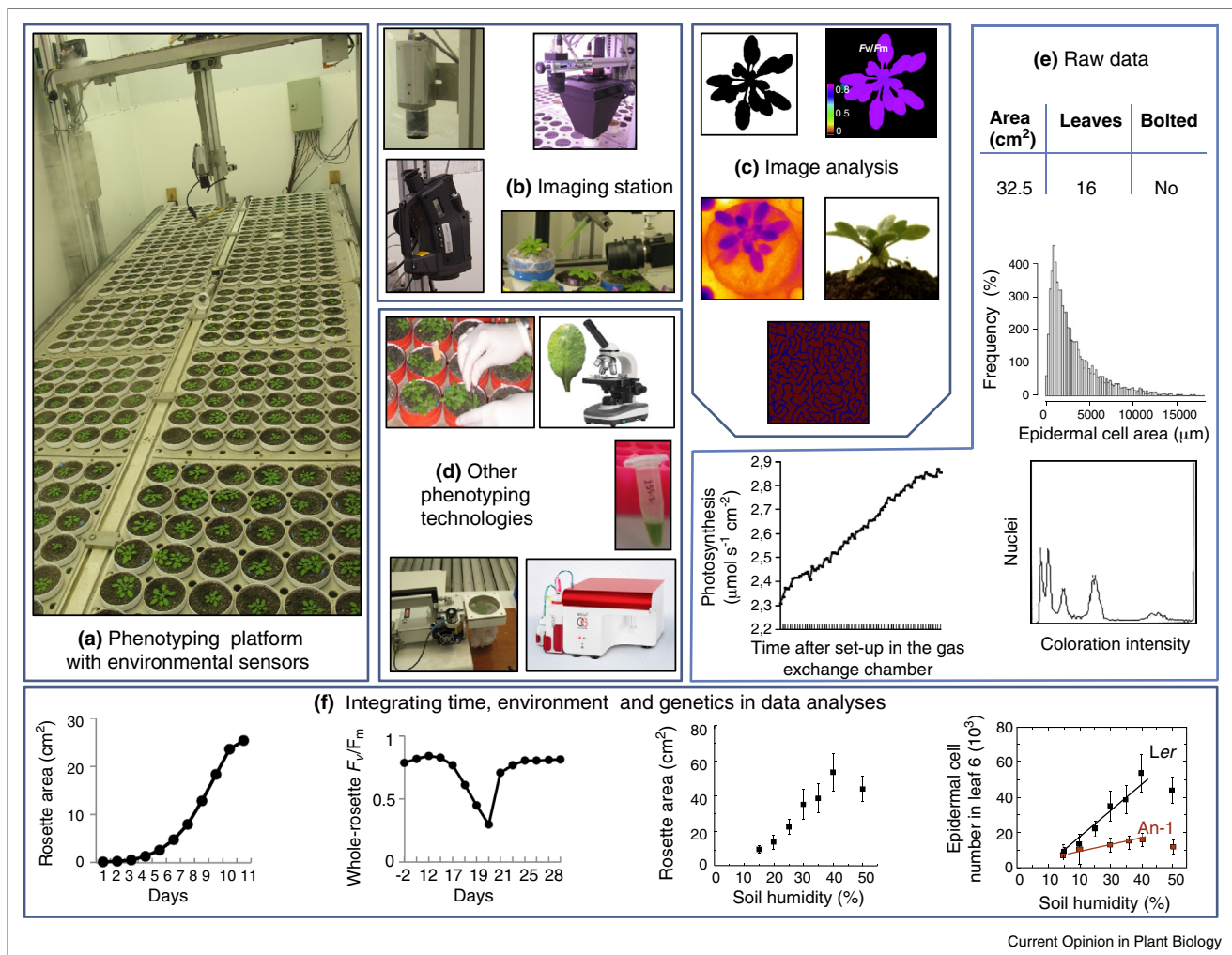
ecology, agronomy and ecophysiology to explore plant functional diversity, compare the performance of species/varieties or study plant responses to the environment. However, the word phenotype, and then phenotyping, has not been often used in functional ecology [5], mainly because average trait values were used to represent each species until now. However, the renewed interest in the role of intraspecific variability in the ecology of plant communities [6], as well as the unprecedented access to genomic data, helped to reincorporate this term in ecological studies. Even if there is nothing really new behind the definition of ‘phenotyping’, nor behind the use of terms such as ‘phenomics’; i.e. the full set of phenotypic features of an individual, their use (and abuse) need a careful inspection in order to avoid them boiling down to ‘high-throughput measurements’ because ‘high throughput measurements’ are instrumental means but are not a goal per se.

Here, we review some advances in plant phenotyping, highlighting that having an automaton with a camera for plant imaging is not a *sine qua non* condition for finding promising associations between a phenotype and its underlying genotype. In addition, measuring one trait at one date on a very large number of genotypes does not necessarily give insights into plant functioning or into the genetic control of this trait. As illustrated by a few recent studies, we show that taking into account environmental and temporal variation of the phenotype and considering the phenotype at different levels of integration, i.e. from subcellular, cellular, tissue, organ to whole-plant level, might enhance our understanding of genotype-phenotype relationships. However, when such datasets are properly acquired, their analyses require a conceptual and statistical corpus, that is not always in the plant biologist’s know-how.

Alleviating the bottleneck caused by the lack of high-throughput tools to measure traits associated with gene function: from phenotyping platforms to phenotyping pipelines of analyses

Plant phenotyping relies on skills and technologies that are used to characterise qualitative or quantitative traits regardless of the throughput of the analyses. To match the rapid increase in genetic resources, the development of plant phenotyping platforms has been initiated since the 2000s and they are now common tools either commercially available or developed by scientific groups (Figure 1a).

Figure 1



An example of multi-trait phenotype pipeline. *Arabidopsis thaliana* plants are grown in controlled environmental conditions with automatic watering, imaging and recording of micrometeorological conditions (a) [9]. The platform is equipped with an imaging station that includes different types of cameras as illustrated in (b) with RGB vertical and horizontal cameras, an infra-red camera and a fluorescence camera. After automatic image acquisition and storage, images are processed to extract useful traits as shown for whole rosette area, rosette fluorescence (F_v/F_m) and temperature (b,c). Other phenotypic traits are measured manually with more or less invasive technologies such as plant gas exchange, microscopic observations or cellular analyses by flow cytometry (d). Tissue microscopic observations also need image processing as shown for the measurements of epidermal cell area (c,e). Raw data are extracted and processed to include temporal variation of the trait (as shown for dynamic changes in growth and whole rosette F_v/F_m (f)), trait response to environmental conditions [as illustrated by the response curve of rosette area to soil water content (f)] or genetic variation of the phenotype [as illustrated by the response curves of epidermal cell number to soil water content for two *A. thaliana* accessions, Ler and An-1 (f)].

In most phenotyping platforms, plants or plant parts are automatically imaged by different types of cameras (Figure 1b) enabling the non-destructive measurements of many plant traits [7]. Depending on the systems, images can be captured at high speeds, thereby offering the possibility to acquire images of many plants over time and therefore allowing the consideration of dynamic aspects. Depending on the experimental facilities, plants do not move but are imaged by the moving imaging station set up on a robotic arm [8,9]; whereas in other facilities conveyor belts drive the plants below a motionless imaging

station [10,11,12,13]. Different orthogonal views of specific plant parts such as whole shoot or root systems are automatically acquired either by using cameras positioned around the plant or by rotation of the plant in front of a camera. The different orthogonal images are combined to extract sets of morphological traits including angles, lengths, widths, diameters and areas [14–16]. Fluorescence imaging allows measuring the photosystem II status *in planta* [8,17,18] whereas thermal infra-red imaging gives access to leaf surface temperature [19]. Hyperspectral imaging systems are also used to capture different plant

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