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Phenotyping: New Windows into the Plant for Breeders

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Abstract

Plant phenotyping enables noninvasive quantification of plant structure and function and interactions with environments. High-capacity phenotyping reaches hitherto inaccessible phenotypic characteristics. Diverse, challenging, and valuable applications of phenotyping have originated among scientists, prebreeders, and breeders as they study the phenotypic diversity of genetic resources and apply increasingly complex traits to crop improvement. Noninvasive technologies are used to analyze experimental and breeding populations. We cover the most recent research in controlled-environment and field phenotyping for seed, shoot, and root traits. Select field phenotyping technologies have become state of the art and show promise for speeding up the breeding process in early generations. We highlight the technologies behind the rapid advances in proximal and remote sensing of plants in fields. We conclude by discussing the new disciplines working with the phenotyping community: data science, to address the challenge of generating FAIR (findable, accessible, interoperable, and reusable) data, and robotics, to apply phenotyping directly on farms.

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PLANT PHENOTYPING HAS COME A LONG WAY

A new era in plant phenotyping began with the increased development of noninvasive technologies. The capacity and throughput of sensor, automation, and computation-based tools grew, along with their availability, affordability, robustness, and scalability (34). Automated, nondestructive, and precise plant phenotyping was first applied in the plant sciences to dissect the dynamics of the spatial and temporal structure–function relations of plants in controlled environments (growth chambers and glasshouses) (38, 143). Numerous infrastructure platforms were developed globally, allowing for deep phenotyping. Highly skilled groups have developed and used specialized equipment for tomographic and high-throughput measurement of structure in three and four dimensions (28, 52, 71, 75, 94, 137). Functional phenotyping quantifies photosynthesis processes, growth, water and nutrient relations, and many more plant characteristics. Global infrastructure platforms have been bundled and made accessible in recent years by initiatives such as the International Plant Phenotyping Network (IPPN); the European Plant Phenotyping Network (EPPN); and the EPPN’s successor, EPPN2020 (see the Related Resources). Ongoing large and coordinated actions continue to provide continental-scale organization, as in the European Infrastructure for Multi-Scale Plant Phenotyping and Simulation for Food Security in a Changing Climate (EMPHASIS) (118). These initiatives also maintain active databases of available technologies and phenotyping experiment installations for users. Most of the phenotyping installations available today are in controlled environments. Surveys of the plant phenotyping community by IPPN (see https://www.plant-phenotyping.org/ippn-survey_2016) have identified noninvasive field phenotyping, root phenotyping, data management, and extraction of information as crucial bottlenecks—specifically when moving toward breeding applications. Noninvasive plant

Phenotyping: the activity of using a suite of methods to quantify features of organisms (e.g., plants) that are expressed and observable

Deep: describes data with many layers from multiple sensors and time points and/or on many individuals

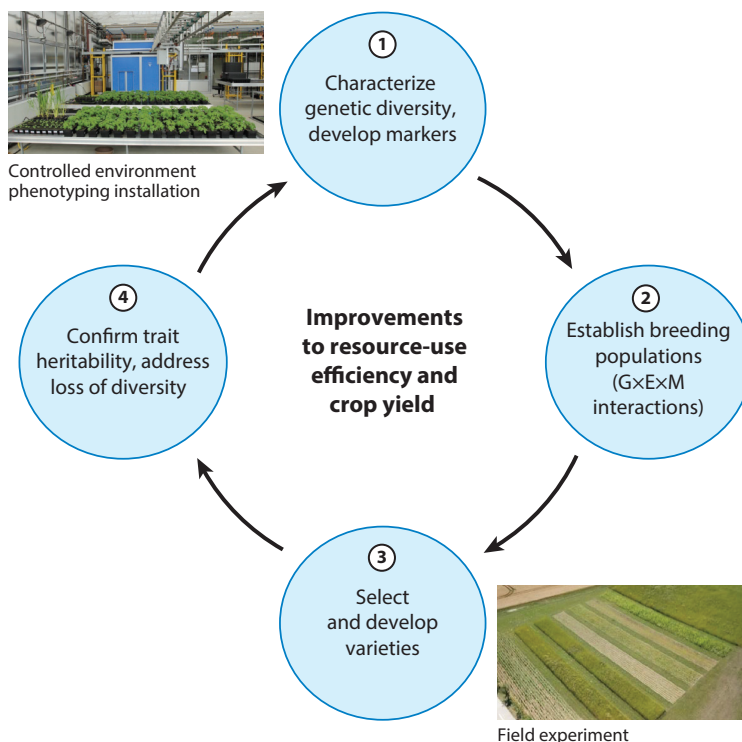


Figure 1

A process model of plant phenotyping to improve crop varieties. The process of improving crop varieties via plant phenotyping includes (①) characterization of genetic diversity, (②) designing experiments for the development of breeding populations, (③) using efficient selection procedures, and (④) assessing trait heritability. Abbreviation: G×E×M, genotype × environment × management. Photos copyright Forschungszentrum Jülich.

phenotyping today is used primarily for the processes depicted in **Figure 1** and, as such, is used mainly in prebreeding.

Introducing and maintaining beneficial genetic diversity are at the core of prebreeding, and much of the plant phenotyping community is engaged in characterization of genetic diversity (**Figure 1**, step ①). Phenotyping provides information about experimental populations (**Figure 1**, step ②) (51, 136) that help include desired phenotypes that do not have molecular markers (e.g., 109). Entirely new automated instruments have been engineered to increase the speed and precision of selection of complex and combined phenotypes (**Figure 1**, step ③). Automated instruments can measure multiple genetic aspects of seeds in seed banks (53) and the dynamics of whole-plant allocation in large crop plants (44). The high throughput of automated phenotyping installations can assess large numbers of plants for heritability. Field validation is addressed with well-designed, specialized trait-demonstration field facilities (108), where high-throughput field phenotyping can be implemented (e.g., 25, 54). Phenotyping has come a long way within prebreeding for numerous species and environments and agriculture, as well as for horticulture systems globally. Its use directly in breeding is becoming better understood and applied.

We begin this review with a brief history of phenotyping, showing the evolution of needs and technologies within breeding and prebreeding. We then cover contemporary and future

Prebreeding: refers to activities to identify desirable features and genes from plants so that information, selection technologies, and plants can be used in breeding to produce varieties for farmers

Trait: a characteristic of an organism that may be measured when expressed at the individual level using phenotyping

Proxy: a variable used to model data correlated to another variable that is more difficult or laborious to estimate

Genome-wide association studies (GWASs): studies to predict genomic loci that are associated with a phenotype, usually based on large panels of genotypes

phenotyping in controlled environments and fields and explain how data science is rapidly growing to link the phenotyping community to genomics and breeding. We finish by describing the emerging alliance among plant phenotyping, robotics, and farm interventions, which is moving phenotyping into a new era in which breeding and agronomic management will work together.

PHENOTYPING FOR BREEDING AND PREBREEDING

The Historical Context

Phenotyping for breeding new cultivars has two challenges: what to measure and how to measure. Breeders add and remove traits to their germplasm to increase yield and quality. Key early phenotypes selected in crop domestication included dietary and cooking properties (e.g., removal of toxins, ease of milling, baking properties) and seed features (e.g., removal of shattering, control of dormancy) (141). Disease incidence and flowering time are significant determinants of yield, and they continue to be scored by breeders mainly by eye. The most famous functional phenotype directly applied in breeding is arguably plant height, selected by Norman Borlaug in the 1950s to support heavier wheat heads that arose from breeding and nitrogen fertilizer application. Height was reduced by approximately 50 cm with the *Reduced height (Rht)* genes and would be easily seen by eye (121). Therefore, breeders select traits directly or indirectly in breeding by using a phenotype; even today, both molecular markers and genomic-based selection depend on initial phenotypic information (21).

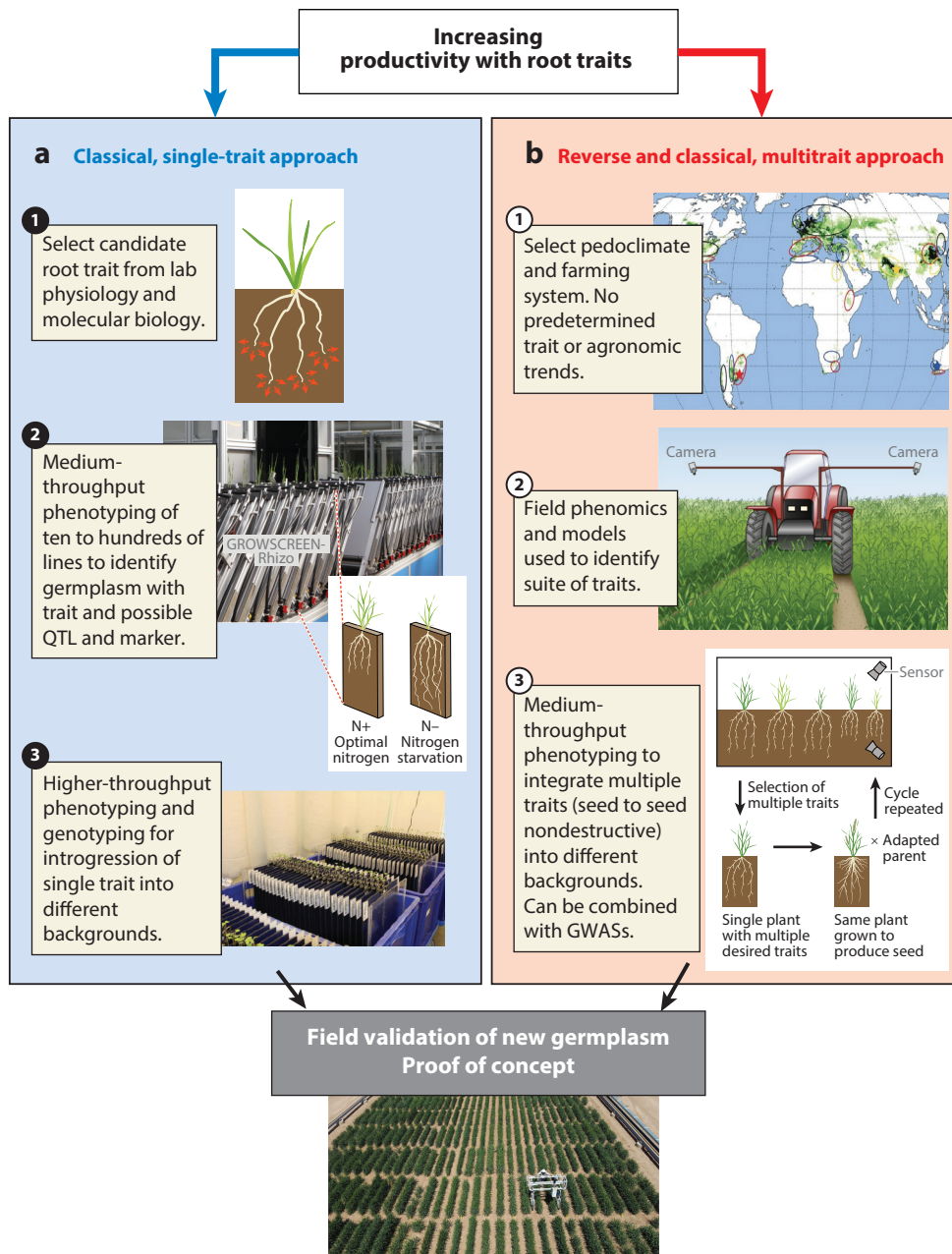
Prebreeding is the use of phenotyping to help speed up genetic improvement in breeding. Donald (27) stimulated the process of prebreeding phenotyping when he introduced the idea of ideotype breeding in the late 1960s. Donald's ideotype included stature and architectural phenotypes that could benefit yield (e.g., leaf erectness). In the 1980s, Richards & Passioura (113) introduced yield identity (yield of water limited crops = water used \times water-use efficiency \times harvest index) to divide yield into its primary, component traits, helping scientists and breeders prioritize phenotypes with a large impact on yield in dry environments. Similarly, Reynolds et al. (110) outlined the primary traits underlying increasing yield in the absence of stressors. Primary traits can be selected directly with their phenotype or indirectly with a proxy (e.g., leaf area selected with leaf width, water-use efficiency selected with carbon isotope signature). Ideotype phenotypes have been the focus of successful prebreeding efforts (see 114 for a review of their selection and application in wheat).

We are not aware of the extent to which prebreeding contributes to the breeding of released cultivars. The process of generating a new plant with a phenotype that increases yield using classical, nonautomated phenotyping within public institutions has been slow: up to 10 to 20 years for challenging environments (48) and traits (133). A main impediment to breeder uptake of phenotyping has been total cost to the breeder (time, expertise) versus price for the farmer (114). However, phenotyping technologies are rapidly gaining capabilities and speed, and it is likely that some will be used by breeders when the cost is low enough per seed and the value of the trait, or combinations of traits [e.g., for genome-wide association studies (GWASs)], is accepted by markets. Indeed, recent approaches have shown that phenomic selection can actually be faster and cheaper than marker-based selection (116).

Novel Opportunities for Breeding from State-of-the-Art Phenotyping

Today's phenotyping technologies can speed up genetic gain within the breeding cycle, in addition to continuing to provide entirely new traits through discovery. Three exciting opportunities are emerging. First is the opportunity to coselect multiple phenotypes in one seed that

is not destroyed (**Figure 2**; see the section titled Phenotyping in Controlled Environments for Prebreeding). Installations that comeasure roots and shoots over time (82) and that track information from parent seed to progeny seed (53) would significantly reduce the time associated with advancing traits through breeding programs. The second opportunity is their integration into speed breeding: methods to reduce generation cycles by manipulating light and temperature



(Caption appears on following page)

Figure 2 (*Figure appears on preceding page*)

Phenotyping roots, from identification of target traits to prebreeding with phenotyping to breeding. (a) The classical pathway for root trait breeding. (●) Conception of a trait of value for productivity (yield per input) from the literature, indoor or outdoor plant physiology, and molecular biology experiments. Illustration by Peter Ryan. (●) Identification of germplasm expressing the trait using medium-throughput phenotyping. Mapping populations can be used to identify the QTL associated with the trait; or germplasm such as Tilling populations can be explored to link the trait to a candidate gene. If a QTL or gene is identified, a molecular marker can be developed. Image of GROWSCREEN-Rhizo platform reproduced from Nagel et al. (82), with permission from CSIRO Publishing. GROWSCREEN-Rhizo is a novel phenotyping robot enabling simultaneous measurements of root and shoot growth for plants grown in soil-filled rhizotrons. (●) Introgression of the trait into genetic backgrounds of elite, modern cultivars with simple, higher-throughput selection tools such as phenotyping or molecular markers. Image of GROWSCREEN-PaGe reproduced from Reference 43 with permission from CSIRO Publishing. GROWSCREEN-PaGe is a non-invasive, high-throughput phenotyping system based on germination paper to quantify crop phenotypic diversity and plasticity of root traits under varying nutrient supply. (b) Contemporary concepts of multitrait improvement that are emerging from the combination of automated controlled-environment and field phenotyping technologies. (①) A climate and region (e.g., a global megaenvironment) are targeted, and yield and agronomic trends are used to identify gaps in productivity gains. Image adapted from Reference 4 with permission from Nature Publishing Group. (②) Deep-field phenomics (multiple layers of information in space and time) is then applied to exemplary field sites to identify a suite of traits, above- and belowground, that can confer productivity gains within the target megaenvironment and agronomic context. The figure depicts sensor cameras passing over a field crop to measure shoot canopy properties repeatedly during a crop life, to quantify phenotypes expressed with environment and genotype. Adapted from Reference 3 with permission from Wiley-Blackwell. (③) Medium-throughput, automated, and noninvasive platforms are applied next to germplasm to coselect above- and belowground traits, including resource-use efficiency. Adapted from Reference 133 with permission from Elsevier. Finally, germplasm developed via either of the two routes in panels *a* and *b* is tested in the field for proof of concept that the introgressed traits led to improved productivity in the target environment. Abbreviations: GWASs, genome-wide association studies; QTL, quantitative trait locus.

conditions (147). Phenotyping has been implemented into speed breeding, but using classical, manual methods (112). Today's technologies could measure multiple phenotypes in each generation with modifications to indoor growing conditions. The third opportunity, highly attractive to ongoing breeding programs, is the integration of high-throughput, precision phenotyping into early-generation selections of small plant numbers in the field (due to small seed amounts) (35). The section titled Field Phenotyping, below, discusses the technologies available to measure single-plant, short row, and plot phenotypes.

PHENOTYPING IN CONTROLLED ENVIRONMENTS FOR PREBREEDING

Plant physiologists and molecular biologists usually use indoor, controlled environments to analyze variables that influence above- and belowground growth in detail. However, for most plant breeding, plant populations are grown outdoors in fields—as many as practically possible to quantify genotype \times environment \times management ($G \times E \times M$) interactions and to simulate yield in crop models (46, 136, 140). In this section, we focus on the challenges of applying phenotyping indoors to crops produced in fields. Phenotyping in glasshouses is expanding for breeding of horticulture crops produced indoors (see 93 for a recent review).

Contrasts between indoor and outdoor environments that are important for plant research are quantified by meta-analyses of variables used in controlled-environment experiments (98). These studies demonstrate the need to systematically address the technical shortcomings of indoor experiments so as to improve the quality and relevance of data for fields. Shortcomings include low light

intensities, temperature profiles mismatched to target environments, insufficient pot volumes, and planting densities that are irrelevant for agronomic practices (56, 100). However, attempting to simulate all outdoor environmental conditions is impossible due to their dynamics. Furthermore, in controlled environments it is rarely possible and meaningful to span complete crop growth cycles to seed and fruit yield for broadacre crops. For grain crops, the majority of data sets from indoor experiments are gathered at the vegetative stage (99). Consequently, controlled-environment phenotyping for direct comparison (correlation and ranking) of genotypic performance measured as yield between greenhouse versus field is often considered to have limited value for breeding.

In contrast, for prebreeding, the use of controlled-environment phenotyping is ideal to dissect physiological traits, analyze breeding progress, and generate genetic diversity with trait-based introgressions (**Figures 1** and **2**). Yield has been dissected into several component, primary traits (discussed above in the section titled The Historical Context). Furthermore, clusters of correlated physiological traits (trait networks) have been described across species and environmental factors using meta-analytics (91, 97, 101, 103). Components and networks of traits can be phenotyped indoors at a certain throughput. Proxies, however, are designed to have greater repeatability than the primary trait, reducing phenotypic variability for each genotype and increasing heritability (62, 138, 139). Transferability from indoor to outdoor for the benefit of plant breeding should be considered in the context of identifying a proxy trait for phenotyping. The proxy approach has frequently been employed for root traits, which are strongly influenced by outdoor, varying soil conditions (see the section titled Root Phenotyping for Prebreeding, below).

Image-based indoor phenotyping platforms provide valuable, complex traits. Crop establishment is a clear example. Good establishment covers the soil, minimizing soil water evaporation and reducing weed competition (115). Establishment traits, collectively referred to as early vigor, include rapid emergence, rapid development of leaf area, early biomass accumulation, and robust elongation of the root system (68). Platforms that specialize in measuring projected leaf area and digital biomass over time at the vegetative stage are particularly well suited for crop establishment analyses (34). Another exemplary application of indoor phenotyping installations is for tolerance to systemic stress effectors such as temperature. Leaf growth indoors at cool temperature can correspond to plant performance in cold conditions in the field, and one study used genotype-specific data to predict the field performance of early vigor at low temperature in maize (14). In this study, temperature and radiation-use efficiency responses were measured and modeled using the phenotyping platform data, increasing the data value for the target field (17, 91). In studies of salinity tolerance and resource-use efficiency, high-throughput indoor phenotyping platforms were successfully used with association mapping to provide candidate quantitative trait loci (QTLs) and genetic markers that could be used in plant breeding (5, 31, 74, 80). A unique and crucial feature of contemporary phenotyping installations is that they are inherently automated to provide time series at varying resolution. Genetic markers for time-dependent heritability and temporal expression during a daylight cycle were first found in *Arabidopsis* (36) through the use of growth profiles of digital biomass data and chlorophyll fluorescence. Such dynamic traits can be identified in crops in the future, either with association mapping studies that require throughputs of hundreds of plants or with germplasm panels.

An emerging trend in controlled environments is the coupling of digital phenotyping with classical physiological measurements to discover entirely new traits for crop improvement. An automated rhizotron platform was used to estimate the loss of diversity during durum wheat domestication for shoot and root traits and their response to nitrogen starvation (44). A platform measuring biomass accumulation and water use was combined with classical methods to assess stomatal functions in order to identify the combined physiological strategies of responses to low

Quantitative trait locus (QTL): a locus associated with a quantitative (phenotypic) trait

water availability in wheat (83). A detailed analysis of shoot and root growth of advanced and commercially available breeding material in maize, combined with a retrospective analysis of tolerance to drought conditions in the field, confirmed field performance and added numerous layers of phenotypic and physiological information at the cell, tissue, and whole-plant levels (7). So far, detailed phenotyping has been applied to relatively few genotypes and well-defined conditions. However, they can be extended to the analysis of genotype panels to complement the selection of parents for crossing strategies by breeders. The breeders obtain information about the variation in population tails across a suite of traits that are much more difficult and time-consuming to measure in the field. Thus, indoor controlled-environment phenotyping remains a valuable tool for well-selected and well-reasoned cases that directly support prebreeding processes (**Figure 1**).

ROOT PHENOTYPING FOR PREBREEDING

Roots: Neglected in the Past Because of Their Limited Accessibility?

Root phenotypes are inherently more challenging to select for crop improvement than those aboveground because they are not visible by eye. Nevertheless, since the 1970s, prebreeding programs around the world have used classical semimanual root and shoot phenotyping to introgress new and beneficial root traits into germplasm for breeding (133). In some cases, phenotypic screens were used to develop molecular markers to improve resistance in breeding lines (e.g., 88), but in others, root traits were directly introgressed into germplasm using root phenotyping. For example, water-use efficiency was selected using a proxy anatomical screen for narrow xylem vessels in seminal roots with a dissecting microscope on seedlings in the laboratory (113); phosphorus use from surface soil layers was selected among cabinet-grown seedling plants using root architecture imaged on paper pouches (64); and aluminum tolerance was selected using a malate exudation screen in the laboratory, leading to the identification of markers for a malate transporter and the generation of new germplasm (122). These examples selected a proxy trait with a phenotypic screen under controlled conditions. Selections were made on genetically diverse germplasm to provide parents for breeding.

Past examples demonstrate that root traits can be phenotyped for prebreeding purposes by discovering how root processes contribute to productivity in targeted field conditions and by applying well-considered physiology to identify a proxy that can be screened across germplasm. Present-day controlled-environment root phenotyping installations are automated and, thus, can greatly speed up proxy selections for root trait improvement compared with the classical methods used in the examples described above (34, 47, 90, 95). Further contemporary phenotyping installations can be used to discover physiological processes that have not yet been exploited in trait-based breeding (e.g., 8). The most exciting aspects of present and emerging controlled-environment phenotyping platforms for root traits are that they can (*a*) image shoots simultaneously on the same plant to identify whole-plant phenotypes (19) and (*b*) quantify dynamics in roots to discover new traits that confer tolerance to stresses (3). A major challenge for root traits, however, remains the speed of translation to field environments (146).

Root Phenotyping in Controlled and Field Conditions Within the Phenotyping Chain Concept

To speed up the translation of root phenotypes to field conditions, it is useful to examine the phases of root phenotyping along both the classical, single-trait and emerging, multitrait routes (**Figure 2**). Root scientists today generally start in controlled conditions and work toward field validation (62) for early, fast progress because doing so avoids complex soil conditions. However,

a number of well-tested examples illustrate that simple controlled-environment conditions do not always lead to better performance in fields (e.g., 42). To overcome the problem of poorly representative laboratory selections, a few root prebreeding programs using classical forward trait selections (**Figure 2a**) began phenotyping in the field. For example, steeper brace root angles, measured using shovelomics in maize, were selected for low-nitrogen field environments (132), and deeper root growth was selected using root–soil coring of mature plants in the field (111). The disadvantages of selections within fields, however, are (a) high variability, which leads to low repeatability and heritability of the phenotype for prebreeding or breeding (152), and (b) the intense resources (in terms of both people and disturbed field sites) required to make direct root measurements in the field. Better proxies are required for root traits where markers cannot be designed directly from field phenotypes. Controlled-environment screens generally select from young plants (43, 112). In some cases, these scale to mature plant traits (113), but in others (e.g., root system length), they scale poorly (149). However, modeling can be used to scale root length from vegetative to mature plant stages (157). Wasson et al. (146) proposed that both field phenotyping and controlled-environment phenotyping can be carried out at the start of a selection program to speed up translation to breeders. Such a laboratory–field program would be further enhanced with (a) crop models at the start of the program to establish environments where traits will be valuable (65) and (b) structure–function root models to link phenotypic data to predicted function (104).

A More Systematic Approach to Root-Based Crop Improvement

Figure 2b depicts the emerging possibility of a more systematic approach to root-based improvement. This reverse approach takes advantage of the state-of-the-art automated phenotyping platforms. Deep-field phenotyping of canopies can lead to discoveries of trait combinations that are then selected for in controlled condition platforms that quantify shoot and root phenotypes simultaneously (43, 82, 83). This process represents a whole-plant approach to root-based crop improvement, in which root and shoot phenotypes are matched and coselected for resource efficiencies. Field phenotyping technologies for shoots are becoming established and widely used (see the section titled Field Phenotyping). Direct measurement of root growth, architecture, and function in the field is a critical bottleneck because the most widely used methods are destructive (131, 145; reviewed in 144), and nondestructive methods have been restricted to large root structures, such as cassava tubers (26).

Can Shoot Proxies Be Used to Select for Improved Root Performance?

Shoot proxies for roots have been used in prebreeding programs. For example, shoot biomass and phosphorus content in low-phosphorus fields were used to identify genomic regions in rice roots. The regions regulate early nodal root emergence, and markers are being used to develop breeding populations for low-input rice in Africa (39, 152). To increase the tolerance of durum wheat to saline soils, Munns et al. (78) used the sodium content in young leaves to identify lines that excluded sodium. These researchers generated markers for two transporters, one within the leaf sheath and another in the roots, which they provided to breeders. These examples, which overcome the challenges of nutrient and elemental stress, show the high value of shoot proxies for selecting for improved root performance.

However, caution is required when using shoot proxies for root traits in general. Phenotyping experiments that simultaneously measure roots and shoots demonstrate an unpredictable relationship between shoots and roots, which is particularly notable for growth (biomass, leaf area, and

Active light detection and ranging

(LIDAR): a method of measuring the outer structure of an object

root elongation) phenotypes. Nagel et al. (81) found that, in controlled conditions, leaf area and root architecture varied in relation to each other in response to light and soil moisture conditions, depending on wheat genotype. Under declining soil nitrogen availability, durum wheat allocated biomass to shoots and roots differently over time (44). Similarly, under field conditions in plowed and unplowed soil cultivation systems, shoot and root vigor responded differently in a released variety of wheat compared with a breeding line (148). On the basis of the few examples in the literature, the utility of shoot proxies for root performance should be approached systematically and with validation in the target field conditions using present and emerging field root phenotyping technologies (144).

FIELD PHENOTYPING

The process of phenotyping shoots in the field for prebreeding has advanced rapidly in recent years, possibly because the technologies can be adapted and used locally (in comparison to building glasshouses and fixed installations) (18). Field phenotyping is used to discover novel traits (e.g., in dynamics), identify germplasm carrying traits beneficial to breeding but challenging for breeders to select (e.g., canopy architecture), and validate traits (e.g., proof of concept). Well-designed field phenotyping stations that have been set up around the world combine different measurement approaches and sensor positioning systems (e.g., 1, 60, 125). Field phenotyping can address dynamic shoot traits throughout the season, including traits not visible to the human eye (e.g., components of photosynthesis) (37), and can combine measurements of different phenotypes by using mobile platforms of multiple sensors (54). A key challenge is that canopies close; as a result, most phenotyping efforts have developed approaches with a top-of-canopy view, which enables good measures of the exposed plant organs but has obvious limitations for lower leaves or fruits hidden from the sensor's field of vision.

Aboveground traits that are regarded as highly relevant by many breeding programs include (a) seasonal development and growth of the crop, including seed establishment and closure of the canopy; (b) photosynthetic use of solar energy during the main growth phase; (c) the timing and dynamics of flower and fruit development; (d) resistance to biotic and abiotic stressors; and (e) the quality and homogeneity of the harvested parts of the crop (**Figure 3**).

The phenotypes depicted in **Figure 3** are discussed here with specific examples. Frequent (daily) measurements during establishment are desirable for quantitative selection of vigor phenotypes because plants develop rapidly in early stages. Drone-based red, green, and blue imagery, in combination with advanced image processing routines, can automatically detect single plants and determine germination rates and timing in the field (55, 66). Automated field phenotyping approaches can detect seed emergence under extreme climatic events such as frost or heavy rain, offering opportunities to directly select for establishment traits suited to agronomic practices and climates not achievable in glasshouse conditions.

Shoot biomass and stem elongation after germination are typically determined with nondestructive measures of the canopy structure and destructive biomass measures to extract growth rates. Unfortunately, as yet there are no widely available and sufficiently precise methods to determine total canopy biomass nondestructively. However, early results from terahertz and subterahertz measurements are available (40). Outer canopy structure is measured with stereo imaging to calculate a three-dimensional (3D) map of the outer visible canopy (15, 77), or with active light detection and ranging (LIDAR) systems. LIDAR is used to estimate biomass (see 41 for a recent review). Stereo imaging can provide color information for segment plant components, for example, for the automatic detection of single leaves (77). LIDAR operates in a spectral window within which the canopy is partly transmissive, and it can provide information about canopy layers

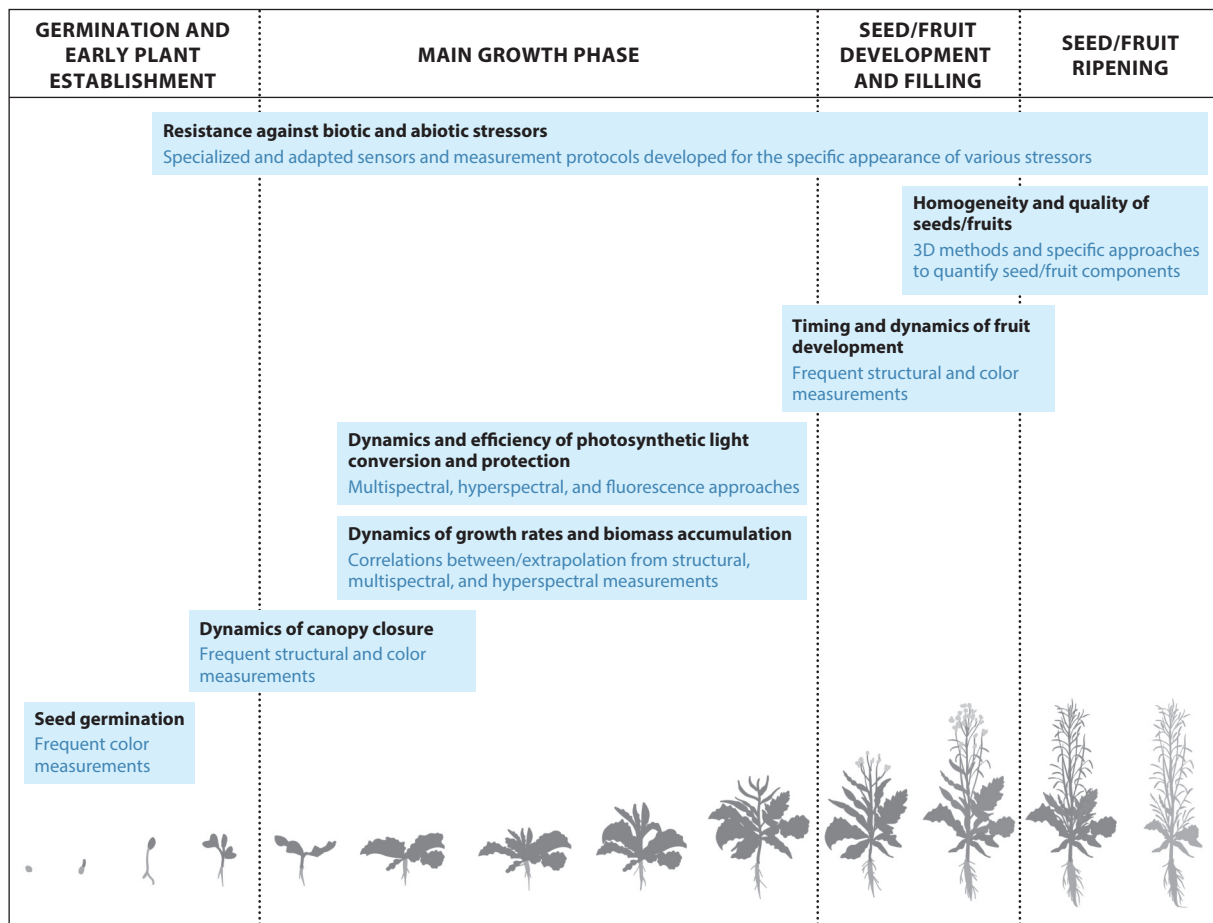


Figure 3

The main components of field phenotyping, covering the dynamics of plant traits throughout the phenological/seasonal cycle. Different phenotypes have specific time windows within the seasonal cycle when they are relevant for the breeder and farmer. Sensor and measurement approaches (*blue text*) are useful within the specific seasonal windows. Plant illustrations copyright Ilya Kalinin (stock.adobe.com).

below the surface (54). Growth rates can be derived from (a minimum of) two time points and by subtracting background soil information (12, 13). Recently, canopy structural measurements were obtained from flying platforms such as unmanned aerial vehicles (UAVs). Structure-from-motion approaches facilitated canopy height and growth measurements, and fast and accurate measurements were obtained from large plot designs (50).

Plant photosynthesis rates are associated with high yield and biomass gain (161), and photosynthetic traits, including optimized nonphotochemical energy dissipation to prevent loss during futile energy conversion (67), remain key targets for breeding. At present, no fast and reliable method to detect photosynthetic carbon-uptake rates is available for large-scale field phenotyping. In contrast, fluorescence-based methods that measure the efficiency of photosynthetic light reactions have become popular (57). Active fluorescence can be used on single leaves with clip-on devices (73), both at canopy level with saturating-light-pulse methods and distal to the canopy with laser-based, single-turnover flashes (106). Recently, solar-induced fluorescence (SIF)

Machine learning:

comprises algorithms and methods to make predictions and/or inferences without specific instructions

Metadata:

data from experimental conditions, such as light during plant growth, that are used to relate other experiments with direct measurement data

was quantified in the field as a new method for phenotyping. SIF passively detects fluorescence emission in atmospheric absorption bands; its advantage over active fluorescence methods is that it is scalable to large fields, aircraft surveys, and satellites (30, 96, 107).

Detection of disease is relevant for many breeding programs but challenging for automated field phenotyping. Disease symptoms are scored using expert knowledge, and the precision required of optical measurements remains a challenge. The most promising approaches combine high-precision optical sensors (often multispectral and hyperspectral cameras) with advanced feature extraction methods, such as adaptive machine learning or linear and nonlinear regression models. Most methods need to be optimized for the specific crop–pathogen interaction. Promising recent studies show that *Cercospora* infection in wheat can be detected by a combination of hyperspectral imaging in the visible and near-infrared spectral range in combination with unsupervised support vector machines (11, 128, 129).

Abiotic stresses, like biotic stresses, are diverse in type, space, and time in the crop cycle. Notable successes in the identification of abiotic stress tolerance were achieved within prebreeding programs using nondestructive canopy temperature and normalized difference vegetation index (NDVI) sensors. Using handheld canopy sensors, physiologists at the International Maize and Wheat Improvement Program identified wheat genotypes with cooler temperatures that were then moved into breeding programs in Pakistan (92). The Australian Commonwealth Scientific and Industrial Research Organisation prebreeding program used green leaf area maintenance (NDVI) to identify germplasm with deeper roots for breeders (63). Challenges for optical, automated stress phenotyping arise from the fact that crops in fields express multiple stresses. For example, a water stress response may be caused by biotic stress. Multispectral or hyperspectral methods may provide solutions (37).

Field phenotyping approaches have recently focused on yield and features closely associated with final yield and quality. For example, color information, 3D measurement techniques, advanced object recognition, and machine learning were used singularly or in combination to detect reproductive organs (158, 159). UAV-based structure-from-motion measurements were used to detect homogeneity of fruit ripening and lodging resistance (79, 155). Time of flowering (anthesis) is an important parameter scored by breeders, requiring time-consuming observation of many plants. Several efforts to automate flowering time scoring for breeders are under way (29). We anticipate that field phenotyping will develop toward whole-season monitoring so as to identify critical time windows for crop development and ultimately to unravel $G \times E \times M$ interactions.

DATA CHALLENGES

Emerging Standards and Standardization

Evaluation of data from one well-defined experiment or from an experimental series is essential for achieving the potential of phenotyping for discovery and breeding (32, 38, 100, 125). This applies to the broad aims of phenotyping highlighted in the section titled Plant Phenotyping Has Come a Long Way, above. Experiments may have few members of a genetic population with repeated measures, or they may have multiple field sites with deep phenomic information from ground and aerial sensors. Data sets may comprise coupled phenotypic and omics data (e.g., 9, 153). The rapid rise of disciplines associated with phenotyping recently led to an agreement concerning the conditions and sharing processes required to make phenotyping data comparable across experiments. Standardized data sharing enables metadata analysis (22) and discoveries of relationships that could not be investigated in the original experimental setup (102). To make phenotyping data and associated metadata analysis feasible and automatable, three conditions need to be met.

First, the plant growth condition metadata must be standardized and recorded so that treatments such as abiotic and biotic stress regimes can be understood and repeated. This holds for standard conditions, which often are not as reproducible as one might think (72). To address this condition in a systematic way, the Minimum Information About a Plant Phenotyping Experiment project (MIAPPE) developed recommendations (23, 61) that are being progressively refined as more and diverse communities embrace and contribute to plant phenotyping. A steering committee and an active community gather input from plant physiologists, breeders, agronomists, and other users for relevant characterization of experimental environments (<https://github.com/MIAPPE>). MIAPPE is supported by, for instance, the ISA-Tab (Investigation/Study/Assay tab-delimited) format (117). Complex data relationships are described in a human-readable format.

Second, a common language must be developed to relate terms in standardized vocabularies. Such vocabularies are used to describe (a) what entity is being measured, (b) how it is being measured, and (c) in which units it is measured. Vocabularies or ontologies can comprise simple examples, such as plant height, or more complex instructions, such as the use of a windless environment for plant measurements (69). Several ontologies describing plant features and expert instructions about plant growth and experimental planning (84, 100) are available to help set up phenotyping information systems that capture phenotypic data and metadata in databases (85). Apart from making entities machine readable, ontologies clarify what is being talked about by providing clear definitions and occasionally vernacular and non-English names. As an example, the plant ontology in Planteome lists Japanese and Spanish translations of English terms for plant parts to supplement the English definitions of, for instance, rosette and cauline leaves (20).

Third, data must be made accessible. A well-standardized and well-described data set that exists only on a personal hard drive cannot be accessed by the community. While there is no single centralized data repository for plant phenotyping data, data should meet the FAIR criteria: findable, accessible, interoperable, and reusable (**Figure 4**) (151). The data sets need to have standardized global identifiers, such as well-known digital object identifiers, and they must be machine readable and have permissive licenses. The FAIR criteria are supported by a general movement toward accessible data by funders including, for instance, the Open Data Initiative of the European Union and the long-established public access policy of the US National Science Foundation. Implementations for FAIR plant data storage exist in open-source examples, such as e!DAL (Electronic Data Archive Library), and can be deployed by a research organization or institute (2) to achieve the FAIR aims.

Phenotyping Data Analysis: Are We There Yet?

A major trend in plant phenotyping is the use of (deep) machine learning (105, 126). Advances in image analysis driven by deep learning improved predictions about plant parameters derived from images ranging from roots (6) to aerial images of fields (58). Data sharing and the use of common (standard) data sets to train models helped improve image analysis precision (135) in these examples, demonstrating that making data sets and their annotations available profits the whole community. The need for data sharing is especially pronounced in machine learning because most machine learning methods for image analysis are supervised (156); that is, they need a ground truth to train the respective models. Ground truth often stems from expert human annotations and measurements and hence is expensive to generate. To overcome the human annotation bottleneck, crowdsourcing is emerging as a novel and cost-efficient way to annotate images (45, 160).

Minimum Information About a Plant Phenotyping Experiment project (MIAPPE): standards to describe a plant phenotyping experiment; includes checklists

Ontology: comprises terms in a standardized vocabulary that are placed in relation with one another

Phenotyping information system: information technology infrastructure used to minimally store and access phenotyping data sets; can include visualization capabilities

Findable, accessible, interoperable, and reusable (FAIR) criteria: recommendations for accessing shared data

Supervised (machine learning): how machine models are trained with outcomes or values assumed to be true (i.e., ground truth); for example, leaf RGB images to predict disease

Ground truth: human annotation or instrument measurements added to data so that a machine can learn patterns and develop a model

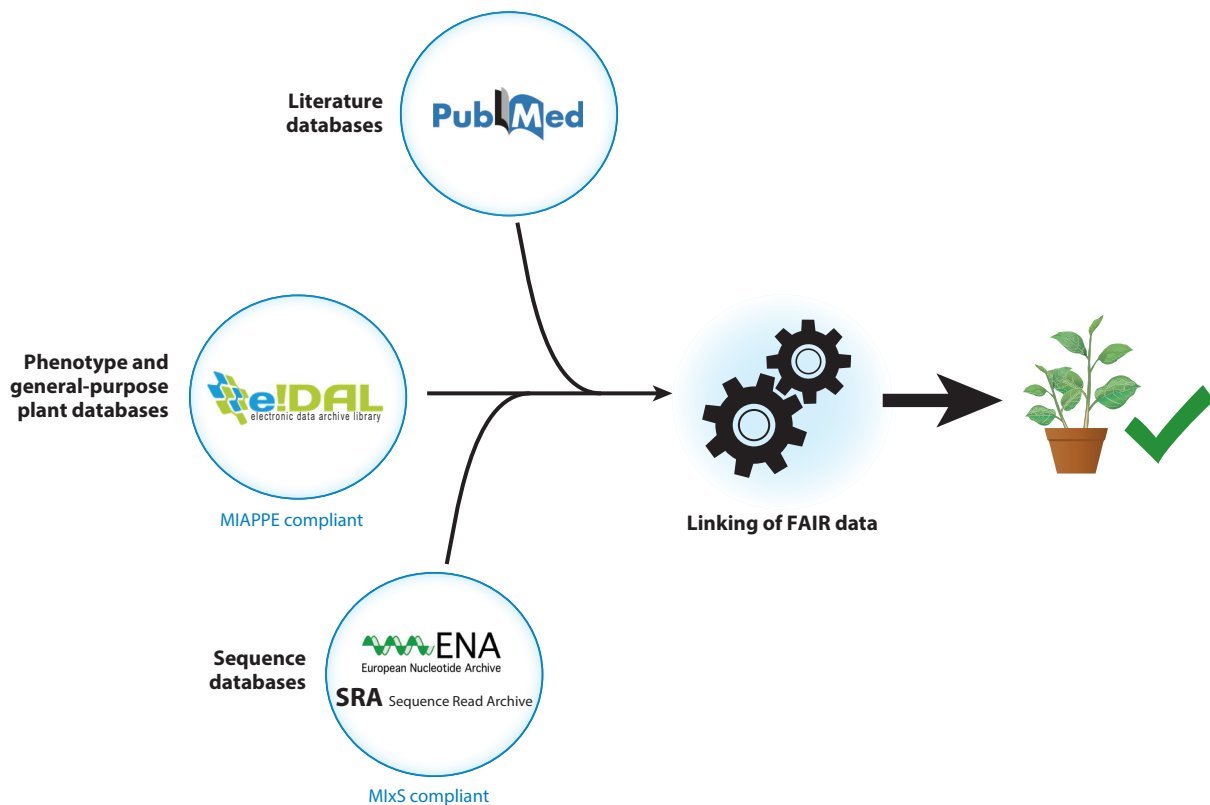


Figure 4

The integration and understanding of phenotypic data require that they be findable, accessible, interoperable, and reusable (FAIR). FAIR data use applies standards—for instance, from the Minimum Information About a Plant Phenotyping Experiment project (MIAPPE)—to enable data integration across sources. These data may include the genomes and sequences centralized in the European Nucleotide Archive (ENA) and Sequence Read Archive (SRA) and governed by Minimum Information about any (x) Sequence (MIxS), information from the literature, and general-purpose data housed in the plant-specific Electronic Data Archive Library (e!DAL). Data integration across these multiple sources may yield better crops and novel fundamental insights into plant processes.

Linking Phenotypes and Genotypes

Methods to bridge phenotyping data to genomics data are progressing rapidly (16) as advances in plant phenotyping are paired with novel developments in plant genome analysis techniques, such as low-cost long-read sequencing (120), long-range chromatin interaction analysis (89), and improved gene annotation (123). In the simplest case, bridging is achieved using classical QTL analysis (24), but more recently multiple experiments have relied on GWASs (150) or more sophisticated genomic selection (76) and other modeling techniques. The GWAS approach alone has led to success stories especially in maize crops (reviewed in 154). Multi-QTL studies, which use statistics to investigate multiple phenotypes, are becoming more popular (127). They require meticulous experimental planning and significant resources. Presently, data integration occurs mostly by association and correlation of multiple QTLs and/or phenotypes in the same population (86, 87, 124, 130), but future approaches may be able to associate and borrow data from different populations. Even for a well-defined experiment, some data integration is essential for statistical

Genomic selection: attempt to predict phenotypes based on large genome-wide marker data sets

ROBOTICS AND DATA SCIENCE FOR PHENOTYPING IN THE FUTURE

Robotics, data science/machine learning, and modern visualization methods will shape future advances in plant phenotyping. Robotics has the potential to act autonomously to accelerate both data acquisition and data analysis, and robotic systems for crop management are becoming increasingly robust and available (142). Autonomous operation on a field might be one of their earliest applications (10). In the future, heavy phenomobiles (54, 119), which are state of the art today, might be replaced by smart-controlled and lightweight fleets of driving and flying sensor carriers (59). When combined with biological knowledge about traits and the sensors of choice, such sensor carriers will allow breeders to overcome some of their biggest problems—namely improving throughput and performing simultaneous, quantitative measurements at different locations. Modern data analysis tools have already found application in the analysis of large imaging data sets in plant phenotyping (105); however, there are many more applications, such as linking phenotypic analysis with environmental and time-series data. The combination of these emerging technologies has the potential to generate closer interaction between breeding science and crop management.

analysis. As phenotyping continues to cross-link with other disciplines, data management, sharing, and challenges for wider use will continue.

MOMENTUM FROM CROSS-LINKING WITH OTHER TECHNOLOGIES

Phenotyping is expanding to management using smart and precision farming, a key development for prebreeding and breeding (142). Novel tools for robotics and automation of phenotyping are being combined with models and computational tools to guide actions taken by farmers on farms (see the sidebar titled Robotics and Data Science for Phenotyping in the Future).

Advances have been made in visualization of weeds in fields for automated and real-time action to kill weeds (33) and in recognition of pathogens on leaves to help farmers apply sprays (70). Phenotypic characterization is crucial in precision horticulture (134). Plant scientists are collaborating with engineers, computer scientists, and vision and robotics researchers in new initiatives toward this aim [e.g., Robotics and Phenotyping for Sustainable Crop Production (PhenoRob)]. The cross-disciplinary momentum associated with applying phenotyping technologies to on-farm management may strongly promote associations between agronomy and breeding. It has long been known that proactively creating agronomy \times breeding synergies on farms is the fastest route to stable and sustainable production security (49).

Phenomobile: vehicle that carries phenotyping instruments; generally operated by a person in fields with experiments to phenotype plants

OUTLOOK AND FUTURE DEVELOPMENTS

Despite significant advances in recent years, plant phenotyping remains a bottleneck for progress in plant sciences and breeding. We still do not have sufficient throughput and capacity to handle large-scale populations with the required accuracy and low cost for targeting traits or their proxies. However, recent developments—ranging from the formation of large-scale networks providing improved technology and access to state-of-the-art methods, to dissemination of technologies through wide industry participation, to phenotyping for root traits in the field, to community-driven integrated data management concepts—indicate how future demands could be met. Efficient scientific and technological progress will require dialogue among users, technology developers, and infrastructure providers. Implementation of practical solutions will require integration

of contemporary phenotyping techniques into the workflow of the breeding-related sciences and breeding itself, and, in the future, agronomy and on-farm management.

SUMMARY POINTS

1. Contemporary plant phenotyping is central to prebreeding in efforts to discover new complex traits, identify diversity that is heritable using high-capacity selection, and generate reusable data. While technologies are rapidly developing, access is being given to users from academia and industry to robust methodologies, technology development, protocols, and data integration.
2. Emerging and future phenotyping methods can be integrated within breeding, especially in the areas of field and early-generation germplasm development.
3. Phenotyping in controlled environments should not aim to mimic the complexity of field conditions; rather, it will contribute to our understanding of specific and dynamic plant–environment interactions, analyses of genetic diversity, and analyses of ex post routes of successful breeding.
4. Noninvasive field phenotyping—although still focused predominantly on aboveground traits—is developing into a robust and accessible tool that supports scientists and breeders in the analysis of crop features and the development of improved properties across heterogeneous and dynamic field situations.
5. Root phenotyping is developing rapidly to improve our understanding of key performance features in controlled environments. Recent developments show some advancement toward field phenotyping, especially in combination with root structure–function models. However, noninvasive root phenotyping in the field is still not possible, and significant advancements are needed to achieve this important target.
6. Data integration is paramount for the integration of plant phenotyping into present-day science and breeding domains. Ongoing community efforts toward this end include a wide range of standardization goals, from the level of generating quality data to their integration in large, diverse multiomics data landscapes.
7. Novel technical opportunities will emerge from the integration of robotics and data science to enhance accuracy and throughput in all aspects of noninvasive plant phenotyping, including integration with agronomy and on-farm management.

FUTURE ISSUES

1. Improving knowledge about genetic resources and their phenotypic potential will continue to be crucial to advance the use of natural genetic diversity.
2. Cooperation and open science are crucial for advancing plant phenotyping as a valuable discipline for plant breeding.
3. Novel technologies and data science will continue to drive progress in achieving the potential of quantitative and noninvasive plant phenotyping.
4. The increasing availability of affordable and robust methods connected to smartphones, mobile computing devices, and open computer architectures opens new routes beyond highly elaborate and expensive phenotyping methods.

5. The integration of robust plant phenotyping technologies into the workflow of breeders, seedbanks, and scientists will continue to gain attention as costs fall and demands for food, feed, and resource efficiency increase globally.
6. The diversity of phenotypic data, the many different forms of the data, and the variability and development of plant features in space and time in interactions with dynamic environments require new approaches beyond classical (bio)informatics.

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The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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57. Defines the photosynthetic traits for phenotyping by the LIFT method.

70. Provides an overview of hyperspectral sensors and imaging technologies for assessing plant-pathogen interactions on leaves and canopies.

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RELATED RESOURCES

1. Breeding API (BrAPI). <https://brapi.org/>
2. European Infrastructure for Multi-Scale Plant Phenotyping and Simulation for Food Security in a Changing Climate (EMPHASIS). <https://emphasis.plant-phenotyping.eu/>
3. European Life Science Infrastructure for Biological Information (ELIXIR). <https://www.elixir-europe.org/>
4. European Plant Phenotyping Network (EPPN). <http://www.plant-phenotyping-network.eu/>
5. European Plant Phenotyping Network (EPPN2020). <https://eppn2020.plant-phenotyping.eu/>
6. French Plant Phenomic Infrastructure (PHENOME-FPPN). https://www.phenome-fppn.fr/phenome_eng
7. G20 Wheat Initiative. <http://www.wheatinitiative.org/>
8. German Plant Phenotyping Network (DPPN). http://www.dppn.de/dppn/EN/Home/home_node.html
9. International Plant Phenotyping Network (IPPN). <https://www.plant-phenotyping.org/>
10. Minimum Information About a Plant Phenotyping Experiment (MIAPPE). <http://www.miappe.org/>
11. Robotics and Phenotyping for Sustainable Crop Production (PhenoRob), German Research Funding Excellence Cluster. <http://www.phenorob.de/>