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# Origins and drivers of crop phenotyping

Roland Pieruschka and Ulrich Schurr, Institute for Bio- and Geosciences (IBG), IBG-2: Plant Sciences, Forschungszentrum Jülich, Germany

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## 1 Introduction

Understanding the phenotype of plants is essential in the context of food or biomass production from crops, for efficient use of resources such as water or nutrients or in understanding plant ecological performance. All these depend on the interaction between plant genetic makeup and the prevailing environment. Understanding multidimensional plant–environment interactions has a long history in the eco-physiological sciences. The subject gained new momentum when genomics technologies became available about three decades ago. An increasing number of plant genome projects were initiated to analyse the genetic makeup of plants. Within the last few decades, about 600 genome assemblies from different plant species have been made available in public repositories (Kersey, 2019). Crop species dominated initially but a wider range of plants, including non-domesticated species, have now been analysed. In parallel with these developments, there have been advances in technologies to modify plant genetics. Recent progress in genetic engineering –specifically CRISPR/CAS9 – provides '…enormous power in this genetic tool, which affects us all. It has not only revolutionised basic science but also resulted in innovative crops and will lead to ground-breaking new medical treatments', to quote Claes Gustafsson, chair of the Nobel Committee for Chemistry. (https://www.nobelprize.org/prizes/chemistry/2020/press-release/).

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However, genetic makeup provides only one element that determines the phenotype of a plant. Genes are the toolbox with which a plant can work when the plant is exposed to challenges – especially abiotic and biotic environment – in real life. Plant phenotyping is the process of quantitatively characterising the structural and functional properties of a phenotype within a dynamic environment. It is the next step beyond genotyping towards an integrated understanding of plant–environment interactions (Fig. 1). Based on a wealth of research, in the late 1990s plant phenotyping started to integrate genomics and eco-physiological perspectives into a more holistic approach. New methods for high-throughput phenotyping were based on technologies like computers, optical sensors and automation. It is worth remembering that computers only became generally accessible in the 1990s – a fact that we often forget given their ubiquity today. High-throughput genotyping revolutionised our understanding of the genetic makeup of plants. This development then increased the need for quantitative assessment of the phenotype as a basis for understanding plant–environment interactions and for breeding applications.

The challenges posed by the complexity of plant structures and functions and their environmental plasticity continue to drive research. This research requires dynamic assessment of individual plant organs, developmental stages, entire canopies or plant processes. These components are interconnected. A change in one has an impact on the others and, in turn, the whole plant and its interactions with the environment. Continuous measurements with non-invasive technology have provided the key to connecting phenotypic dynamics, molecular properties and environmental dynamics to create models to visualise and predict these complex interrelationships and transfer them into applications such as breeding.

Phenotypic data are pivotal to understanding quantitative traits which are under polygenic control. Quantitative description of a phenotype is extremely challenging. It ranges from subcellular, cellular, tissue and organ levels up to the level of the whole organism or even the arrangement of individual plants in a stand. These different levels must be analysed in the context of dynamic

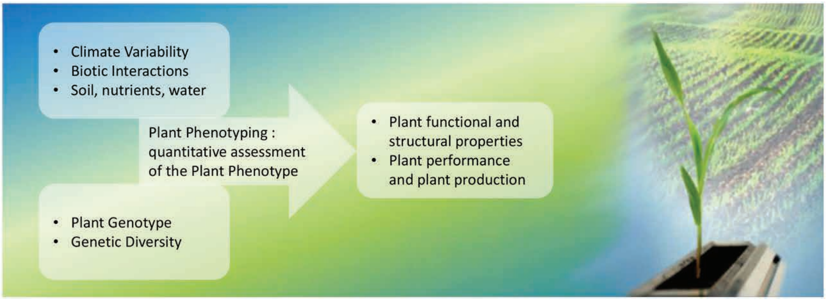

**Figure 1** Multidimensional system addressed by plant phenotyping.

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environmental conditions in space and time (Pieruschka and Poorter, 2012). Houle et al. (2010) described this relation using genotype–phenotype maps to determine the phenotypic state that organisms occupy within the overall space of possible phenotypes, taking into account phenotype response to variation in environmental conditions within a complex multidimensional system (Fig. 1). This level of analysis requires robust and accurate measurement technologies (technology development), integration of technologies in phenotyping infrastructures and applications (phenotyping infrastructures), use of phenotyping systems in interaction with plant material which has been properly characterised in its genetic setup (genotype analysis) and with analysis of its often dynamic (bio-)chemical composition (chemical phenotype). Only by combining all these dimensions in adequate temporal and spatial domains, can a mechanistic understanding of interactions of genetics, structural, physiological and environmental processes be made. Since this is the basis for crop improvement, a concerted effort is essential to further advance the quantitative understanding of crops in a dynamic environment. This is particularly important with multiple grand challenges related to feed and food for a growing population in times of climate change (FAO, 2017).

Selection based on phenotypic traits has been the basis for crop improvement for thousands of years and has been fundamental for breeding from the beginning of crop domestication until genetic tools became available. Wheat is an outstanding example where phenotypic selection based on traits such as large seeds, plants with low toxicity and reduced seed dispersal was essential for adaptation of plants to crop cultivation. The success of using early, non-quantitative phenotyping was vital to the shift from hunter-gatherer to agricultural societies, and it stimulated the development of cities and modern civilisations. The increased understanding of genetics, which became available during the Green Revolution, allowed genetic improvement towards much higher-yielding varieties through the introduction of dwarfing traits with huge increases in wheat yield (Vergauwen and De Smet, 2017). The development of various DNA/gene marker technologies shifted the emphasis of breeders from selection based on phenotypes to marker-assisted methods based on access to cheap sequencing methods (Collard and Mackill, 2008). Phenotypes were linked to DNA-markers which could then be used to assess crossing material without expressing the phenotype at each step of the selection process. This has been critical to the success of modern breeding. One study has shown that, on average and across all major arable crops cultivated in Europe, quantitative phenotyping contributes approximately 74% to overall productivity growth (Noleppa, 2016).

Plant phenotyping has been recognised as one of the major limitations to further advances in breeding and pre-breeding (Watt et al., 2020). Progress in phenotyping requires improved technology and access to state-of-the-art methods and facilities, as well as dissemination of novel technologies to phenotype an increasing diversity of traits under controlled and field conditions above and belowground. These must be combined with integrated data management techniques to allow reuse of data.

This chapter outlines how plant phenotyping has developed over recent decades, driven by factors such as advances in optical sensors, image analysis and automation as well as multidisciplinary cooperation in establishing facilities for high throughput plant phenotyping. The chapter describes successful uses of plant phenotyping and stresses the importance of collaboration in further development, particularly to address emerging potential bottlenecks such as management of data to enable interoperability.

## 2 Technological progress in plant phenotyping

The terms phenotype and genotype were first mentioned over a hundred years ago and quantitative plant phenotyping has been a central element of eco-physiological research ever since (Johannsen, 1903, 1911). Over the past two decades, however, there has been a dramatic increase in the accuracy and speed of phenotyping with new technologies in high-throughput based on huge volumes of genetic information from next-generation sequencing. Since then, plant phenotyping has made impressive progress, developing novel sensors and imaging techniques able to quantitatively measure a wide range of traits at many spatial scales and in many different temporal dimensions. Quantitative phenotyping to understand the interaction between plants and environmental conditions is now possible, using low and high-throughput phenotyping for quantitative screening of a high number of genotypes under well-defined conditions at cellular, organ, plant and canopy levels under a variety of environmental conditions.

This progress in phenotyping can be seen in the massive increase in the number of publications addressing plant phenotyping from around 2010 (Costa et al., 2019). This period coincides with the development of tools for quantitative assessment of plant traits that allowed the matching of phenotypic analysis with genetic information from DNA sequencing.

Non-invasive imaging sensors and computer vision technologies have significantly improved measurement of plant traits. These were based on the rapid increase in affordable and robust imaging systems in the 1990s following the development of digital imaging sensors (Blais, 2004). Non-invasive technology initially focused on recording time series at the level of single organs in single (or a few) plant(s). Schmundt et al. (1998) were able to demonstrate the temporal and localised character of growth in leaves of *Ricinus communis* and tobacco with growth restricted to the base of the leaf and to a few hours at the end of the night and the start of the day. The ability to obtain high-resolution time-lapse videos, paired with development of algorithms in image analysis, represented a substantial advance in understanding growth processes. The progress was possible by linking image analysis expertise with plant physiology. Similar examples include characterisation of growth of primary roots (Walter et al., 2002) and functional imaging of photosynthesis (Genty and Meyer, 1995).

Newly developed imaging systems and the increasing number of image analysis programs led to the next step in the evolution of phenotyping. These phenotyping approaches were integrated into automated systems allowing increasingly high throughput. Automated systems first addressed phenotyping of small plants such as *Arabidopsi*s to measure growth dynamics (Granier et al., 2006) or *Arabidopsi*s and tobacco seedlings to measure growth and photosynthetic properties (Jansen et al., 2009). These marked an important step towards measuring genetic variability. The importance of imaging approaches in plant phenotyping can be seen in the growth in publications using the terms plant phenotyping with different types of imaging over the last decade (Fig. 2). This analysis shows that functional imaging (spectral, hyperspectral, thermal) also grew over the same decade. Merging these different imaging modes (sensor fusion) may become an important tool in the future, enabling simultaneous monitoring of the dynamics of structural and functional properties by combining measurement of 3D plant structure with spectral measurements (Paulus, 2019). Increased use of imaging can be expected with the development of affordable, mobile technologies providing high-quality images (Mueller-Linow et al., 2019; Reynolds et al., 2019).

Many of the ongoing developments in plant phenotyping are driven by developments in non-invasive sensors providing information from the entire electromagnetic spectrum. A wealth of information can be obtained from data from reflected, transmitted or emitted radiation. The magnetic resonance

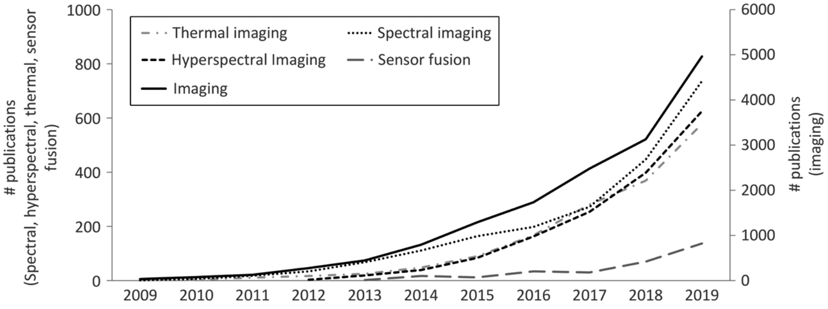

**Figure 2** Number of publications using imaging technology. Web of Science (Clarivate Analytics) was used for a simple evaluation of publications within the last 10 years with search terms: phenotyping x imaging, spectral imaging, hyperspectral imaging, thermal imaging and sensor fusion.

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properties of nuclei provide information for instance on *in situ* root properties (Fiorani et al., 2012). Two-dimensional or three-dimensional representations of plant features show structural properties that can be combined with functional imaging techniques in providing unique information on structural-functional or agronomic traits (Paulus, 2019). Advances in automation, robotics and computing capacity have led to advances in: i) combining experimental design with growth facilities to simulate relevant environments at a sufficient capacity to support large-scale phenotyping; ii) the integration of non-invasive technologies into standardised experimental protocols (key for best practice in phenotyping); and finally, iii) data analysis, management and storage capacities (Fiorani and Schurr, 2013).

Plant phenotyping will always require a wide range of technologies, expertise and knowledge about plant systems and the environments. In this context, the diversity of technologies and infrastructures mirrors the diversity of traits and crops. This is in strong contrast to the 'genomics world', where the unifying principle of nucleic acids provides a common focus for analysis. While analysing nucleic acids of crops in greenhouses and field conditions uses the same techniques, phenotyping in field or controlled environment conditions requires very different approaches. Therefore, plant phenotyping will always be a field of activity, which requires strong consideration of how to bring together the necessary infrastructure and expertise for the multitude of relevant traits. It is a very challenging task to understand the diversity of phenotypes in response to different environmental cues. This requires addressing a diversity of traits that change dynamically during the lifetime of a plant in a dynamic environment. To decipher this interaction, we need to interpret various structural and functional traits, spectral ranges, the development of various organs, etc. The number of outcomes (phenotypes) from the potential combinations of genotype, environment and phenotype is enormous. It is essential to identify the relevant traits, environmental scenarios and technologies that advance our understanding, improve our models and provide data that are reusable.

The approach needs to be complemented by the optimisation of the costs of plant phenotyping tools and facilities. Low-cost phenotyping will mostly be limited to a few common traits that can be measured with affordable, often manual tools. In contrast, high quality and high throughput analyses of functional and structural traits require higher initial investment costs for instance in sensors, vehicles and automation technologies, but may deliver more robust, higher quality and relevant results with lower operational costs over the long term (Reynolds et al., 2019). Complex phenotyping also requires investment in expertise and software. Image analysis instruments, e.g. need to be tailored to their experimental setting to address specific phenotyping problems which differ according to crop, environment and genotype. One software solution often cannot be transferred from one crop or treatment to another. This means that acquiring images is often easier (and less costly) than quantitative analysis of images, with the latter becoming a potential bottleneck (Choudhury et al., 2019; Minervini et al., 2015). The use of artificial intelligence in image analysis problems may help to address this challenge. Machine learning approaches have emerged as a tool to analyse and find patterns in large amounts of data in plant phenotyping (Singh et al., 2018). Machine learning techniques may play a prominent role in the future of image-based phenotyping in, e.g. detection of biotic and abiotic stress (Ubbens and Stavness, 2017). These approaches, however, require choices about target features to be extracted. They depend on the availability of high-quality reference data sets to provide the learning algorithm with the optimal description of the data and problem in question (Pound et al., 2017). Variability in methods may also create standardisation problems.

Despite substantial progress, plant phenotyping still faces challenges which are inherent in the complexity and diversity of plants and traits and the nearly countless environmental scenarios that need to be quantified. There is an increasing range of technologies available with the potential to address these challenges but it still require significant development in software solutions and data analysis.

While analysing gene sequences require essentially one basic approach across all plants or living organisms, with advances in one area potentially benefitting all others, the gap between phenotyping and genotyping may remain large. Pooling of infrastructures and expertise is essential for plant phenotyping to increase efficiency. This requires utilising synergies by pooling investment in new facilities, sharing specialised technology, software solutions and knowledge on physiology. This also includes the development of technological and scientific expertise in conjunction with best phenotyping practices to benefit knowledge and technology transfer (Fig. 3).

The development of common standards to enable interoperability will reduce costs and help close the gap between phenotype and genotype. Interoperability of data and model development will become integral elements in designing phenotyping experiments to address knowledge gaps. These considerations show the importance of the phenotyping community organising broad networks to integrate knowledge and facilities. The challenges of quantifying the diversity of relevant plant phenotypes cannot be addressed in a single research institution or country. Open collaborative approaches between plant phenotyping centres are key to address gaps in plant research and translation of this knowledge into applications.

## 3 Community integration in plant phenotyping

The first phenotyping centres started to emerge in the early 2000s. From the beginning, these centres needed to build on strong multidisciplinary expertise.

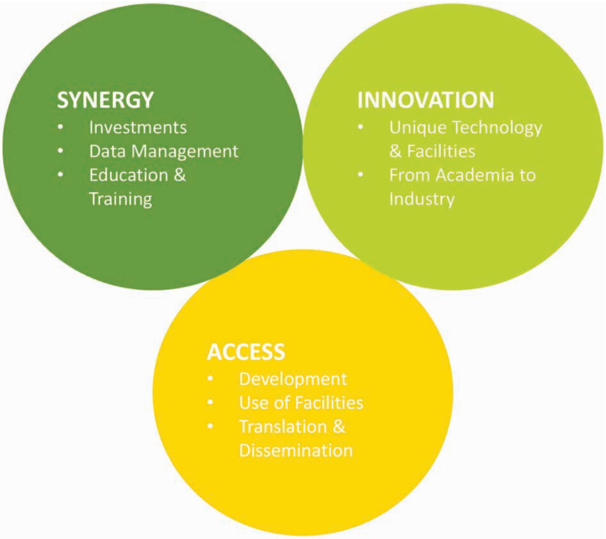

**Figure 3** Community integration to foster synergies, innovation and access (modified from EMPHASIS: (https://emphasis.plant-phenotyping.eu/).

These included integration of (novel) sensors, establishing facilities simulating relevant environmental conditions (often in contrast to constant conditions used in in many experimental facilities) and specialised platforms for deep and high-throughput phenotyping under controlled and field conditions. The resulting research had to link genetic, biochemical and phenotypic data. Challenges remain in the need to address different plants and a diversity of environmental conditions. It is particularly challenging to balance a high level of flexibility with harmonisation of experimental procedures and data management to allow reusability of data. This is another important role of centres with high phenotyping expertise. They often form important nuclei for knowledge and technology transfer. This task cannot be addressed by a single research group or organisations and requires community integration across different levels (Fig. 3). This integration has been achieved in several countries from the early 2000s with the establishment of national infrastructures to integrate the expertise of different institutions. These national infrastructures pool both technology and expertise to address the needs of users from both academia and industry. An important aspect is the support by funders and policymakers to optimise research investment, reduce duplication and enable sustainable operation of the phenotyping infrastructure within a country.

One of the first national infrastructures established in 2009 was the Australian Plant Phenomics Facility (APPF, https://www.plantphenomics.org.au/).

This combined The Plant Accelerator in Adelaide as the first automated high-throughput phenotyping system, the High Resolution Plant Phenomics Centre (HRPPC) at Commonwealth Scientific and Industrial Research Organisation (CSIRO, Australia) which combined expertise in plant science and engineering to develop and build phenotyping technologies and, finally, the Australian National University (ANU) with expertise in phenomics, bioinformatics, hardware and software development and data visualisation. The German Plant Phenotyping Network (DPPN, https://dppn.plant-phenotyping-network.de/index.php?index=6) started in 2012 with three complementary sites to combine infrastructure and methods, using a range of technology platforms to address different plant phenotyping approaches. PHENOME (France, https://www.phenome-emphasis.fr/phenome_eng/) was established in 2013 as a federated network of phenotyping platforms at five different sites in France. Since then, many countries have initiated building of a national plant phenotyping infrastructure to integrate national research. Table 1 lists national and regional plant phenotyping initiatives. The challenge is to integrate the activities across borders.

In Europe, in parallel with the establishment of national centres, discussions were initiated about developing cooperation between centres. The process of integration was facilitated by the EC-funded projects EPPN (2012-2015) and EPPN2020 (2017-2021), which developed best phenotyping practice and enabled excellence-driven access to phenotyping facilities under controlled environmental conditions (EC, 2016). These projects provided 200 opportunities for access to enable experiments, resulting in over 80 publications (https://eppn2020.plant-phenotyping.eu/EPPN_Publiations). Most users were from academic institutions addressing a wide range of scientific questions. Facilities providing access within EPPN2020 also have a strong interaction with industry. On average, about 30% of the experiments within the plant phenotyping facilities include industry partners – in most cases based on bilateral agreements (EPPN2020, personal communication). Since projects such as EPPN or EPPN2020 usually have a limited duration, and national infrastructure efforts are usually limited to a certain country or region, it is important to develop ways to allow long-term and sustainable development of a regional infrastructure. The European Strategy Forum for Research Infrastructures (ESFRI) is a Europe-wide instrument to improve scientific integration across Europe (and beyond), to strengthen its international outreach and enable long-term sustainable operation across borders (ESFRI, 2017). The integration of plant phenotyping within Europe has been developed within the framework of European Infrastructure for Multi-scale Plant Phenotyping and Simulation (EMPHASIS), added to the ESFRI Roadmap in 2016 and expected to become operational during 2022 or 2023 (ESFRI, 2016). The main objectives of EMPHASIS (see Fig. 4) are to:

- develop an infrastructure to coordinate and enable access to facilities and services across borders, make investments in new infrastructure more efficient;
- link data acquisition to a pan-European information system and modelling by developing best phenotyping practice; and
- develop, evaluate and disseminate knowledge and technology to support the commercial sector as well as provide new technological solutions both for phenotyping and related disciplines such as precision agriculture.

**Table 1** Plant phenotyping networks/Initiatives

| National networks/Initiatives: | |
|---|---|
| APPF: Australian Plant Phenotyping Facility | http://www.plantphenomics.org.au/ |
| APPN: Austrian Plant Phenotyping Network | http://www.appn.at/ |
| BePPN: Belgian Plant Phenotyping Network | - |
| CPPN: China Plant Phenotyping Network | - |
| CzPPN: Czech Plant Phenotyping Network | http://www.czppn.cz/ |
| DPPN: German Plant Phenotyping Network | http://www.dppn.de/ |
| NaPPI: Finland National Plant Phenotyping Infrastructure | http://blogs.helsinki.fi/nappi-blog/about/ |
| Phen-Italy: Italian Plant Phenotyping Network | http://www.phen-italy.it/ |
| PHENOME-EMPHASIS | https://www.phenome-emphasis.fr/ |
| Phenom-UK | https://www.phenomuk.net/ |
| Regional networks / Initiatives: | |
| EMPHASIS | https://emphasis.plant-phenotyping.eu/ |
| EPPN: European Plant Phenotyping Network | https://www.plant-phenotyping-network.eu/ |
| EPPN2020: European Plant Phenotyping Network 2020 | https://eppn2020.plant-phenotyping.eu/ |
| LatPPN: Latin American Plant Phenotyping Network | (Camargo and Lobos, 2016) |
| NaPPNord American Plant Phenotyping Network | https://nappn.plant-phenotyping.org/ (Carroll et al., 2019) |
| Nordplant | https://www.nordplant.org/ |
| Global networks / Initiatives: | |
| IPPN: International Plant Phenotyping network | https://www.plant-phenotyping.org/ |

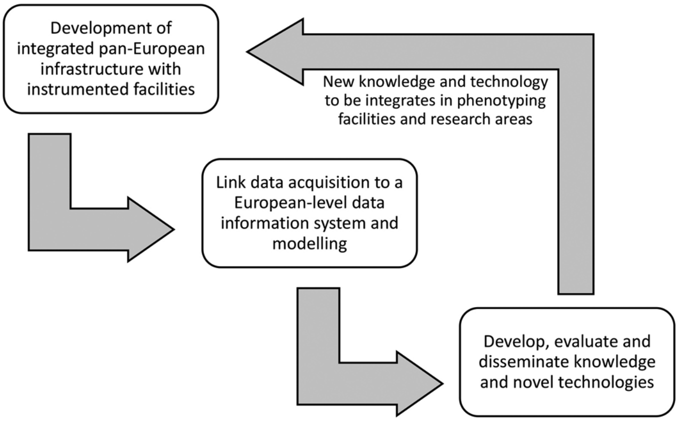

**Figure 4** Integration of distributed plant phenotyping research infrastructure (Example from EMPHASIS, modified from: https://emphasis.plant-phenotyping.eu/).

EMPHASIS has a strong European focus. However, cooperation beyond Europe is important and an integral part of the ESFRI internationalisation strategy (see RI-VIS project: https://ri-vis.eu).

There is also a strong need for development of phenotyping networks outside Europe. Latin American Plant Phenomics Network (LatPPN), e.g. focuses on Latin America and the Caribbean countries covering a wider range of climatic conditions and potentially any crop (Camargo and Lobos, 2016). Another example is the North American Plant Phenotyping Network (NaPPN) to promote collaboration between groups in North America to support agricultural and other sciences (Carroll et al., 2019). National and international networks are listed in Table 1. With the increasing number of national and continental networks, there is an opportunity to integrate at a global scale. This role is taken by the International Plant Phenotyping network (IPPN). The IPPN has the goal of linking different regional networks and providing a communication and exchange platform. The IPPN includes academic members from phenotyping centres across the globe as well as key companies involved in phenotyping. The network addresses different topics with dedicated working groups organising workshops, round table discussions, training, etc. A key initiative is the organisation of the International Plant Phenotyping Symposia, starting in 2009 and bringing the global plant phenotyping community together to exchange information and ideas. The symposia are often complemented by publication of the latest research in dedicated special issues in different journals (Pieruschka and Lawson, 2015; Pommier et al., 2020; Reynolds and Schurr, 2019). Working groups develop integrated views on particular areas of research and support the exchange between experts and users of plants phenotyping.

## 4 Plant phenotyping as a tool for enhanced and sustainable crop production

Sustainable intensification of crop production is a major challenge to ensure the amount and quality of plant biomass needed for human nutrition and other uses. There is an urgent need to design new varieties which are high yielding and adapted to contrasting environmental conditions, including those associated with climate change, which makes efficient use of resources and are compatible with new agricultural management systems. We highlight three research areas that have substantial potential in advancing the development and application of phenotyping solutions and play a key role in advancing plant breeding:

- utilisation of genetic resources;
- phenotyping of roots; and
- phenotyping under field conditions.

In each of those areas, we summarise the benefits plant phenotyping is delivering and discuss potential future developments.

### *4.1 Phenotyping to support utilisation of genetic resources*

Genetic resources for food and agriculture are the raw materials on which the world relies to improve the productivity and quality of crops. The conservation and sustainable use of genetic resources for food and agriculture is therefore at the centre of food security and nutrition. Modern, high-yielding agricultural crop varieties have resulted in reduced genetic diversity, including the potential of crop adaptation to future environmental conditions compared to natural populations (Jump et al., 2009). Utilisation of genetic resources in gene banks with future value is essential in preserving the evolutionary potential of crops. There are about 7.4 million accessions locked in storage rooms in more than 1750 gene banks worldwide (FAO, 2010). These resources are substantially underutilised because of a lack of access to information. In particular, lack of phenotyping data about accessions is an important limiting factor in the use of genetic resources for crop improvement and basic research.

An essential step towards the utilisation of plant genetic resources is the informed selection of the most promising genetic resource. Passport records of accessions usually include provenance, genotypic data and phenotypic observations if available. Quantitative phenotyping during successive rounds of seed multiplication is rarely performed because of limited resources and capabilities. However, it may contribute substantially to complementing passport data with a relevant description of trait, which would improve the development of core populations and consequently the translation of novel traits (genes, alleles) into pre-breeding and breeding programmes (Mascher et al., 2019; Rebetzke et al., 2019).

New, more affordable techniques for single seed phenotyping will facilitate description of relevant traits of accessions, which would make the translation of novel traits into pre-breeding and breeding programmes more effective. Single seed phenotyping is often based on image analysis of 2D shape parameters such as seed length, width and surface area, which can be recorded using high throughput methods and used for quantitative trait locus (QTL) analysis as demonstrated with rice (Tanabata et al., 2012). Assessing seed properties using 3D techniques such as stereoscopic imaging is more challenging, especially for small seeds, but provides useful additional information (Roussel et al., 2016). Seed imaging connected to a robotised platform including weighing of seeds provides a useful tool to measure a number of traits (Jahnke et al., 2016). This may then be linked to an X-ray CT scanner to investigate the internal structure of seeds (Gargiulo et al., 2019). Irregularly shaped seeds with rough surfaces are difficult to assess accurately with image-based tools, though seed volume can be measured acoustically (Sydoruk et al., 2020).

To complement seed phenotyping, high throughput phenotyping of plants during regeneration cycles may provide useful additional information on traits to add to accession passport data. Low-cost solutions based on smartphone applications are widely available with increasing resolution and processing capabilities. The Plant Screen Mobile, e.g. provides a portfolio of segmentation options that allows simple geometric calibration to extract traits such as projected leaf area and shape parameters (Mueller-Linow et al., 2019). Those data can be used as a proxy for leaf area, biomass or growth when recorded over time and, when combined with environmental data, they provide a flexible and easy tool in providing quantitative phenotypic data (Jun and Park, 2017).

There is therefore a range of increasingly affordable technologies that can be used in gene bank pipelines to characterise single seeds and plant traits during regeneration cycles. Those approaches have the potential to substantially enhance the utilisation of genetic resources and make translation of novel traits into pre-breeding or breeding programmes more effective. Collaboration between gene bank curators and technology developers is important to identify the relevant steps in preservation and utilisation of genetic resources.

## *4.2 Exploring the hidden part of the plant: root phenotyping*

Quantitative assessment of root structural and functional properties relates directly to properties such as water and nutrient use efficiency which are key to plant productivity. While changes in shoot properties have been extensively studied, analysis of roots has been neglected. However, the development of new crop cultivars with improved root properties is an important strategic goal for global agriculture (Kuijken et al., 2015).

High throughput analysis can be achieved with seedlings grown in agar-filled Petri dishes where root system architecture and growth can be quantified with a good temporal resolution, including traits such as branching angles and frequency of lateral roots (Nagel et al., 2009; Nagel et al., 2020). Growth in cylinders filled with transparent gel allows measurements of 3D root properties (Clark et al., 2011). While growth in agar-filled Petri dishes is limited to a few days, pouches using germination paper (with roots growing along the paper) allow experiments over weeks (Gioia et al., 2017; Le Marie et al., 2016). Root growth in artificial systems provides an opportunity to simulate aspects of the root environment such as nutrient availability. However, it can be challenging when using the root traits from one growth system to predict those in another growth system (Liu et al., 2017). Well-defined experimental settings to study root properties in soil are essential to allow comparison.

In controlled conditions plants can be grown in soil-filled pots (Shi et al., 2018) rhizotrons (Nagel et al., 2012) or rhizotubes (Jeudy et al., 2016) with transparent walls that allow measurement of root traits. The root system fractions visible from the transparent parts of the pots or rhizotrons are species dependent. However, the variation of roots growing along the transparent part of the pot or rhizotron correlates well with a number of traits such as root biomass or total root length (Nagel et al., 2012). These experiments require careful preparation but provide the opportunity to measure root and shoot properties simultaneously. Analysing the growth of maize under drought conditions, e.g., revealed a significant reduction in total root length as well as rooting depth and width, together with significantly reduced leaf growth parameters. Such an approach has the potential to identify key candidate traits for future breeding programmes (Avramova et al., 2016).

New approaches for root phenotyping have recently been developed to study 3D root structure and function *in vivo* in soil-filled pots using X-ray computed tomography (CT) or magnetic resonance imaging (MRI) (Metzner et al., 2015; Mooney et al., 2012). Widely used in medicine and the life sciences, both methods involve 3D reconstruction of scanned objects (Kherlopian et al., 2008). These methods produce high-quality 3D images of root systems and an opportunity for deep phenotyping of root responses to a range of relevant environmental conditions. MRI can also be combined with positron emission technology (PET) where carbon transport into roots can be measured by tracing the short-lived radioactive carbon isotope (11)C (Jahnke et al., 2009).

Root phenotyping often starts using controlled conditions with the goal to transfer knowledge to the field (Kuijken et al., 2015). There are several approaches to phenotyping of roots under field conditions. Digging out the roots (shovelomics) or coring are crude but effective methods and can be used to reveal biologically important variation and genome regions affecting root architecture (Burridge et al., 2017) or identify variation in deep root traits to speed up selection of genotypes for breeding programs (Wasson et al., 2014). Deep rooting genotypes can also be identified using indirect methods such as a tracer or herbicide placed at a certain depth in the soil: root activity can be assessed by measuring the responses of shoots above ground (Chen et al., 2019). An interesting approach is root observation through long transparent tubes that are placed diagonally in the soil at differing depths, allowing measurement of the time when roots are visible at different depths. The approach can be combined with water and nutrient stress analysis, providing direct measurements of both root growth and stress symptoms in the canopy (Svane et al., 2019).

There is therefore a range of methods to assess root properties in a detailed and systematic way and then translate a better understanding of root properties into crop improvement. These approaches are essential for the development and validation of models on how root phenotypes interact dynamically with the environment, acquire resources and thus influence plant growth and yield (Postma et al., 2017). The capacity for high throughput phenotyping of roots is currently rather limited. It is essential to use available data and models to identify the main gaps in knowledge that need to be addressed experimentally. Phenotyping facilities and technology that simultaneously measure roots and shoots must be developed for a better understanding of global plant productivity and translation of this understanding into applications (Tracy et al., 2020; Watt et al., 2020).

### *4.3 Plants under dynamic environment: field phenotyping*

Plant performance is strongly affected by environmental conditions. Plants grown under controlled conditions can be manipulated in a well-defined way that cannot be replicated in the field. The translation of results from controlled to field conditions is challenging because of the highly dynamic environment in the field (Poorter et al., 2016). There are some facilities where some aspects of the environment can be controlled such as the $CO_2$ concentration in Free Air $CO_2$ Facilities (FACE, (Muller et al., 2018)) or control of water and nutrient availability in rain-out shelter facilities (Beauchêne et al., 2019). However, in most cases field phenotyping focuses on plant canopies growing in a highly dynamic environment usually over extended areas where both the environment and the traits of interest must be assessed in a quantitative way. Here we focus on summarising the current development of field and airborne platforms as well as sensor networks in experimental field sites and discuss potential requirements for future developments.

Requirements for quantitative assessment of plant traits in the field can be easily described but are challenging to achieve in practice. There is a need for a dedicated ground and airborne carrier system for sensors complemented by environmental monitoring (Araus et al., 2018; Cendrero-Mateo et al., 2017; Jin et al., 2020). Ground-based phenotyping systems may be categorised as phenopole-based, phenomobile and stationary systems. Phenopoles are simple fixed or mobile 'sticks' with an attached sensor that must be fixed manually. Phenomobiles may involve automatic, human or tractor-based movement. Both systems may include an integrated GPS system to deliver high-quality data. Stationary systems include cable-suspended sensors (Kirchgessner et al., 2017) or dedicated gantry systems (Virlet et al., 2017) which provide high-resolution spatial and temporal data but are often restricted to a specific field-side because the carrier system is usually not transferable. Unmanned aerial vehicles (UAVs) have recently become increasingly important in field phenotyping. This has become possible because of increasing flight times, increased payload capacity and decreasing costs. An additional factor is the development of miniaturised sensors covering a wide range of the electromagnetic spectrum, as well as using thermal imaging and hyperspectral imaging to assess a diversity of functional and structural traits in the field at high spatial and temporal resolution. This has resulted in the increasing use of this technology (Yang et al., 2017).

Assessing genetic variability of crops under field conditions usually requires multiple experiments across different sites and countries, which need to take into account year-to-year and site-to-site climatic variability. This requires comparable environmental characterisation of individual experiments in addition to harmonised trait assessment over multiple years to assess the performance of genotypes in crops such as maize (Millet et al., 2016) and allow prediction of yield under a wide range of environmental scenarios (Millet et al., 2019). Further development of multi-site experimental capacity is essential and requires harmonisation of experimental procedures so that data are comparable and reusable. Further advances will come from multi-scale monitoring of plants and the environment using autonomous robotics combined with big data analysis through artificial intelligence. With the G5 technology on the horizon, it will be possible to transfer data to servers for complex analysis in real time, providing opportunities for use in precision farming.

There is currently substantial development in technology for plant phenotyping including ground and airborne systems with a wide range of sensors to analyse a diversity of traits. Further development in robotised systems will boost plant phenotyping and related disciplines such as precision farming. Assessment of genetic variability of crops requires multi-site experiments and, despite the availability of phenotyping technology and environmental sensors, there is a need to harmonise experimental procedures, data acquisition and management, particularly considering that experiments often need to be performed on multiple sites over multiple years.

## 5 Future trends

Plant phenotyping is becoming an integral tool in the plant sciences and related disciplines, including in breeding and precision farming. Phenotyping can exploit advances in vision systems, machine learning and robotics to improve efficiencies and accuracy. There is no one-size-fits-all solution. Achieving sustainable plant productions requires three key elements:

- phenotyping and environmental observations of diverse crops and traits of interests in dedicated facilities;
- hardware and software solutions to address the diversity of required solutions; and
- multi-scale systems.

These are summarised in Fig. 5.

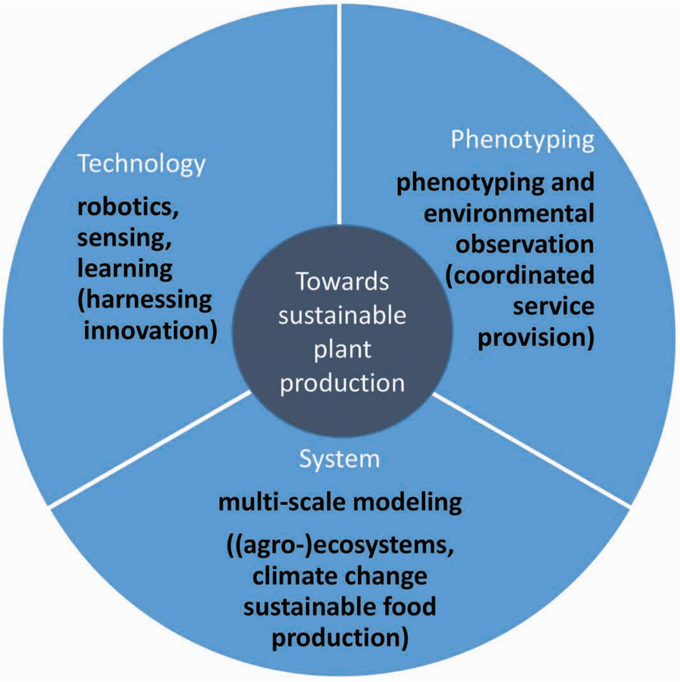

**Figure 5** Phenotyping, systems and technology as three integral elements required to advance sustainable plant production.

Plant phenotyping is an important tool in understanding plant–environment interactions. Given the diversity of facilities, tools and methods, a coordinated approach is needed to effectively utilise these resources for sustainable plant production. This includes sharing facilities to minimise duplication of costs and resources, with investment focussed on developing new facilities which will have the most impact. The integration of robotics and data science will help to achieve higher throughput and accuracy (Watt et al., 2020). Coordination is essential to enable harmonisation from experimental design to data acquisition and reusability of data in models (Bolger et al., 2019; Tardieu et al., 2017). Analysis of genotype–phenotype relationships in diverse environments is not feasible through experiments alone (Houle et al., 2010). There is therefore a need for interoperable phenotyping data for modelling to identify gaps that dedicated experiments can then fill.

## 6 Where to look for further information

### 6.1 Conferences

The IPPN organises biannual International Plant Phenotyping Symposia in different regions across the globe, usually hosted by a dedicated plant phenotyping centre in a specific region. The symposia are often linked to special issues (Pieruschka and Lawson, 2015; Pieruschka and Poorter, 2012; Pommier et al., 2020; Reynolds and Schurr, 2019). There are also several regional events organised by regional networks such as the North American Plant Phenotyping Network (NAPPN, https://nappn.plant-phenotyping.org/) or research infrastructures such as EMPHASIS (https://emphasis.plant-phenotyping.eu/).

### 6.2 Journals addressing plant phenotyping

According to a latest bibliometric study plant phenotyping was mentioned in 174 journals (Costa et al., 2019). The top five journals were: Frontiers in Plant Science, Journal of Experimental Botany, Plant Methods, Plant Theoretical and Applied Genetics, PLoS ONE. Specific plant phenotyping journals addressing plant phenotyping are:

- Plant Phenomics (https://spj.sciencemag.org/journals/plantphenomics/).
- The Plant Phenome Journal (https://www.wiley.com/en-us/The+Plant+Phenome+Journal-p-9780JRNL79529).

### 6.3 Plant phenotyping initiatives

There are several plant phenotyping networks and initiatives on a country, regional and global level as summarised in Table 1.

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