Picturing the future of food

Anna L. Casto | Haley Schuhl | Jose C. Tovar | Qi Wang | Rebecca S. Bart | Noah Fahlgren | Malia A. Gehan

Donald Danforth Plant Science Center, 975 N. Warson Road, Saint Louis, MO 63132, USA

Correspondence
Noah Fahlgren, Donald Danforth Plant Science Center, 975 N. Warson Road, St. Louis, MO 63132, USA.
Email: nfahlgren@danforthcenter.org
Malia A. Gehan, Donald Danforth Plant Science Center, 975 N. Warson Road, St. Louis, MO 63132, USA.
Email: mgehan@danforthcenter.org

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Abstract
High-throughput phenotyping (HTP) has emerged as one of the most exciting and rapidly evolving spaces within plant science. The successful application of phenotyping technologies will facilitate increases in agricultural productivity. High-throughput phenotyping research is interdisciplinary and may involve biologists, engineers, mathematicians, physicists, and computer scientists. Here we describe the need for additional interest in HTP and offer a primer for those looking to engage with the HTP community. This is a high-level overview of HTP technologies and analysis methodologies, which highlights recent progress in applying HTP to foundational research, identification of biotic and abiotic stress, breeding and crop improvement, and commercial and production processes. We also point to the opportunities and challenges associated with incorporating HTP across food production to sustainably meet the current and future global food supply requirements.

1 INTRODUCTION

Increases in food demand are driven by an increasing global population. By the year 2050, the current world population of 7.6 billion is projected to reach 9.7 billion (United Nations & Social Affairs, 2019). Notably, more than 820 million people are currently undernourished, and the prevalence of malnutrition has remained just under 11% after a decade of steady decline (FAO, 2019). In addition, more than 2 billion people worldwide experience moderate to severe food insecurity, putting them at risk of undernourishment (FAO, 2019). The increasing demand for food, fuels, and fiber due to a growing population and shifting diets, and the disruption of agricultural systems due to the effects of climate change threaten to increase food insecurity further (Godfray et al., 2010). Global crop yields have steadily increased since the 1960s, but this trend is not projected to be sufficient to meet future demand (Ray et al., 2013). Furthermore, past trends indicate that increases in crop production will lead to increased land clearing, deforestation, and land use, which are already at unsustainable levels (Foley et al., 2011; Tilman et al., 2011).

Food systems include all activities involved in the production, processing, distribution, consumption, and disposal of food (FAO, 2018). A challenge facing food systems is that food production, nutritional quality, processing, and distribution need to be increased and improved to eliminate current and projected food insecurity, and improvements need to be achieved sustainably. One facet of increasing the sustainability of food systems is the inclusion of new technologies and new applications of technologies. Here we focus on how imaging technologies are being used to improve production,
quality, and processing of crops that are an integral part of the food system (Figure 1). Many of the same imaging technologies are being used in research, production, and post-harvest assessment of crops, but these research communities are often siloed and do not interact as frequently as one might expect.

Phenotyping, the assessment of physical, physiological, morphological, and qualitative properties of crops, is a fundamental aspect of research, breeding, and food quality assessment. A plant phenotype is the observable manifestation of a plant’s genetic information interacting with its environment. Manually measuring and assessing crop phenotypes can be expensive in terms of time and labor. A relatively simple measurement such as plant height can be done with a ruler, but this phenotype becomes more challenging when height measurements are required across fields of plants over time (a challenge of scale). High-throughput phenotyping (HTP), and particularly image-based HTP methods, has the potential to revolutionize plant research, food production, and quality assessment by significantly reducing the need for human intervention, thereby accelerating processes and minimizing error at all stages in the global food system (Araus & Cairns, 2014; Contador et al., 2015; Humplík et al., 2015b; Pu et al., 2015).

High-throughput phenotyping covers a broad set of technologies that involve data collection (e.g., imaging and sensors, robotics, etc.), data analysis (e.g., computer vision, machine learning, etc.), and data interpretation (e.g., modeling). Therefore, the development of HTP platforms requires robust interdisciplinary collaboration between plant science, agricultural science, engineering, computer science, data science, mathematics, and other fields of research (Carroll et al., 2019). High-throughput phenotyping has made significant progress in recent years to better inform research (Bucksch et al., 2014; Chaerle et al., 2006; Devadas et al., 2015; Fujita et al., 2018; Ghosal et al., 2018; Granum et al., 2015; Lamb & Brown, 2001; Mutka et al., 2016; Pérez-Bueno et al., 2019; Raji et al., 2015; Strock et al., 2019; Vadez et al., 2015; Yasrab et al., 2019), breeding (Campbell et al., 2015; Holland et al., 2003; Kumar et al., 2015; Mir et al., 2019; Pauli et al., 2016; Rounsley & Last, 2010), and decision-making (Rady et al., 2017; Schimmelpfennig, 2016; Simko et al., 2015; Zhang et al., 2019) throughout crop development and production.

This review provides a summary of high-throughput phenotyping technologies. This review identifies areas of phenomics that need more community attention.

2 HTP TECHNOLOGIES AND ANALYSES

Image-based HTP technologies can be used across scales from cells (e.g., chlamydomonas phenotyping) to fields (Dhondt et al., 2013). Cell-scale, organ, and whole plant-scale, growth chamber, greenhouse, and field-scale applications are amenable to different HTP platform strategies (Figure 2), but in general HTP technologies use three main platform strategies for acquiring data: (a) moving an imaging platform to stationary plants; (b) moving plants to a stationary imaging platform, and (c) using an array of imaging devices over stationary plants. Most field-based platforms rely on mobile imaging platforms including handheld devices, ground and aerial vehicles, gantries, and satellites (Shakoor et al., 2017). The advantage of field-level systems is the ability to phenotype large populations with replication in relevant field conditions. For a detailed overview of field-based phenotyping platforms and sensors, we recommend a recent review by Shakoor et al. (Shakoor et al., 2017).

Platforms for controlled-environment research experiments can include mobile imaging platforms but more commonly move plants through imaging stations (Acosta-Gamboa et al., 2016; Brien et al., 2013; Cabrera-Bosquet et al., 2016; Chen et al., 2014; Das Choudhury et al., 2018; Fahlgren et al., 2015; Fujita et al., 2018; Tisné et al., 2013; Vello et al., 2015; Yang et al., 2014). These highly automated platforms are costly but offer the advantage of controlled environments and precise automated treatments, such as water and nutrients that can be applied uniformly and frequently. Compared with field-scale experiments, controlled-environment systems can be limited in terms of replication and plant size. In addition to conveyor systems, arrays of low-cost computers and cameras have been used to collect data in controlled-environment systems (An et al., 2017; Minervini et al., 2017; Tovar et al., 2018). Array-based imaging systems can simultaneously collect data on large numbers of plants if many cameras are set up but can require more technical expertise for management. Array-based imaging can also be used to collect 3D information (e.g., stereo imaging). As a final option, researchers may use manual imaging techniques to avoid the upfront cost.
High-throughput phenotyping (HTP) technologies and applications span across the entire food system from predicted yield estimations to post-harvest food quality assessments. The HTP technologies include digital, near-infrared, fluorescence, thermal, multi/hyperspectral, and 3D imaging.

Once an appropriate platform strategy is identified, researchers must select an imaging technology. Many imaging options are described in Table 1. In each case, a universal tradeoff exists between throughput and resolution (spatial, spectral, and temporal). For large morphological differences, low-resolution phenotyping will likely suffice. In contrast, more subtle phenotypes may benefit from high-resolution imaging, including technologies that expand beyond the visible range of the electromagnetic spectrum (Figure 3). There is also a tradeoff between the size of the cell and the scale at which imaging is performed.
| Technology          | Description                                                                 | Features (scale: 1–5, low–high)                                                                 |
|---------------------|------------------------------------------------------------------------------|---------------------------------------------------------------------------------------------|
| Digital imaging     | Ubiquitous, low-cost, and easy-to-use. Typical sensors capture broad spectrum | Cost: Data size: Acquisition rate: Data processing: Data interpretation:                      |
|                     | blue, green, and red light intensity in a 2D pixel array. Images are         |                                                                                             |
|                     | compatible with a broad set of available tools.                              |                                                                                             |
| Near-infrared       | Sensors capture broad near-infrared spectrum light intensity in a 2D pixel    | Cost: Data size: Acquisition rate: Data processing: Data interpretation:                      |
|                     | array. Images are often lower-resolution than standard digital cameras but   |                                                                                             |
|                     | still compatible with a broad set of available tools. Data can be used to    |                                                                                             |
|                     | estimate relative plant water content (Seelig et al., 2008).                 |                                                                                             |
| Fluorescence        | Specialized imaging chambers and/or platforms are required to combine an      | Cost: Data size: Acquisition rate: Data processing: Data interpretation:                      |
|                     | excitation source and a detector. Induced chlorophyll fluorescence can be    |                                                                                             |
|                     | measured. In some systems, multiple images are acquired and need to be input |                                                                                             |
|                     | into a formula (e.g., $F_v/F_m$) for interpretation (Baker, 2008).           |                                                                                             |
| Thermal             | Thermal cameras contain a 2D array of infrared radiation sensors called      | Cost: Data size: Acquisition rate: Data processing: Data interpretation:                      |
|                     | microbolometers (Syllaios et al., 2000). The electrical resistance of the   |                                                                                             |
|                     | sensor material changes in response to long-wave infrared wavelengths.       |                                                                                             |
|                     | Thermal image data can be converted to grayscale images for use with         |                                                                                             |
|                     | existing software packages.                                                 |                                                                                             |
| Multi/Hyperspectral | Sensors can capture and discriminate wavelengths in the visible, near-infrared | Cost: Data size: Acquisition rate: Data processing: Data interpretation:                      |
|                     | (NIR), short-wave infrared, ultraviolet (UV), and other ranges. Multispectral |                                                                                             |
|                     | sensors refer to sensors with >3 bands but fewer than 30. Hyperspectral      |                                                                                             |
|                     | imaging systems capture >30 bands and the more sophisticated systems can     |                                                                                             |
|                     | capture more than 1,000 bands. Hyperspectral systems are substantially more   |                                                                                             |
|                     | costly than multispectral sensors but give the advantage of significantly    |                                                                                             |
|                     | higher band resolution and greater number of bands. Hyperspectral imaging     |                                                                                             |
|                     | technologies have varied and complex systems for data acquisition (Lu & Fei, |                                                                                             |
|                     | 2014; Ravikanth et al., 2017). Data files are not standard images and        |                                                                                             |
|                     | require more specialized knowledge and software to use (Curran et al., 1997;  |                                                                                             |
|                     | Mershon et al., 2015; Pauli et al., 2017; Wang et al., 2018; Woolley, 1971). |                                                                                             |
| LIDAR/Laser scanner | Sensors measure the distance from the camera to points in 3D space by       | Cost: Data size: Acquisition rate: Data processing: Data interpretation:                      |
|                     | illuminating objects with laser light and measuring the time of reflectance   |                                                                                             |
|                     | (Lin, 2015). The resulting point cloud data contain potentially billions of   |                                                                                             |
|                     | points, resulting in large datasets that need specialized tools for analysis  |                                                                                             |
|                     | (Lin, 2015).                                                                |                                                                                             |
| Tomography          | Tomographic techniques utilize penetrating electromagnetic waves to image    | Cost: Data size: Acquisition rate: Data processing: Data interpretation:                      |
|                     | 2D sections of plants and reconstruct 3D structures. Examples used in plant   |                                                                                             |
|                     | phenotyping include MRI, X-ray CT, PET, and OPT (Clark et al., 2011; Jiang    |                                                                                             |
|                     | et al., 2019; Li et al., 2019; Tracy et al., 2015; van Dusschoten et al.,    |                                                                                             |
|                     | 2016; Wang et al., 2015). Data processing is complex, but relatively easily   |                                                                                             |
|                     | interpretable.                                                              |                                                                                             |
target object and the amount of detail that can be gathered. High-resolution imaging may better identify variation in certain phenotypes, which could be useful when the variation is used for genetic mapping, but also comes at the cost of data storage and computation of larger quantities of data. Li et al. (2014b) and Yang et al. (2020) provide detailed classifications of plant phenotyping applications by imaging technology and plant species under study, but the breadth of potential research questions and applications of image-based phenotyping is wide and expanding.

After data collection, individual images can be analyzed manually to measure features of interest with tools like ImageJ, a free image analysis software (Schneider et al., 2012). Manual analysis has the advantage of being flexible and utilizing human pattern recognition abilities to identify complex structures, but analyses with higher degrees of automation are often desirable due to the size of datasets from HTP platforms, which are often on the order of tens to hundreds of thousands of images. Automated analyses can also help reduce bias and maintain experimental consistency. Hundreds of software tools have been developed for a wide range of plant image analysis tasks and many are cataloged at https://www.quantitative-plant.org/ (Lobet et al., 2013). In general, there is a tradeoff between the levels of automation and flexibility image analysis tools provide. Software dedicated to a specific task (e.g., measuring a single flattened leaf) is often more automated but is also less adaptable to new tasks, whereas software that can be adapted to a broad set of problems are often less approachable since choosing components, building workflows, and customizing parameters require technical knowledge. Once a tool has been identified and parameterized, many software programs have capabilities that can be used to batch process hundreds to millions of images. Despite a large number of available options, many tools are not actively maintained after publication (Lobet, 2017). Sustained development and maintenance of flexible image analysis tools require both expertise in software engineering and the target domain. A major challenge associated with HTP software is to unify development efforts where possible and build tools around a common interoperability framework that allows developers to build on previous efforts; otherwise the community is constantly reinventing frameworks rather than functionality.

Most forms of computer vision software begin with the segmentation of the target object from the background scene. Once objects of interest (cells, plant organs, individual plants, plots, or entire fields) are separated from the background, characteristics are quantified to measure or model underlying traits that may contribute to growth, yield, and/or tolerance to biotic or abiotic stressors. In addition to traditional computer vision approaches, machine learning tools are increasingly popular within the HTP field (Marcuzzo et al., 2009; Tsafiratis & Scharr, 2019). Machine learning approaches allow prediction, classification, or quantification of traits that are otherwise difficult to measure with traditional image analysis techniques but come at a much higher cost of computation,
time, and expertise. Generally, machine learning algorithms define models to describe patterns within data and are trained using labeled data (supervised) or trained using the inherent structure of the data (unsupervised). Trained models are applied to unseen data or new datasets with similar patterns to make predictions (Bishop, 2006). Deep learning algorithms, which are a subset of machine learning methods, use an artificial neural network architecture to bypass the requirement for feature engineering during model building (LeCun et al., 2015). Deep learning tools require significantly larger training datasets than other machine learning techniques. Transfer learning (Harris et al., 2008), where models build off one another, may allow for models to be repurposed for similar problems without the need for collecting large ground-truth datasets each time. The availability to collect large quantities of labeled training data is a major bottleneck that limits the use of machine learning methods in HTP of crops because annotation can be labor-intensive, species-specific, and can require plant biology expertise. However, crowdsourcing and the development of synthetic data sets are promising avenues to mitigate these issues (Giuffrida et al., 2018; Toda et al., 2020; Tsaftaris & Scharr, 2019; Ubbens et al., 2018; Ward et al., 2018; Zhou et al., 2018). In general, the HTP field will experience accelerated progress if more datasets are made public and if efforts in phenotyping software development focus on making tools that are freely available to other researchers, sustainable, flexible across platforms and species, and well-documented (Tsaftaris & Scharr, 2019).

3 | HTP-ENABLED RESEARCH, BREEDING, AND CROP IMPROVEMENT

Many opportunities exist for improved efficiency within the food system. For example, plant gene discovery, identification of beneficial microbes, and precision gene editing are all likely to yield novel strategies for increasing food production and decreasing agricultural inputs. Similarly, improved methods for quickly and reliably predicting yield will be useful to genomic selection and to accelerate the timeline for conventional crop improvement. Phenotyping has historically been a rate-limiting step in the development of crops because manual measurements to quantify phenotypes are low-resolution and time and labor-intensive. Manual measurements can also introduce variation due to differences in measurement technique, fatigue, and human error. High-throughput phenotyping technologies are being touted as the solution for many of these challenges, but it is not the technologies themselves, rather the standard adoption of analysis methods, that will ultimately lead to widespread use. The field of plant phenomics, which focuses on best practices for data collection and analysis methodologies, is still actively developing.

### 3.1 Feature identification: Using HTP to quantify plant morphology

One of the most important and challenging questions HTP technologies have been applied to is the estimation of crop yield. In some cases, where yield is related to biomass, such as in pea (*Pisum sativum* L.) and wild tomato (*Solanum pimpinellifolium* L.), projected plant area correlates well with yield (Humphlik et al., 2015a; Johansen et al., 2019; Sankaran et al., 2018). However, yield is a complex trait and the relationship between yield and image-derived features (e.g., biomass, color, height, etc.) is often species-specific. In addition to yield estimation methods that use visible plant traits, spectral reflectance information is also used. Healthy, photosynthetically active plants absorb most red and blue light and reflect other wavelengths of light, so several indices based on the ratios of absorbed and reflected wavelengths have been developed that correlate with yield, plant health, and photosynthetic performance with varying success (Condorelli et al., 2018; Johansen et al., 2019; Pauli et al., 2016; Sankaran et al., 2018). Sankaran et al. used unoccupied aerial systems (UAS)-based multispectral imaging of dry bean under drought and nitrogen stress to calculate green normalized difference vegetation index (GNDVI) of dry bean plants over time (Sankaran et al., 2018). Interestingly, they found that GNDVI had the highest correlation with yield at 60 days after planting (DAP) in both control and drought treatments, but the correlation decreased by maturity at 75 DAP (Sankaran et al., 2018). Correlations between reflectance features and yield present an opportunity for yield prediction and early selection of better performing genotypes. However, the study by Sankaran et al. (2018) also demonstrates that there is a dynamic relationship between crop yield and spectral features, and that selection of measurement time points is a critical consideration during phenotyping.

In addition to HTP advances applied to aboveground plant features, root phenotyping holds further potential for improving overall plant health and yield. Root phenotyping is challenging due to the subterranean location of roots and because of the complex, obscured, and overlapping phenotypes inherent in root structures (Bucksch et al., 2014). Low-cost imaging has been applied to roots grown in clear media, but soil-grown roots generally require more costly technologies such as X-ray, CT, or MRI imaging. Technologies and methods for image-based root phenotyping have been reviewed recently in depth (Atkinson et al., 2019). Measurements such as root number, length, and angle are difficult features to extract, but there are recent examples of success. Due to the branching structures of root systems, several analysis packages have used a path or graph-based approach to measure root phenotypes from 2D images (Bucksch et al., 2014; Das et al., 2015; Seethepalli et al., 2020). Yasrab et al. utilized a deep learning approach to navigate complex root...
structures by segmenting images into the background, first-order root, and second-order root classes (Yasrab et al., 2019). Segmented images were used to quantify total first-order and second-order root length, convex hull area, maximum width, maximum depth, first-order and second-order root count, and centroid depth (Yasrab et al., 2019). The model was originally trained on wheat (Triticum aestivum L.) in growth pouches but displayed the potential for transfer learning to new species and image types (Yasrab et al., 2019). Using a fraction of the number of images for additional training, the model was effectively used with rapeseed (Brassica napus L.) seedlings also grown in growth pouches and arabidopsis [Arabidopsis thaliana (L.) Heynh.] grown on agar plates (Yasrab et al., 2019). The ability of deep learning networks to adapt to different plant species via transfer learning is encouraging since it would suggest that researchers can build upon existing models, which alleviates much of the burden of new annotation and training work. Continued advancement in imaging technologies and image analysis will further complement or reduce the need for manual phenotyping, which is still a large bottleneck in root morphology research.

3.2 Feature identification: HTP applied to biotic stresses

Biotic stress or plant pathogen infection is a major cause of crop loss (Savary et al., 2006) and high-throughput phenotyping is already being used to work toward earlier detection of plant disease and accelerate research in plant pathology including the development of disease-resistant crops. The most straightforward application of HTP for detection and quantification of plant–pathogen/insect interactions is perhaps the use of red, green, blue (RGB) images taken with digital cameras. Color digital imaging has been successfully used to detect plant insect pests (Cao et al., 2015; Ebrahimi et al., 2017; Fennell et al., 2018) and to monitor insect behavior throughout infestation (Thoen et al., 2016). These technologies have been reviewed in detail by Goggin et al. (Goggin et al., 2015). Analysis of RGB images is also being adopted by research labs to aid other basic research endeavors. Researchers are able to use low-cost cameras and widely available image analysis software to accurately quantify disease phenotypes like leaf area affected by chlorosis that might otherwise be scored visually. For example, Mutka et al. used ImageJ (Schneider et al., 2012) to analyze images from a low-cost Raspberry Pi microcomputer and camera to track cassava bacterial blight symptom development over time (Mutka et al., 2016). Again, many of the tools available to analyze RGB images of plants are cataloged on the Quantitative Plant database (Lobet et al., 2013; Lobet, 2017).

In the case of studying root interactions with soil-borne (edaphic) pests and pathogens, root phenotyping systems can be applied. Laser ablation tomography (LAT), which is capable of detailed and efficient 3D imaging, has been used to destructively analyze root anatomy under infection with edaphic pests and pathogens (Strock et al., 2019). The high resolution of LAT scans can collect compositional information at a level of precision that is difficult to match with non-destructive techniques. Laser ablation tomography is suited to this problem because edaphic organism infestation impacts ultraviolet (UV) excitation of root tissues, thus resulting in differential autofluorescence emission (Strock et al., 2019). Laser ablation tomography has been used to quantify and classify root tissues and anatomical features for crop roots infected with pathogens and pests, such as Fusarium, cyst nematode, and western corn rootworm (Strock et al., 2019). These same techniques can be applied to a wide range of plant species and pests since the autofluorescence spectra emitted from various tissues are contrasting, allowing for differentiation between tissues in resulting images.

Stress can manifest as a complex of phenotypes. One of the major challenges for image-based phenotyping of biotic stress is accurately discriminating between stresses. For example, many pathogens cause leaf chlorosis that is easily confused with nutrient stress and vice versa. Traditionally, plant biotic stress has been identified and quantified using a limited number of techniques that all rely heavily on visual assessment. These approaches are time-consuming and susceptible to human error, even for trained plant pathologists (Koch, 1876; Ravichandra, 2013). Recent phenotyping methods aim to increase the sensitivity, reliability, and specificity of stress detection and classification. In a promising example of biotic and abiotic stress discrimination, Ghosal et al. (2018) used RGB images of detached leaves from healthy and stressed soybean [Glycine max (L.) Merr.] plants to train a deep convolutional neural network (DCNN) to classify leaves into nine biotic and abiotic stress categories. The DCNN was also able to accurately classify images of other plant species with iron and potassium deficiency, which supports transfer learning as a viable option for researchers to build on existing deep learning models (Ghosal et al., 2018).

The use of sensors that extend beyond the visible range (Figure 3) may be particularly useful in stress detection and discrimination. Most biotrophic and hemibiotrophic pathogens invade plant tissues prior to eliciting symptoms visible to the human eye. A significant goal in the field of phonomics is to identify infections early enough to enable proactive disease management. Fluorescence imaging has been used in the field to detect plant biotic stresses since many pathogens and pests impact photosynthetic productivity, which can be assayed by measuring chlorophyll fluorescence. For example, Raji et al. (2015) used sunlight-induced chlorophyll fluorescence images to detect early stage mosaic disease in cassava (Manihot esculenta Crantz) in the field. In another recent example, hyperspectral indices were used to
discriminate and quantify stripe rust severity and nitrogen deficiency in wheat crops under field conditions (Devadas et al., 2015). The reflectance in mid-green to red wavelength regions significantly correlated to rust infection severity, whereas the NIR region provided the strongest correlation with levels of nitrogen deficiency (Devadas et al., 2015). These results are encouraging, but the challenge that still remains is how to scale these methods (e.g., use of spectral indices and mathematical models to rate disease) to the field so they can be used more broadly. Hyperspectral image sensors are highly sensitive to external conditions, and a model fit to data collected in one crop species or location likely will have limited applications to other systems without recalibration.

Thermal imaging is another approach for detecting plant diseases using non-visible spectrum wavelengths because pathogen infection often triggers stomatal closure in plants, which results in a decrease in transpiration rate and change of leaf temperature. Thermal imaging has been used to detect biotic stress responses in plants caused by bacteria (Pérez-Bueno et al., 2019), fungi (Granum et al., 2015), and viruses (Chaerle et al., 2006). It also has been used to detect grain infested by rusty grain beetle and cowpea seed beetle (Chelladurai et al., 2012; Manickavasagan et al., 2008). In some cases, data fusion, the process of integrating data from different sources, can provide more reliable, accurate, and useful information. For example, Mahlein et al. (2019) used hyperspectral, fluorescence, and thermal imaging to monitor *Fusarium* head blight of wheat in controlled conditions. Compared with individual sensors, the combined multi-sensor parameters from hyperspectral-fluorescence or hyperspectral-thermal imaging significantly improved the accuracy of detection (Mahlein et al., 2019). Although research into early detection of plant diseases is promising, the current cost of imaging technologies such as hyperspectral and thermal sensors and the challenges associated with analyzing these image types (e.g., data fusion, data size etc.) limit their widespread use.

### 3.3 Feature identification: HTP applied to abiotic stresses

Drought is one of the largest causes of global crop loss (Challinor et al., 2014) and is one of the most studied abiotic stresses (El Aou-Ouad et al., 2018; Gago et al., 2015). Drought can be acute or occur progressively, and plant responses to drought stress are dynamic throughout spatial and temporal scales. Non-destructive HTP can measure plant responses to stress over time and help untangle the temporal effects of water limitation on plant phenotypes. In one approach, Vadez et al. (2015) measured drought responses using NIR laser scanners to create 3D point clouds that estimate leaf area of plants grown outdoors in pots placed on analytical scales. Point clouds can be used to estimate leaf area because they are large sets of coordinates in three-dimensional space that represent the external surfaces of objects. The continuous measurement of leaf area and water loss allowed researchers to measure differences as small as 13% in leaf area and diurnal transpiration rate (Vadez et al., 2015). Notably, Vadez et al. (2015) studied four crop species—peanut (*Arachis hypogaea* L.), cowpea (*Vigna unguiculata* (L.) Walp.), pearl millet (*Cenchrus americanus* (L.) Morrone), and sorghum (*Sorghum bicolor* (L.) Moench)—and showed consistently strong correlations with ground truth measurements of leaf area. This result was important because it is not always the case that a specific method will work well on different species or even across developmental stages of the same species (Sankaran et al., 2018). Drought stress has also been studied in root systems, using various phenotyping approaches, including non-invasive X-ray computed tomography (CT), which are reviewed extensively in Wasaya et al. (2018).

Temporal thermal imaging in controlled environments allows detailed investigations of plant water-use efficiency under drought because well-watered plants typically have a lower leaf temperature compared with water-limited plants since leaf temperature is related to transpiration and stomatal conductance. Controlled, automated environments also allow for precise measurements of how plants respond to water limitation. Fujita et al. (2018) combined thermal imaging and the automated watering system in the Riken Integrated Plant Phenotyping System to determine that stomatal closure in arabiadopsis plants occurs at a specific water content of 1.5 g of water per 1 g of dry soil. Establishing the specific conditions that trigger stomatal closure in a plant species enables researchers to identify variation in drought responses in natural accession or mutant populations, which subsequently allows for the underlying genetic contributors of drought response to be identified. Thermal imaging also allows nearly instantaneous measurement of the temperature of individual plants or entire fields. The speed of thermal imaging compared with manual leaf/canopy temperature measurements decreases variability that is introduced by fluctuations in the environment (wind, shade, etc.) during measurements (Deery et al., 2016; Sankaran et al., 2018).

Abiotic stresses can affect photosynthesis by damaging photosystems, changing chlorophyll content, and altering stomatal aperture. Fluorescence imaging has been used to monitor photosynthetic parameters such as the quantum efficiency of photosystem II ($F_v/F_m$) under several abiotic stresses (Baker, 2008). In a study of two morphologically similar pea varieties under cold stress, $F_v/F_m$ measurements decreased in both varieties during cold treatment; however, one variety showed a smaller decrease in $F_v/F_m$ and faster growth (measured by projected area from RGB images) (Humphlik et al., 2015a). Fluorescence imaging was also shown to be sensitive enough to distinguish between
changes in chlorophyll fluorescence in two morphologically similar varieties (Humplík et al., 2015a) and was able to detect significant changes in light-adapted photosynthetic parameters after just one day of salt stress (Awlia et al., 2016). These examples demonstrate the sensitivity of chlorophyll fluorescence imaging for detecting abiotic stress at the plant level. Portable chlorophyll fluorescence sensors have been available for many years for use on single leaves, and specialized growth/imaging chambers now allow multi-plant fluorescence imaging; however, field-level image-based measurements of $F_v/F_m$ are still logistically difficult due to the need for canopy-scale dark adaptation and saturating light pulses. One technology that may address this limitation is laser-induced fluorescence transient (LIFT) technique, which allows remote or platform-based measurement of chlorophyll fluorescence in the light without canopy-scale saturating light pulses (Kolber et al., 2005). There are still many opportunities for new technologies to fill such gaps in phenotyping capabilities and increase throughput even further.

3.4 Population scale: Gene discovery, breeding, and selection

As genotyping technology has improved and become more affordable, the scale at which researchers can identify genetic variation in plant populations has increased rapidly (Rounsley & Last, 2010). However, quickly and accurately measuring large-scale phenotypic variation has not improved at the same pace, creating the “phenotyping bottleneck.” Combined with current advances in genotyping, HTP can accelerate and improve genetic studies for breeding and gene discovery. One way in which image-based phenotyping improves genetic association studies is that HTP improves the reproducibility of measurements. A comparison of hyperspectral image traits from UAS and tractor-mounted cameras found that both HTP platforms increased trait reproducibility compared with hand measurements of chlorophyll content and biomass in a mapping population of durum wheat (Triticum durum Desf.) (Condorelli et al., 2018). This decrease in variation between replicate measurements increased the variation explained by all loci associated with variation in this quantitative phenotype (quantitative trait loci, QTL) identified in the study (Condorelli et al., 2018). In addition to increased accuracy, HTP facilitates the non-destructive measurement of a phenotype over time, which allows for observation of the changing effect of QTL throughout a season. For example, Pauli et al. (2016) imaged a cotton (Gossypium hirsutum L.) population in well-watered and water-limited conditions with hyperspectral and thermal cameras several times throughout a season and observed that canopy temperature QTL changed over time. If canopy temperature QTL had been mapped at a single time point likely many important drought-associated genetic regions would have been missed.

A genome-wide association study (GWAS) is a genetics approach to associate variations in the genome to a phenotype. Campbell et al. (2015) used daily RGB imaging along with single nucleotide polymorphisms (SNPs) of a population of rice (Oryza sativa L.) plants to identify SNPs associated with changes in growth rate during salt stress. The ability to associate SNPs with longitudinal growth curves based on temporal image data increased the number of significant SNPs identified (Campbell et al., 2015). By using daily fluorescence imaging, they identified a significant SNP on Chromosome 1 just 2 d after salt treatment, and by Day 14 this SNP became the most significant association identified in the study (Campbell et al., 2015). This is an example of temporal information increasing confidence in identified SNP since it was identified on more than 1 d (Campbell et al., 2015). Hyperspectral indices have also been used as phenotypes in GWAS studies. Normalized Difference Spectral Index (NDSI) is a hyperspectral index shown to have a high correlation with protein content (Sun et al., 2019). The same significant SNP association was identified for rice protein content when using NDSI estimates and traditional measurements of rice protein content (Sun et al., 2019). This result further demonstrated the feasibility of using hyperspectral traits as a substitute for destructive protein content measurements in GWAS, breeding, and post-harvest assessment (Sun et al., 2019). Many additional examples exist for HTP applied to gene and QTL discovery, which are reviewed in Mir et al. (2019). In summary, the application of HTP with plant genetic studies is already advancing plant science and is expected to continue to play a significant role in future basic research applications.

Additionally, HTP is being applied to breeding programs. Rapid assessment of breeding populations and varieties with HTP methods can help breeders make decisions more quickly with fewer resources. The advantage of image-derived phenotypes decreasing measurement variability also applies when phenotyping breeding populations, thus increasing heritability estimates (Holland et al., 2003). For example, handheld IR thermometer readings took ~30 min for one operator to measure 768 plots whereas an aerial thermal camera imaged the same area in seconds, and as a result, broad-sense heritability ($H^2$) nearly tripled when estimated based on the thermal camera data (Deery et al., 2016). Temporal imaging also allows the estimation of dynamic changes in $H^2$ over time and between image types (Chen et al., 2014).

Developing new cultivars can take many years, so predictive models that help breeders select varieties earlier can be useful for improving the efficiency of breeding. In an example of this, NIR spectra measurements and ground truth measurements acquired over 4 yr were used to develop models for soluble sugar concentration and dry matter concentration in apples (Malus domestica Borkh.) that would inform
breeders about which seedlings to remove from early stages of cultivar development (Kumar et al., 2015). Predicted sugar and dry matter concentrations correlated well with actual concentrations at the end of the experiment (Kumar et al., 2015). Earlier culling of less promising cultivars decreases the resources needed to develop new plant varieties.

The ability to capture genetic variation for prediction of future crop performance makes HTP technologies a powerful tool for accelerating plant breeding. Unsupervised machine learning could remove the labor-intensive step of phenotyping breeding populations in crops like strawberries, where manual visual characterization is currently the standard approach. Feldmann et al. (2020) clustered strawberries based on traits extracted from 2D RGB images, such as height and width, horizontal and vertical biomass distribution, and outline-based descriptors, with a mathematical method called the principal progression of k clusters. This study is a good example of translating approaches developed for human facial recognition to plant science.

Capacity for measuring phenotypes is often a limiting factor in both selection for breeding programs and linkage and association studies. Phenotyping large populations by hand requires large amounts of time and labor, but larger populations have clear advantages and are often required for both breeding and genomic studies. Evaluating larger populations can give breeders more information when making selections. Population size becomes especially important in genomic studies where larger populations (>500 individuals) enable detection of medium to small effect QTL and epistatic QTL (Würschum, 2012). Implementation of HTP pipelines open up the opportunity to take advantage of large populations and more efficient investment of time and labor.

4 COMMERCIAL AND PRODUCTION APPLICATIONS

4.1 Applications: Precision agriculture

Precision agriculture refers to the field of crop science that is focused on the collection and utilization of data to make decisions about crop management. One of the most meaningful outcomes of precision agriculture is that it can potentially reduce pesticide and herbicide use and slow the development of resistance to these chemicals. Remote sensing techniques (i.e., those that detect and monitor the characteristics of a plant or group of plants by measuring reflected and emitted radiation from a distance) allow stakeholders to respond to variability in crops including pests, soil conditions, disease, weeds, and other stressors because it is possible to map environmental heterogeneity to GPS coordinates (Lamb & Brown, 2001). The ability to target herbicides to weeds rather than spraying an entire field is already being used by a number of companies (e.g., Robert Bosch GmbH, Blue River Technology, Inc.) and has the potential to save millions of dollars in herbicide costs worldwide and vastly reduce the negative environmental impacts of herbicide use (Clark & Tilman, 2017; Kortekamp, 2011). These companies use imaging and artificial intelligence to identify and differentiate weeds from crops. Through localized herbicide spraying and keeping a record of which herbicides have been sprayed where in the field, they are able to identify herbicide-resistant weeds and use herbicide rotation to eliminate these resistant weeds. Similarly, early detection of plant disease or other biotic stresses in the field can allow producers to rapidly target affected areas for treatment and potentially reduce the yield losses.

Current applications of precision agriculture on U.S. farms include GPS-based yield and soil mapping, GPS tractor guidance systems, and variable rate technology for applying pesticides and fertilizers (Schimmelpfennig, 2016). These technologies have had small positive impacts on yield and profits for the average-sized U.S. farm (Schimmelpfennig, 2016). Wider implementation of existing precision agriculture methods and adoption of new technologies, especially new image-based technologies, remains difficult due to several factors: (a) the upfront cost of deploying wireless sensor networks and HTP platforms; (b) the costs associated with data storage; and (c) the level of technical expertise required (Elijah et al., 2018; Kamilaris et al., 2017). Additionally, for precision agriculture to be put into practice, methodologies need to be robust enough for producers to risk their livelihoods. Extension programs have been at the forefront of translating new research and technology to stakeholders, so greater investment in these programs may be a way to address the barriers associated with implementing new precision agriculture technologies (Aker, 2011). Currently, the avenue to derisked implementation of precision agriculture technologies is to outsource to commercial companies so the burden of investing in HTP platforms, sensor networks, and expertise does not rest on individual stakeholders. Precision agriculture applications of HTP imaging technologies require: (a) data collection and analysis to be done close to real-time; (b) analysis algorithms to be robust to variation in crop growth stage, environment, genotype, and imaging angle; and (c) results from data analysis need to be clear for management decision-making. These challenges are not insignificant, even for companies that have access to large datasets and the data collection platforms (Perry, 2020).

Current research around precision agriculture technologies has the potential to be useful for the management of abiotic and biotic stress. For example, aerial spectral analysis has been successfully used in research applications to detect the laurel wilt disease of avocado (Persea americana Mill.) fields in the early stage of disease with minimal symptoms (De Castro et al., 2015). However, detection of disease needs to be early enough for targeted pesticide application
to be possible without greater crop loss. Thermal imaging is another promising approach for detecting plant diseases because pathogen infection often triggers stomatal closure in plants, which results in a decrease of transpiration rate and change of leaf temperature. As previously mentioned, thermal imaging has been used to detect biotic stresses in plants caused by bacteria (Pérez-Bueno et al., 2019), fungi (Granum et al., 2015), viruses (Chae et al., 2006), and insects (Chelladurai et al., 2012; Manickavasagan et al., 2008).

Variable-rate pesticide and fertilizer application is currently used in precision agriculture but relies on chemical tests of plants and soil to create management maps that are used to prescribe fertilizer application (Schimmelpfennig, 2016). Traditional plant and soil-based testing for nutrient deficiency are labor-intensive, relatively expensive, and slow. Ideally, real-time information on plant and soil status would inform variable rate technologies. Detecting nutrient deficiencies with imaging technology could make variable input programs more efficient. Hyperspectral imaging has accurately estimated plant nitrogen concentration in rice paddy fields (Yu et al., 2013). However, the correlations between nitrogen content and spectral reflectance have been shown to be growth stage-dependent in rice, wheat, and maize (Zea mays L.) (Inoue et al., 2012; Li et al., 2014a; Wei et al., 2019). Hyperspectral analyses have also been used to predict nitrogen content in leaves of wheat and apple (Li et al., 2018; Tan et al., 2018).

Variable rate technology could also be applied to irrigation. Canopy water content of a field of maize was successfully estimated by field reflectance spectra measurements when compared to fresh and dry weight measurements of leaves, stems, and fruits over 2 yr (Zhang & Zhou, 2019). Using the same vegetation indices on all crops is unlikely to be equally effective across all crops and environments and would need to be optimized. The Genomes to Fields Initiative does an excellent job of highlighting the current need for publicly available, well-documented, multi-year, multi-environment datasets that catalog the phenotypic variation in genotype × environment interactions (Lawrence-Dill et al., 2019).

4.2 Applications: Decision making on postharvest quality

Post-harvest and post-storage evaluation of crops are important but labor-intensive steps in food systems where food waste can be substantial (Jarolmasjed et al., 2018; Nourbakhsh et al., 2016). Often the evaluation step involves visual assessment or chemical analyses for grading, pricing, or quality control. Current research in post-harvest food assessment is focused on using technologies that will improve the speed, accuracy, and robustness of decision algorithms that often need to be executed in real-time. Spectral and fluorescence imaging has been applied to examine post-harvest damage of produce (Jarolmasjed et al., 2018; Rady et al., 2017; Simko et al., 2015; Zhang et al., 2019). For example, Lettuce decay indices (LEDI) based on either hyperspectral reflectance or chlorophyll fluorescence were found to be highly correlated with visual ratings of leaf decay after cold storage (Simko et al., 2015). Cold/freezing injury has also been accurately identified after harvest by hyperspectral imaging in peaches (Nourbakhsh et al., 2016) and corn seed embryos (Zhang et al., 2019). Near-infrared (NIR) spectral analysis has been used to detect codling moth infestation in apples after harvest and storage with relatively high accuracy (Rady et al., 2017). Hyperspectral measurements are also promising as a detection method for a physiological disorder called bitter pit in stored apples (Jarolmasjed et al., 2018). Bitter pit begins as a breakdown of internal membranes and later appears as brown spots on the apple flesh (Jarolmasjed et al., 2018). Hyperspectral analysis was able to classify harvested apples as “healthy” or “bitter pit” with up to 100% accuracy, depending on the number of spectral features included in the predictive model (Jarolmasjed et al., 2018). Considerable resources have been wasted on storing and transporting asymptomatic apples that later develop visible bitter pit symptoms and these resources could be saved by implementing hyperspectral imaging for postharvest quality checks (Jarolmasjed et al., 2018).

Replacing manual post-harvest chemical analyses with HTP imaging technologies could also significantly reduce the resources needed to evaluate and grade crops before they reach consumers. For example, RGB imaging and hyperspectral scanning have been applied to quantify the chemical profiles of grapes during the growing season and after transport to wineries (Kemp et al., 2010; Martínez-Sandoval et al., 2016; Porep et al., 2015). Digital color imaging has also been used to analyze the sugar content of citrus fruits since there is a correlation between sugar content of citrus fruit and color (Wang et al., 2016). Multi/hyperspectral analysis is being widely applied in research to estimate chemical composition of harvested crop products. For example, hyperspectral sensors have been used to accurately estimate the protein content in wheat kernels (Caporaso et al., 2018a) and to screen cereal grains for quality and safety (Feng et al., 2019). Casporaso et al. (2018b) nondestructively analyzed sucrose and caffeine content of coffee beans using NIR and hyperspectral imaging. Although prediction accuracy of compound concentrations with hyperspectral data was lower than with traditional destructive techniques, hyperspectral imaging provided valuable information on spatial and bean-to-bean variability of sucrose and caffeine that could be valuable to breeders and roasters. Replacing destructive chemical analysis with hyperspectral imaging/scanning has the potential to improve the speed and reduce the cost of postharvest analyses, but additional work is needed to improve the accuracy of the analyses so that HTP is implemented in more post-harvest pipelines.
5 | DISCUSSION

Technologies associated with HTP are often the primary point of focus and excitement. However, without enabling domain knowledge, analysis, interpretation, and decision-making algorithms, these technologies will not reach their full potential. These challenges present the phenomics community with important opportunities for future work. As a point of comparison, we point to DNA sequencing technologies. In the 1970s and 1980s, DNA sequencing was mostly limited to cutting edge research labs and highly trained scientists. During the last 50 yr, the technologies that enable sequencing have expanded, the financial cost per base pair has decreased, and software applications have been developed to empower easy analysis and interpretation of the data. Although the theoretical impact of HTP technologies has not yet been met, the phenomics community has started to formally organize, which is critical to future progress (Carroll et al., 2019; Roy et al., 2017). These phenotyping communities are attempting to facilitate interactions between public and private entities and to identify and overcome common bottlenecks in applying HTP to food systems.

Expanding and supporting training in plant phenotyping, such as the efforts led by the International Plant Phenotyping Network (https://www.plant-phenotyping.org/IPPN_Training_Education) will facilitate adoption and development of new applications. One of the most challenging and rewarding aspects of working HTP phenomics is that it is an integrative field of study that touches on engineering, physics, mathematics, statistics, computer science, and domain expertise in plant science. This means that to work in this field requires some ability to communicate effectively across fields that all have their own jargon. This is important because a common language allows the community to better identify common issues in phenomics. There are excellent examples of formal education programs (e.g., https://www.predictivephenomicsinplants.iastate.edu/) that are beginning to bridge the expertise necessary for plant phenomics; however, expanding these opportunities to reach students and researchers around the globe is also necessary to both recruit more talent into the HTP community, and for expanding the use of HTP across the globe.

Despite the potential broad applicability of HTP tools, we also must take care to avoid setting up false expectations, because they may result in alienating important members of the community. For example, although there is a heavy reliance on technology (imaging technologies, platforms), there is still significant human labor and domain expertise involved in developing phenomics standards, methods, and trait models. Further, when discussing HTP analysis software, terms like “user-friendly” and “fully-automated” are often only true to a target audience and not broadly applicable. For example, to a computer scientist, Python is a user-friendly language and yet can be headache-inducing to a coding novice. “Open source” is commonly considered synonymous with “free.” However, code that is written in MATLAB may be freely available but cannot be used without purchasing proprietary software. Similarly, resources may be “conditionally” open source or open access. For more on the topic of open data and software, we recommend reading the FAIR guidelines (Wilkinson et al., 2016). In addition to access to tools, software sustainability after publication is another challenge for phenomics and bioinformatics in general. Lobet (2017) does an excellent job of describing the problem of software sustainability after publication, because often software development halts when a student graduates or after an experiment has been completed (Lobet, 2017). Furthermore, even if a tool is publicly available and continues to be maintained, a tool with no documentation is unlikely to be widely adopted by a community. We understand the appeal of creating tools that are “new,” but value also needs to be placed on tools that have clear and documented plans for sustainability, growth, and community inclusion.

The full potential of HTP is far from realized and with the current global pandemic it is even clearer that infrastructure, technologies, and analysis methods that allow researchers and stakeholders to remotely monitor and make decisions about their plants and crops will be critical going forward. Finally, many of the technologies used for HTP are expensive and research-oriented, which limits adoption by stakeholders across the food system. Therefore, more interactions between communities are needed to understand bottlenecks in the adoption of technologies and to ensure that hardware and analysis tools are built that address real domain problems that researchers and stakeholders face. Despite these challenges in picturing the future of food, we see that phenomics holds enormous potential for improving global food security by impacting foundational and applied research, enabling precision agriculture, and additional applications across the food system.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.
AUTHOR CONTRIBUTIONS
Anna L. Castro: Visualization, Writing-original draft, Writing-review & editing; Haley Schuhl: Visualization, Writing-original draft, Writing-review & editing; Jose C. Tovar: Visualization, Writing-original draft, Writing-review & editing; Qi Wang: Visualization, Writing-original draft, Writing-review & editing; Rebecca S. Bart: Visualization, Writing-original draft, Writing-review & editing; Malia A. Gehan: Visualization, Writing-original draft, Writing-review & editing.

ORCID
Noah Fahlgren https://orcid.org/0000-0002-3238-2627
Malia A. Gehan https://orcid.org/0000-0002-5597-4537

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