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BASIC PRINCIPLES AND MAIN APPLICATIONS OF PLANT PHENOMICS

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Abstract. In recent years, a new area of plant biology, the so-called plant phenomics, has been rapidly progressing and allowing for non-invasive, fast and high-throughput analysis of the plant physiological parameters by their phenotype. It uses modern knowledge of biology, information technology and engineering solutions for deep digital analysis of phenotypes. The impulse for the development of digital phenotyping was the creation of new types of sensors that are sensitive to various regions of the electromagnetic spectrum, as well as methods of processing and obtaining meaningful information from them. The introduction of RGB, NIR, hyperspectral and other cameras make it possible to obtain physiologically significant information for individual organs, entire plants and their populations both in laboratory and in the field. Computer vision and machine learning technologies allow highly automated analysis of datasets, excluding the human factor, and revealing previously unknown features of plant growth, development, regulation and stress reactions.

Keywords: *Plants, plant phenomics, phenotyping, plant physiology, imaging, convolutional neural network*

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1. Introduction

Phenomics is a new field of knowledge between biology, bioengineering and programming, aiming at the analysis of phenotypes (phenotyping), their formation during the ontogenesis and modifications in response to environmental factors (Fiorani and Schurr, 2013). Phenomics of plants is of particular interest, as plants are characterised by an exceptional variety of phenotypic manifestations. The major focus of plant phenomics is digital phenotyping, quantification and deep analysis of morphological and physiological traits of plants during development, senescence, response to damages and stresses. An automated high-throughput phenotyping automatically processes much more data than any classical physiological technique. It generates massive and informative datasets on size, shape, biochemical and physiological parameters of individual plants and populations (Walter *et al.*, 2015). Plant phenomics helps to establish previously unknown patterns of plant functional physiology and regulation (Li *et al.*, 2014). Recent combination of plant phenomics with other omics sciences, such as genomics, proteomics and metabolomics allows to discover new fundamental principles of plant organisation and physiology (Großkinsky *et al.*, 2018; van Bezouw *et al.*, 2019).Such complex but tightly regulated processes as leaf senescence (Kim *et al.*, 2016), transcriptional regulations of genes involved in protein synthesis and cell wall metabolism (Baute *et al.*, 2016), metabolomic changes of tomatoes under the action of plant-derived protein hydrolysates (Paul *et al*., 2019) have been studied in detail owing to introduction of multi-omics approach.

Phenomics is one of the modern branches of experimental biology, although it is based on the principles and approaches that were historically used by people. The evolution of human species is closely connected to agriculture development, domestication of animals and cultivation of plants, the history of which, according to various estimates, goes back from 9000 to 11000 years (Houle *et al*., 2010). Ancestors selected plants based on specific characteristics.For example, people chose bigger and brighter fruit. With human development, the approach to finding food becomes more meaningful: plants with higher yields, resistance, and nutritional value were selected and cultivated. As a result, valuable plant organisms accumulated useful internals (beneficial features, useful qualities) over time (Johannsen, 2014). The development of human civilisation depended to a large extent on continuous improvement of breeding and detailed selection of highly effective phenotypes of agricultural plants. These were the first stages of phenotyping – the classification and selection of plants with a given phenotype (the indicated phenotype). During the era of systematics (18-19th centuries), plant phenotypes were classified to make a division on taxons. Before the invention of methods and approaches of genetics, cytology, molecular and cell biology, etc. selection was based directly on the assessment of phenotyping characteristics accessible to a naked eye, ruler or microscope (Arend *et al*., 2016). With the development of science and technology, especially in the last century, methods of studying the external features of organisms have moved to the next level, have become more complete and deeper, integrated with biochemical, physiological, genetics, bioinformatics and other studies (Normanly, 2012). Nowadays, accumulated knowledge about phenotypes culminated by the development of high-throughput phenotyping systems and sophisticated plant phenomics software allowing transformation of the total field of plant physiology and botany onto digital form.

2. Objects of phenomics at different levels of plant organization

Despite the fact that phenomics is a relatively young direction of plant biology, the range of objects studied is wide enough and constantly increasing (Table 1). It can be classical model plant species and important agricultural, ornamental plants, objects of medical biotechnology, etc. (Barmeier & Schmidhalter, 2017; Berger *et al*., 2007; Corona *et al*., 2019; Dutta *et al*., 2017; Scharr *et al*., 2016; Schneider *et al*., 2019; Stewart & McDonald, 2014; Volpato *et al*., 2021). Algae, monocotyledonous and dicotyledonous higher plants, both herbaceous and woody forms, are subject to phenotyping. The object can be a whole plant, its individual organs (leaves, roots, flowers or fruits) or plant population, depending on research strategies (Chacon *et al*., 2013; de Medeiros *et al*., 2020; Dhondt *et al*., 2013; Doh *et al*., 2019; Falk *et al*., 2020; Fujita *et al*., 2014; Li *et al*., 2020; Mahlein *et al*., 2012; Parmley *et al*., 2019; Virlet *et al*., 2014).

The main organ responsible for photosynthesis and plant productivity is the leaf, which is also the main source of carbon exchange and transpiration (Table 1). Yield can be predicted from photosynthetic activity, transpiration and leaf area (Lane *et al*., 2020; Parmley *et al*., 2019; Rincent *et al*., 2018). At the moment, phenomics is able to determine these indicators based on RGB, NIR/SWIR, fluorescence and hyperspectral images (Perez-Sanz et al., 2017). A number of reports dealt with phenotyping of shoots and leaves of the model (*Arabidopsis thaliana*) and important agricultural plant species, the assessment of their morphological and physiological parameters (Barmeier & Schmidhalter, 2017; Berger *et al*., 2007; Corona *et al*., 2019; Manacorda & Asumendi, 2018; Metzner *et al.*, 2014; Stewart & McDonald, 2014; Vanhaeren *et al*., 2015; Volpato *et al*., 2021; Yao *et al.*, 2018). Even simplest commercial phenotyping systems provide detailed information about the shape and size of leaves, growth movements of plants. For example, using non-destructive rosette imaging in the visible spectrum, differences in the color and shape of *Arabidopsis* leaves were shown under the influence of various stress and regulatory factors (Vanhaeren *et al*., 2015), and the spectrum of genes responsible for this was identified for different plant species (Coneva *et al.*, 2017; Wilson-Sanchez et al., 2014). Owing to phenotyping methods, it became possible to study in detail the photosynthesis, respiration and transpiration on intact plants of a number of species without damaging them, to observe dynamics of these processes under various influences and at the different life cycle stages (Dobrescu *et al*., 2017; Du *et al.,* 2020b; Herrit & Fritschi, 2020; McAusland *et al*., 2019).

Table 1. Phenotyping at different levels ofplant organization

Studied species	**Phenotyping object**	**Imaging techniques**	**Measured parameters**	**Key findings**	**Reference**
			Subcellular and cellular level		
Arabidopsis thaliana L. Heynh.	Chloroplasts of mutant plants with abnormal morphologies	CCD camera, monitoring red light reflectance	Chloroplast movement and division, chlorophyll fluorescence	Chloroplast division mutants with abnormal morphologies differed markedly from the wild type in their light adaptation capabilities	Dutta et al., 2017
Pisum sativum L.	Chloroplasts, mitochondria and vacuoles of leaves	MultispeQ, 3D confocal laser scanning microscope	Chlorophyll content, quantum yield, non-photochemical quenching, transpiration, water content of the leaves	Method for estimation of organelle functional stoichiometry and to determine differential subcellular dynamics within cultivars in a high-throughput manner	Schneider et al., 2019
Chlamydomonas reinhardtii P.A.Dang.	Flagella of swimming mutants	Dark-field light microscope	Flagella motility, beat frequency and rate; cell localisation	Techniquesfor the analysis of behavior of motile cells was designed	Fujita et al., 2014
			Organ and tissue level		
Arabidopsis thaliana L., *Nicotiana tabacum* L.	Leaves	Digital RGB camera	Leaf shape and size, nastic movements	Detection of leaves, analysis of leaf quantity and morphology	Scharr et al., 2016
Triticum aestivum L.	Leaves damaged by *Zymoseptoria tritici*	Digital RGB camera	The number and size of pycnidia, total leaf area, green leaf area	Automated quantitative disease assessment	Stewart and McDonald, 2014

Glycine max L. (115 breeding lines)	Roots	Digital RGB camera	Length, surface area, volume, root branching, angles of root bending	Relationship between root traits and genotype descriptors	Falk et al., 2020
Beta vulgaris L.	Leaves	Hyperspectral camera	Symptoms of foliar diseases	Non-invasive detection of leaf damages caused by *Cercosporabeticola*, *Erysiphe betae*, *Uromyces betae*	Mahlein et al., 2012
Sorghum spp. (55 accessions)	Inflorescence	X-Ray computed tomography	Panicle area, major and minor axis length, convex hull area, solidity, depth, circularity, volume, etc	Automated identification of major botanical races of sorghum by characterisation of panicles	Li et al., 2020
Dianthus caryophyllus L.	Flowers	Digital RGB camera	Flower area, major and minor chord lengths, flower solidity and convexity	Correlations between morphometric parameters in flowers and petals	Chacon et al., 2013
Citrus spp.	Fruits	Digital RGB camera	Presence of specific diseases in citrus fruits assessed by artificial neural network	High quality detection systems for identification of anthracnose, black spot, canker, scab, melanose	Doh et al., 2019
Glycine max L., *Triticum aestivum* L., *Arachis hypogaea* L., *Pinus koraiensis* Siebold & Zucc., *Pistacia vera L., and Prunus tenella* Batsch	Fruits and seeds	X-Ray computed tomography	Length, width, thickness, radius, surface area, volume, compactness, and sphericity of fruits and seeds	3D image analysis software for automatic segmentation and quantification of morphological parameters	Liu et al., 2020
Brassica napus L.	Roots	Electrical impedance tomography	Morphological parameters (shape, length, area, density) and electrical impedance	Method for non-invasive analysis of root development and investigating infected plants distinctive characteristic	Corona et al, 2019
Brachiaria ruziziensis Germ. & C.M. Evrard	Seeds	Digital X-ray analysis	Seed area, perimeter, circularity, width, height, solidity, integrated density and seed filling	Correlation between relative density, integrated density, seed filling and physiological attributes of seed quality	de Medeiros et al., 2020

Organismal level					
Hordeum vulgare L.	Leaves, culms, ears	PhenoTrac with spectral sensors (VIS + NIR; flash and canopy sensor and hyperspectral camera)	Organ specific dry weights, N accumulation number of ears m^{-2}, normalised difference vegetation index	Correlations between plant organs and the final grain yield	Barmeier and Schmidhalter, 2017
Arabidopsis thaliana L.	Rosette with leavesdamaged by *Pseudomonas syringae*	Chlorophyll fluorescence sensor	Photosynthes is parameters (FV/FM, Rfd, and NPQ)	Earlier detection of plant-pathogen interactions comparing to human eye (6 h vs 24 h)	Berger et al., 2007
Population level					
Triticum aestivum L. (breeding lines)	Field wheat population	UAV-Based digital RGB camera	Plant height, canopy color	Prediction plant height and revealing genotype-environment interaction	Volpato et al., 2021
Malus domestica Borkh (520 hybrids).	Population of apple trees	RGB, near-infrared, and thermal infrared cameras	Temperature, water potential	Identifying abiotic and biotic factors inducing water stress in trees	Virlet et al., 2014

To study the photosynthesis, various advanced chlorophyll fluorescence detection techniques (PAM, LIF, etc.) and analysis methods(JIP-test) were integrated with the phenomics approach, which significantly increased the productivity and accuracy of analysis (Bauriegel *et al*., 2010; Breia *et al*., 2013; da Silva, 2015; Perez-Bueno *et al*., 2019; Pieruschka *et al*., 2014; Pineda *et al*., 2008; Rascher & Pieruschka, 2020; Räsch *et a*l., 2014; Virlet *et al*., 2015). Multispectral imaging method of phenomics made it possible to reveal the genetic basis of transpiration mechanisms in apple trees under conditions of water deficit (Virlet *et al*., 2015). The chlorophyll fluorescence imaging in combination with thermography makes it possible to identify healthy and infected melon plants with high accuracy from leaf images (Pineda *et al.*, 2008). By decreasing the FV/FM parameter, the distribution and progression of late blight (*Fusarium* spp.) is observed in winter wheat populations (Bauriegel *et al.*, 2010). Using PAM measurements, tissue-specific distribution pattern of photosynthetic competence has been determined, as well as the ability to photosynthesis in various tissues of grape berries was studied in detail (Breia *et al.*, 2013). Laser-induced fluorescence transients (LIFT) and laser-induced fluorescence spectroscopy (LIFS) are the methods of imaging of chlorophyll fluorescence excited by artificial light systems, but, unlike PAM, it uses a laser, not a LED (Perez-Bueno et al., 2019). These methods are used for remote (telescope or tower) measurements of chlorophyll fluorescence parameters of trees (Pieruschka *et al*., 2014; Rascher & Pieruschka, 2020) or agricultural plants (Räsch *et al.*, 2014). JIP test is a reliable mathematical model for analysis of quick (< 1 s) chlorophyll fluorescence changes (Strasser *et al*., 2004). JIP test has been applied in different studies of heat treatment (Stefanov *et al*., 2011) and nitrogen deficiency (Redillas *et al*., 2011).

Phenotyping of the root system has been progressing over the last two decades (Tracy et al., 2020). Modern root phenotyping allows digital analysis of macroscopic (size, architectonics, branching) and microscopic (structure of trichoblasts, tissues, stele) root parameters. In recent years, 3D modeling of root architecture has been successfully combined with the molecular analyses of genes encoding receptors and other regulatory systems controlling rapid root growth responses (Clark *et al*., 2011). Introduction of modern phenomics approaches makes it possible to identify previously unknown complex characteristics of roots that determine the productivity and stress resistance of agricultural crops, which is necessary for effective implementation of agro-amelieorative measures and development of sustainable agriculture (Paez-Garcia *et al*., 2015; Tracy *et al*., 2020). Hyperspectral imaging allows for encoding physical and chemical properties of root systems (Bodner *et al*., 2018). Magnetic resonance imaging is used for root system architecture imaging of soil-grown plants (van Dusschoten *et al*., 2016). Many studies also use PET or X-ray CT (McGrail *et al.,* 2020; Takahashi & Pradal, 2021).

Flower phenotyping is widely used in the ornamental floriculture (Chacon *et al*., 2013). It is also important for determining flowering time in cereals to predict productivity in the early stages of plant development (Wang *et al*., 2019). In the case of fruits, phenomics is most often used for economically important edible plants such as tomatoes, grapes and others (Feldmann *et al.,* 2020; Migicovsky *et al*., 2017; Nankar *et al.,* 2020). A number of methods have been developed for the analysis of images of seeds to assess their quality (Joosen *et al.,* 2012). Phenotyping systems make it possible to automatically define the shape, size and other morphological indicators of various types of seeds, which revealed a number of completely new patterns of their formation (Tanabata *et al.,* 2012).

An importantarea of phenomics is the study of woody plants, as a rule, on a population scale in gardens or woodlands (Sankaran *et al.,* 2019; Santini *et al*., 2019; Zhang *et al.,* 2020b). Large-scale study of the state of plants in forest stands is almost impossible due to the topology of the areas, the characteristics of the trees (too large for manual assessment), the inaccessibility of some regions, the large amount of data and their high heterogeneity. Modern phenotyping methods, provided by the latest achievements of science, engineering and information technology, are able to overcome these limitations (Dungey *et al.,* 2018). For example, using three machine learning methods set of 2.7 million observations composed of 62 variables describing climate, forest management, tree genetics, and fine-scale terrain information extracted from environmental surfaces, management records, and remotely sensed data was analysed to identify the most important drivers of forest productivity (Bombrun *et al.,* 2020).

3. Major principles of digital phenotyping

Major principles of modern high-throughput techniques include non-invasiveness, use of wide range of imaging sensors capturing comprehensive and accurate information about plants, modern data processing and deep data analysis tools using computer vision and machine learning approaches (Mochida *et al*., 2019a; Perez-Sanz *et al*., 2017; Rascher *et al*., 2011). One of the major advantages of phenotyping systems is their non-invasiveness, which means *in situ* exploration of plant morphology and physiology (Mochida *et al.*, 2019b). Possibility of non-invasive plant research is closely connected with the equipment used, a wide range of imaging sensors, capturing information about plants, including RGB-, multi- and hyperspectral cameras, LIDAR technology, thermography and fluorescence imaging, MRI, PET, CT, LIFT, LIFS (Perez-Sanz *et al.*, 2017; Roitsch *et al*., 2019). Modern phenomics approaches allow for a deep studying of the processes of formation and functioning of aboveground shoots and, what is more difficult and important, belowground roots in its natural conditions, without any damage or interference with the natural flow of physiological processes (Rascher *et al.*, 2011). For example, classical for phenotyping, RGB imaging enables a fast and precise determination of the leaf area, and *Arabidopsis*, tobacco, cereals shoot fresh and dry weights (Humplik *et al*., 2015b) or allow detection and identification of disease symptoms in plants (Mahlein, 2016). Equipment that is more sophisticated provides more complex and informative data revealing complex physiological problems (Atkinson *et al.*, 2019; Dhanagond *et al*., 2019; Rascher *et al*., 2011; Shinohara *et al*., 2020; Takahashi & Pradal, 2021; Totzke *et al.,* 2017; Woo *et al.,* 2008). For example, magnetic resonance imaging, computed tomography or positron emission tomography can resolve root structure in 3D (Atkinson *et al*., 2019; Takahashi & Pradal, 2021), white neutron beam radiography and tomography provide information about water content both in roots and rhizosphere (Shinohara *et al*., 2020; Totzke *et al*., 2017). Non-invasive phenotyping allowed for unraveling QTLs drought tolerance responsibility in barley (LemnaTec-Scanalyzer 3D system) (Dhanagond *et al*., 2019), PAM fluorometry successfully screened for various photosynthetic traits (Rascher *et al*., 2011), chlorophyll fluorescence imaging helped to predict survival of soil-grown plants under drought treatment (Woo *et al.,* 2008), etc. Figure 1 shows the standard stages for obtaining and processing plant images for phenotyping.

The principle of non-invasiveness becomes the basis for narrower section of phenomics – volatomics, a promising method to measure the emission of volatile organic compounds, photosynthetic gas exchange and transpiration (Jud *et al*., 2018).

Complex data requires modern processing approaches that provide high throughput and high accuracy of its analysis. In last years, phenomics prevailing trend is the use of computer vision and machine learning algorithms (Chandra *et al*., 2020; Demidchik *et al*., 2020). Originally, digital phenotyping started from simple obtaining and processing of digital images. Then, these procedures were automated and bundled with brief image annotation and analyses. Further technological advances were in adding neural network modules and improving machine vision techniques. Currently, automated imaging with the analysis by artificial intelligence software has become a routine and allow to investigate a multitude of important physiological phenomena, including leaf development (Ubbens *et al*., 2020), chlorosis caused by iron deficiency (Bai *et al.,* 2018), reactions on drought (Ludovisi *et al.*, 2017), plant-pathogen interactions (DeChant *et al*., 2017), flowering (Xu *et al*., 2018), fruit ripeness (El-Bendary *et al*., 2015). Aspects of using neural network in plant phenomics are described in the paper in the section "Image analysis and use of neural networks in plant phenotyping"

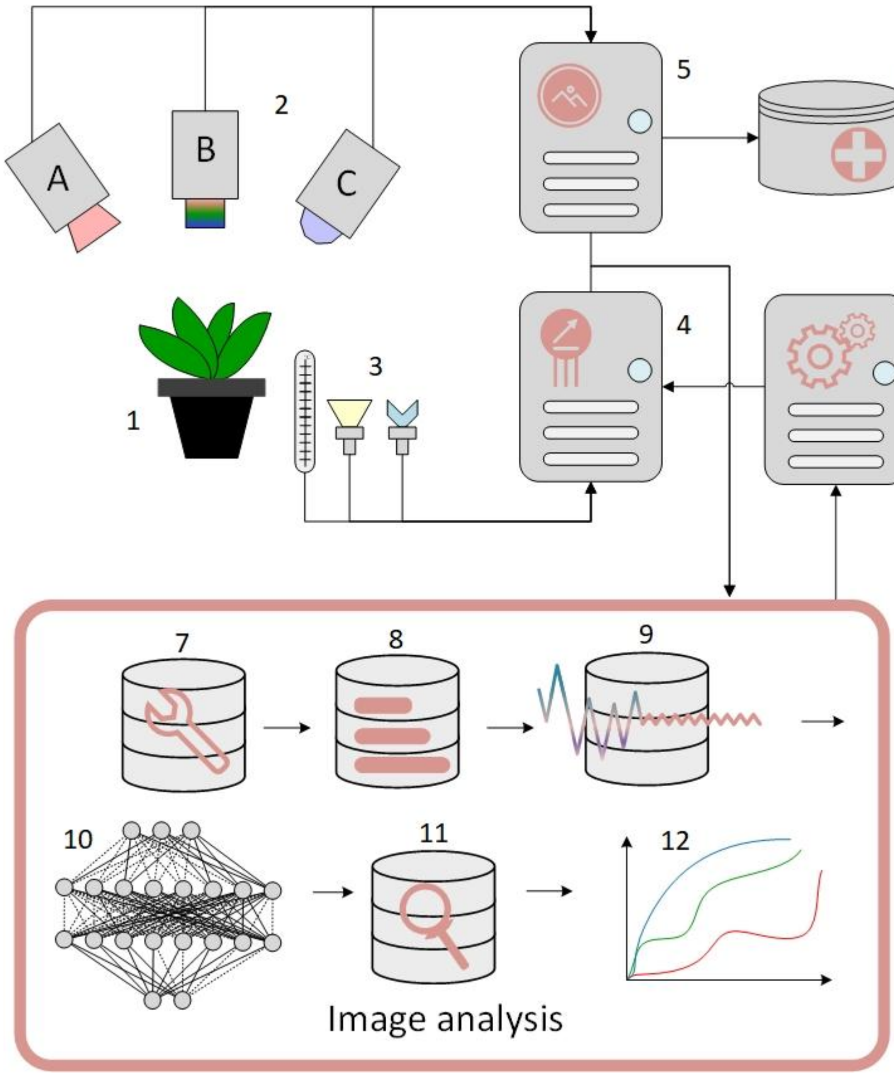

Fig. 1. Typical stages of digital plant phenotyping
1. Object of phenotyping. 2. Imaging station with different sensors (A - NIR, B - RGB, C - Hyperspectral, etc.). 3. Sensors for monitoring the environment (light, temperature, humidity). 4. Server for the analysis of information from environmental sensors. 5. Server for collecting and processing information from the imaging sensors. 6. Data warehouse. 7. Cleaning and correcting errors in data. 8. Sorting of information. 9. Normalisation of data. 10. Searching for patterns by artificial neural network. 11. Data analysis. 12. Visualisation and presentation of results. 13. Server for changing control of the system by computer and operator

4. Phenotyping systems and commercial platforms for digital phenomics

High-performance plant phenomics is often based on specific hardware and software systems called ‘phenotyping platforms’ (Shashko *et al*., 2020). They provide collection and processing of information about plant phenotypes. Modern phenotyping systems generally divide into indoor and outdoor set-ups (Großkinsky *et al*., 2015). Their size and automation can be different as well as their sensor set can vary a lot. Laboratory systems include manually operated platforms (Yang *et al.*, 2020) and automated platforms with mobile sensors or conveyors with plants (Du *et al.*, 2020a;

Nagel *et al*., 2020), while large-scale field systems can be composed of portal crane system (Sadeghi-Tehran *et al.*, 2017), ground robot (Xu *et al*., 2020), towers (Li *et al*., 2021) or aerial vehicles (Yang *et al*., 2017). A large number of commercial companies and research centers are represented on the world market for phenomics equipment, focusing on both fundamental and applied purposes and problems of plant biology, and producing various products from single cameras and sensors to large-scale modular systems. The major producers of phenotyping platforms are the following: Lemna Tec (Germany), Photon systems instruments (Czech Republic), Optimalog (France), Crop Design (Belgium), Phenoscope (France), WIWAM (Belgium), Phenospex (Netherlands) and WPS (Netherlands) (Demidchik *et al*., 2020; Shashko *et al*., 2020).

The most developed area of phenomics with the widest base of equipment is laboratory phenotyping (Rouphael *et al*., 2018). The use of indoor systems of various sizes with fully controlled environmental conditions makes it possible to create an ideal model for studying the influence of biotic and abiotic factors and their combinations on plants (Fiorani & Schurr, 2013). There are two major groups of these systems: 'sensor-to-plant' and 'plant-to-sensor' (Du *et al.,* 2020a; Nagel *et al.*, 2020). The 'sensor-to-plant' concept is based on transporting imaging modules to plants while 'plant-to-sensor' system means movement of container with a plant to the imaging position. First type is generally presented by conveyor pipelines, such as multisensory Hyper AIxpert (Lemna Tec) and Plant Screen Modular System (PSI). Using these platforms, an in-depth study of the mechanisms of supplying the water leaf of cereals has been carried out (Fahlgren *et al*., 2015) and detailed description of chlorophyll fluorescence changes in Arabidopsis leaves in response to water deficit has been performed (Mishra *et al.*, 2016).

Plant-to-sensor platforms are very diverse, they can be represented by small stationary boxes with stationary plants and sensors, can be equipped with robotic arms and include cultivation chambers. Manually operated systems are of this platform type and still widely used for digital phenotyping because they allow for very accurate resolution for quick measurements of small batches (Agnew *et al*., 2017). Some commercial platforms require manual installation of plant pots. As a rule, plant-to-sensor systems have a lower throughput than conveyors, but they eliminate mechanical stress in plants from active location change. Thus, using a box-type platform Image AIxpert (Lemna Tec), the dynamics of the phenotypic responses of C4 plants to nitrogen deficiency and drought was studied in detail (Neilson *et al.,* 2015); and a group of genes that control the geometry of the tomato leaves was found (Coneva *et al*., 2017).

In recent years, the number of studies in open areas has increased, it is the so-called high-throughput field phenotyping (Yu *et al*., 2017). The most common field platforms use ground wheeled or airborne vehicles with several types of sensors to measure plant characteristics. Typical examples of ground platforms are Scanalyzer Field (Lemna Tec) and Plant Screen Field (PSI), determining the shoot architecture and the symptoms of stress (Virlet *et al*., 2016), the mechanism of cold resistance (Humplik *et al.*, 2015a), the patterns of phenotype formation in plants with a known genotype (Cendero-Mateo *et al*., 2017). Some authors show that sub-meter resolution satellite multispectral imagingis a promising application in field phenotyping, especially when genotypic response to stress is prominent (Sankaran *et al.,* 2019). Satellite phenotyping has a number of advantages, including fast/automatic data collection from large areas, as well as their limitations (Zhang *et al*., 2020a).

The forestry uses unmanned aerial vehicles (UAV) or flying drones to search for and phenotype the damaged areas, genetic variation, canopy architecture, photosynthetic pigments, photosynthetic efficiency and water use of the forest (Araus & Cairns, 2014). Genetic variability screening of the morphophysiological characteristics of mature forest trees has been carried out using a UAV (Santini *et al*., 2019). Farmers monitor the state of crops and soil composition by satellite imaging (Sankaran *et al*., 2015). In decorative floriculture and landscape design, high-throughput phenotyping systems have beencombined with machine learning and computer vision approaches for variety verification, identification of plant diseases and for selection plants with high physiological state (Maeda-Gutierrez *et al*., 2020; Taghavi *et al*., 2018).

5. Characteristics of phenotyping cameras and sensors

To solve phenotyping problems, modern developments in the field of imaging are used.For the detection and analysis of plants, RGB, fluorescence, thermal and hyperspectral types of imaging have beenadapted (Bai *et al*., 2018; Berger *et al*., 2007; Bodner *et al*., 2018; Ludovisi *et al*., 2017; Perez-Bueno *et al*., 2019; Santini *et al*., 2019; Volpato *et al.*, 2021; Yao *et al*., 2018). The principle of different imaging methods is the same for different technologies. Camera sensor captures and converts photons falling on it into an electrical signal, which isdecoded by computer to build an image (Linhares *et al.*, 2020).

A characteristic feature of RGB imaging is the use of Bayer filter, which divides the entire spectrum into blue, red and green in such a way that each photodetector receives part of the photons of the desired wavelength (Filoteo-Razo *et al*., 2015). Based on the resulting colour matrix, the image is recreated. Often a white light source is used in conjunction with an RGB camera to provide a standardised amount of light to ensure accurate colour separation (Bora *et al*., 2015).

In fluorescence imaging, an object, such as plant leaves, is irradiated by the higher energy light (of the excitation wavelength), which can then be emitted as the fluorescence (an emission wavelength). Fluorescence photonsare detected by the sensor and analysed. In contrast to conventional visible imaging, fluorescence imaging is independent of ambient light and provides single-channel images subject to segmentation analysis using simple threshold-setting approaches (Rousseau *et al*., 2013). A special parameter of thermal imaging is the use of focusing lenses made of special materials such as germanium, calcium fluoride, crystalline silicon, special plastic. Such a lens transmits wavelengths in the range from 700 to 14000 nm (Combs & Shroff, 2017).

In hyperspectral imaging, the spectrum is split into hundreds or thousands of narrower spectra, which are detected by photodetectors on the sensor (Lodhi *et al.*, 2019). Thus, each photodetector collects a vector of wavelength values for each pixel. These values form a 3:3 matrix called a data cube that stores information about each pixel across the entire wavelength range (Elmasry *et al*., 2012).

6. Image analysis and use of neural networks in plant phenotyping

A large number of commercial open-source programs, applications and libraries are available for phenotyping (Falk *et al*., 2020). One of the most commonly used ‘computer vision’ libraries is Open CV, which provides a wide range of functionality for working with both still images and streaming video. The library contains more than five thousand functions and algorithms, among which there are both classical and modern methods of analysis (Pulli *et al*., 2012). A number of programs for phenotype image analysis are wholly or partly based on this library, for example the Bellwether Phenotyping Platform (Phenomics Center of Wageningen University; Netherlands).

A number of commercial and free computer programs for the analysis of biological images are used in modern phenomics (Mochida *et al*., 2019). The "Quantitative-plant" website summarises other image analysis software (https://www.quantitative-plant.org/software). One of the most popular programs is ImageJ (National Institutes of Health, USA). ImageJ is capable of performing various manipulations with an image, such as increasing its clarity, detecting borders, automatically adjusting the brightness and contrast parameters. ImageJ allows to determine length, area, calculate statistical parameters and to create graphs based on the obtained data. J Microvision software quantitatively assesses and classifies images, conducts the dynamic analysis and combine the multiple images. Bio Image XD provides batch analysis of images without the knowledge of programming languages. This program carries out the 3D rendering, noise reduction and various arithmetic operations (Costa *et al.*, 2019).

Nowadays, the neural networks have been involved in a multitude of phenotyping studies on plant physiology, including plant growth (Dobrescu *et al.*, 2017; Nagel *et al*., 2020; Vanhaeren *et al*., 2015), development (Metzner *et al*., 2014), reproduction (Doh *et al.*, 2019; Feldmann *et al*., 2020; Liu *et al*., 2020), photosynthesis (da Silva, 2015; Du *et al.*, 2020b; Herrit & Fritschi, 2020; McAusland *et al*., 2019; van Bezouw *et al*., 2019), water exchange and mineral nutrition (Cotrozzi & Couture, 2019; Munns *et al*., 2010; Neilson *et al*., 2015; Virlet *et al*., 2015), mechanisms of regulation of productivity and stress resistance (Dutta *et al.*, 2017; Humplík *et al*., 2015a; Rascher & Pieruschka, 2020; Virlet *et al*., 2014; Yao *et al.*, 2018).

Apart from machine vision techniques, a number of applications for phenomics are based on 'machine learning' methods. The machine learning is a vast class of artificial intelligence methods that enable a computer to learn from its own 'experience', as well as examples and analogies (Feldmann *et al.*, 2020). It is an integrated and systematic approach to data analysis and it uses probability theory, statistics, and theories of decision, visualisation and optimisation (Pound *et al.*, 2017). The learning opportunity automatically improves the accuracy of calculations based on previous results, due to which the machine learning is actively used to solve very complex problems, where data structure and patterns of their relationships are not known (Arel *et al.*, 2010; Bombrun *et al.*, 2020; Doh *et al.*, 2019; Feldmann *et al.*, 2020). One of the key machine learning techniques is the so-called 'neural networks', in particular, their narrower direction, a 'convolutional neural networks' (CNN) designed specifically for a high-precision image analysis, including biological applications (Mirowski *et al*., 2008). The CNN has been successfully applied in the detection of control mechanisms and a detailed description of the stages of leaf development (Singh *et al*., 2016), exploring the relationship between genotype and phenotype in a number of species (Taghavi *et al.*, 2018), the identification of pathogen-induced damages in corn leaves (DeChant *et al.*, 2017), the establishment of inflorescence development mechanisms (Xiong *et al.*, 2017), computer reconstruction of the whole plant model using the algorithms of segmentation (Jin *et al.*, 2018). CNNs are also applicable in the field research, in particular, in assessing the quality of seed material in the breeding of a wide range of agricultural plants, and identifying the quantitative mathematical characteristics of the cotton flowering process (El-Bendary *et al.*, 2015; Feldmann *et al.*, 2020). Several CNN-based programs achieved accuracies of plant stress identification as 99%, for example, 99.4% for GoogLe Net and 99.7% for ResNet-101 (Singh *et al.*, 2018). There are many open-source ‘deep learning’ libraries and platforms (Tensor Flow, Keras, Theno, etc.), allowing non-programmers to develop own CNN models.

Most of the work involving neural networks is based on RGB imaging analysis, but there are studies analysing a wider range of electromagnetic spectrum (Mirowski *et al.*, 2008). Significant progress has been made in the use of machine learning in the analysis of hyperspectral images to determine the maturity and varietal differences in tomatoes, peppers and apples (see special edition of Expert Systems with Applications, 2015, Volume 42, Issue 4). Recently, the mechanisms of the primary reactions of the black poplar to the lack of moisture were determined using thermal imaging data from aerial vehicles (Ludovisi *et al.*, 2017). Compared with conventional segmentation methods, CNN-based approaches increase the accuracy of root phenotyping by up to 30% (Smith *et al.*, 2020; Wang *et al.*, 2019). More accurate segmentation of the root system architecture (RSA) allows calculations of important phenotypic traits of the root in response to various factors. CNNs have also been adapted for segmentation of RSA on X-ray images for reconstruction of the root three-dimensional architecture (Douarre *et al.*, 2018).

Classification tasks are a significant part of CNN use in the digital biology. For example, Wheat Net was developed and applied, which predicts the percentage of bloom in wheat images. For the training of Wheat Net, eleven classes were annotated for each stage of wheat flowering. As a result, Wheat Net showed an accuracy comparable to using manual counting by plant biologists (R^2 = 0,987 and R^2 = 0,982, respectively). This suggests of a great potential for including CNN in commercial plant phenotyping applications used for crop breeding and genomics research (Wang et al., 2019). CNNs can also be used to monitor specific plant development events, such as lodging of cereals (Maeda-Gutierrez *et al.*, 2020). The Lodge Net software has been developed, which allows determining and predictinglodging and regular areas, using different image classification scenarios (Mardanisamani *et al.*, 2019). Currently, some CNNs have achieved as much as 87% and 99% accuracy for stress identification and classification (DeChant *et al.*, 2017; Fuentes *et al.*, 2017; Lu *et al.*, 2017).

CNN regression models were used for estimation of sugar/acid ratio in citrus (Xu *et al.*, 2018). To this end, an ‘excitation-emission matrix’ technique (EEM) was used. EEM images were used as input for CNN training. Sugar/acid ratio was determined using trained CNN models for twenty test samples and the results showed that the CNN-based regression model achieved the lowest prediction error as compared to the conventional regression models (Itakura *et al.*, 2019). Another study investigated, using a fully CNN, the blueberry bruising and calyx segmentation. In this research, the model was based on the VGG-16 network and it demonstrated that CNNs provided accuracy up to 81.2%, while the support vector machine gave only 46.6% (Zhang *et al.*, 2020b).

Overall, these studies have demonstrated that CNN has great potential for solving the most difficult problems arising at various stages of phenotyping. In particular, some types of CNN have simplified the process of extracting phenotypic traits from images, which will improve the processing and analysis of plant imaging data.

7. Major achievements of plant phenomics

Even simple digital RGB imaging technologies give an opportunity to automatically identify *Arabidopsis* leaves and evaluate total rosette area, relative leaf growth rate and as a result to compare growth behavior of different genotypes (Arvidsson *et al.,* 2011). Evaluation of leaf growth parameters using chlorophyll fluorescence imaging allowed discovering the differences in total projected leaf area and potential quantum yield of PSII in stress conditions, caused by drought, chilling and altered spectral composition (Jansen et al., 2009). Root growth assessment in solid medium was a big challenge before the development of specialized phenotyping techniques. It is possible to track root growth motions, its physiological traits and biomass production in gel medium using non-invasive video imaging (Ma *et al*., 2019; Yazdanbakhsh & Fisahn, 2009), to quantify root system parameters in soil using magnetic resonance imaging (Pflugfelder *et al*., 2017; van Dusschoten *et al*., 2016), positron emission tomography (Garbout *et al*., 2012) or X-ray computed tomography (Mooney *et al.,* 2012).

Chlorophyll fluorescence imaging is commonly used for photosynthesis phenotyping and gives the advantages of fast and high-throughput measurements in contrast with traditional methods of assessing photosynthesis parameters (Du *et al.*, 2020b; McAusland *et al*., 2019). Using these technique cultivar specific differences of PSII efficiency and the rate of induction and relaxation of non-photochemical quenching in *Triticum aestivum* were observed under controlled gaseous conditions (McAusland *et al*., 2019). Modified chlorophyll fluorescence imaging was used even in the field for monitoring of photosynthesis reaction dynamics in changing light and temperature conditions and this method allowed for revealing specific genotype x environment interactions (Keller *et al.,* 2019). Handle equipment like Fluorpen (Qubit systems INC, Canada) is also widely used for photosynthesis characterisation, for example, contrasting responses to elevated air temperatures were observed among four soybean genotypes (Herrit & Fritschi, 2020) or photochemical efficiency of grain sorghum was measured in a field setting (Herritt *et al*., 2020).

Significant part of phenotyping research aimed at revealing features of plant stress physiology caused by different types of biotic and abiotic stressors (Khanna *et al*., 2019; Pineda *et al*., 2021; Singh *et al*., 2018). Modern phenomics approaches allowfor automatically collecting and analysing huge amounts of data in high spatial and temporal resolution about plant growth under stress condition or combination of multiple stress factors such as drought, weeds and nutrient deficiency (Cotrozzi & Couture, 2019; Khanna *et al*., 2019). Chlorophyll fluorescence, RGB, and infrared cameras capture data about variety of traits reflecting plant growth, photosynthetic efficiency, rosette morphology, and temperature in wild type and *hsp101Arabidopsis* mutants under heat stress treatment and it was observed that early changes in photochemical quenching corresponded with the rosette size at later stages (Gao *et al*., 2020). Plant responses to biotic stress factors, from pathogens (viruses, bacteria, and fungi) to pests (herbivory) were analysed both in lab and field including detection and identification of stress factor and evaluation of its impact on plant physiology (Méline *et al.,* 2020; Mochida *et al.,* 2019; Mutka & Bart, 2014; Perez-Bueno *et al.,* 2019). Chlorophyll fluorescent imaging is usually used for these purposes (Méline et al., 2020; Mochida *et al.,* 2019), but thermal (Pineda *et al.,* 2021) and hyperspectral imaging (Kuska *et al.,* 2015) can also be used.

8. Concluding remarks and future challenges

Plant phenotyping has shown rapid progress in the past two decades. Phenomics has evolved from very simple manual digital approaches to new high-performance systems, called high-throughput phenomics platforms, capable of monitoring and assessing thousands of plants. Both lab and field phenotyping systems tend to use more sensors with wider range of spectra, which are constantly expanding the range of researcher possibilities. The introduction of NIR sensors made it possible to discover completely new patterns of plant life, such as root volume values correlated well with root dry weight. Hyperspectral camera provided information about leaf water concentrations of major macro- and micronutrients. Intriguingly, the combinations of sensors, which are being used recently, are taking physiological and morphological tests to a new level, providing unprecedented set of new digital data on plant phenotype.

Revolutionary changes in plant phenomics have been made in recent years with the help of artificial neural networks. Their introduction into the usual practice of analysis of phenotypes made it possible to identify integral physiological parameters, such as the simultaneous and interconnected growth of the shoots or roots of one organism, the formation of flowers and fruits, the physiological response to stress or regulatory factors.

Future challenges of phenomics mainly consist in the development of interconnected and correlated studies based on a combination of omics studies. It is also important to connect phenomics data and methodology with a real physiological context. Further development of artificial intelligence and standardisation of measurements may help in this direction. Incorporation of phenomics techniques into plant biotechnology and agriculture will also be a crucial step forward.

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