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Review

Applications of hyperspectral imaging in plant phenotyping

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Our ability to interrogate and manipulate the genome far exceeds our capacity to measure the effects of genetic changes on plant traits. Much effort has been made recently by the plant science research community to address this imbalance. The responses of plants to environmental conditions can now be defined using a variety of imaging approaches. Hyperspectral imaging (HSI) has emerged as a promising approach to measure traits using a wide range of wavebands simultaneously in 3D to capture information in lab, glasshouse, or field settings. HSI has been applied to define abiotic, biotic, and quality traits for optimisation of crop management.

Highlights

Hyperspectral imaging captures both spectral (λ) and spatial (*x*, *y*) information and merges these into a 3D data matrix termed a 'hyperspectral data cube' (hypercube).

A 3D hyperspectral data cube consists of 2D of spatial information plus one spectral dimension that contains information for hundreds of spectral bands.

Hyperspectral imaging has been applied to detect abiotic, biotic, and quality traits in plants in indoor and outdoor growing conditions.

Hyperspectral imaging can be applied from a cellular to landscape scale to determine plant traits.

Data processing and mining tools are still evolving, with machine learning and deep learning algorithms being used in order to assist scientists in predicting traits.

Understanding plant traits requires measurement of rich and complex phenotypic information

Plant phenotyping is a transdisciplinary research domain that uses **noninvasive imaging** (see Glossary) and sensor-derived time-series data often combined with high-throughput measurements to analyse plant anatomy, physiology, and biochemistry. The aim is to determine the structure, performance, and tolerance to limitations of an individual plant or group of plants in a laboratory, in a glasshouse, or in the field. The devices used must be scaled appropriately for the traits, species, and cultivation settings to be analysed. Consequently, a range of handheld devices, stationary systems, tractors and buggies, unmanned aerial vehicles, zeppelins, aircraft, and satellites are used. Absorption, reflection, emission, or transmission of electromagnetic waves from or in plant tissues differ, depending on physiological status, and can be informative to measure parameters such as biomass, biochemical components, biotic and abiotic stress, leaf characteristics, yield traits, root morphology, or photosynthetic efficiency [1–12]. Often applications are categorised by the range of electromagnetic **wavebands** measured, which include UV, visible light (VIS), and IR [13] (Figure 1). **Hyperspectral imaging (HSI)** (Box 1) is an emerging technology that provides the ability to measure traits across a wide range of wavebands simultaneously, enabling more detailed characterisation of plant performance and environmental interactions.

Principles of HSI applied to plant phenotyping

Principles of HSI

HSI is a noninvasive, fast, high-throughput, and remote sensing plant phenotyping method. It captures both spectral (λ) and spatial (*x*, *y*) information and merges these into a 3D data matrix termed a 'hyperspectral data cube' (hypercube). A hypercube includes hundreds to thousands of contiguous images, narrow spectral bands, and 2D images of spectral information in UV, VIS, near IR (NIR), and short-wave IR (SWIR) regions (250–2500 nm) (Figure 1) [14,15]. HSI is nondestructive, based upon the interaction of light with plant tissues and their biochemical components [16]. Both structural and physiological information about plants can be extracted due to the ability of HSI to record both spatial and extensive spectral data [17]. Applications include

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estimating carbon, oxygen, hydrogen, or nitrogen concentrations; calculating vegetation indices; identifying species; and detecting plant responses to adverse conditions [18–21]. For example, HSI was used to generate distribution maps of water and nitrogen in wheat tissues [22].

A standard HSI system relies on five major components: the light source, objective lenses, hyperspectral sensor, an imaging spectrograph, and a computer [17]. The light sources can be either natural sunlight or artificial light provided by halogen lamps or light-emitting diodes. Reflected radiation from the plant is captured by objective lenses and split or dispersed into wavelengths by the imaging spectrograph. Hyperspectral sensors then capture those wavelengths and convert them into quantitative electrical signals [23]. Hyperspectral sensors currently on the market may have two main types of detectors, a charge-coupled device (CCD) or a complementary metal oxide semiconductor (CMOS) and an indium gallium arsenide sensor as a SWIR camera. All are made from photodiodes. The major difference between them is the method used to transform light into digital signals. While CMOS amplifies and converts light to a digital signal at each pixel, CCD transports the charges across the chip, and the charges are read and converted to a digital signal at one corner of the array. The differences of the mechanisms means that CCD sensors are more light sensitive, resulting in higher-quality and lower-noise images. However, CMOS sensors use much less power and can be less expensive than CCD chips [24]. Consequently, CMOS is slowly replacing CCD technology.

Hyperspectral cameras are commonly divided into spectral regions, including VIS (400–700 nm), NIR (700–1100 nm), and SWIR (1100–2500 nm). Photosynthetic pigments, xanthophyll, chlorophylls, and carotenoids absorb strongly in the VIS region. Water content and nitrogen can be detected in NIR and SWIR regions [25]. SWIR can quantify properties of plant materials such as phosphorus, hemicellulose, protein, and mineral contents [26,27].

Other spectroscopy technologies

Other analytical techniques can also be used for plant phenotyping, including IR spectroscopy, NMR, and Raman spectroscopy. The most widely used application of IR for plant phenotyping is NIR spectroscopy, which generates a spectrum from both short (780–1300 nm) and long (1300–2500 nm) NIR wavelengths. IR spectroscopy radiates different regions of IR wavelengths, then measures absorption or reflection by molecules, which occurs as they bend, vibrate, and rotate. These instruments are sensitive (detecting 0.1% concentration of chemical components), so they can be applied in an industrial setting using handheld devices. NIR spectroscopy is sensitive in identifying the presence of water and also the physical structure of cells, as its light is able to penetrate deeper than other instruments that use the same spectrum of wavelengths. However, it is worth noting that NIR spectroscopy fails to provide robust data regarding the chemical composition. Therefore, acquisition of robust information is only possible if data from different regions of IR spectroscopy are collected and combined. Furthermore, due to interference between adjacent peaks in the spectrum, IR is often used in combination with other techniques [28]. Nonetheless, the utility of IR in plant phenotyping is undeniable. For example, the approach has been used to identify cell wall components in wheat endosperm [29,30].

The information provided by Raman spectroscopy can be used to complement IR spectroscopy, contributing to construction of molecular 'fingerprints.' Similar to IR spectroscopy, Raman spectroscopy exposes the sample to a spectrum of light ranging from UV to NIR, then measures the extent of light scattering caused by transitions in the bond vibrations of molecules. Unlike IR spectroscopy, Raman spectroscopy measures isolated bands that are not affected by adjacent peaks or external parameters. Its use is often popular in biochemical and structural analysis, as it is a noninvasive technique. The data provide insights into structure, concentration, and interaction

Glossary

Data mining: process of finding anomalies, patterns, and correlations within large datasets to predict outcomes.

Deep learning: a subset of machine learning referring to the use of multiple and 'deep' layers of a neural network, which are cascaded to extract high-level information, and for pattern recognition and data predictions.

Hyperspectral imaging (HSI): an imaging technique that collects spectral and temporal information of reflected light arriving from the imaged surface through hundreds of spectral channels. Often used to interpret the chemical and physical properties of the imaged object.

HSI data cube: the resulting dataset produced by an HSI camera, which consists of two spatial and one spectral dimension. The main limitation of the data cube is extremely large dimensions because of the high resolution of spectral data.

Indoor phenotyping: phenotyping undertaken in an enclosed and partially or fully controlled environment, which includes glasshouses/greenhouses, growth chambers, and labs. Plants can be illuminated entirely or partially by artificial lighting. Typically, imaging is undertaken using automated systems and handheld devices.

Machine learning: an algorithm that can be trained and self-adjust for progressive learning based on experience and input data in the form of text, numbers, images, video, and so forth.

Noninvasive imaging: nondestructive imaging of plants using one or more techniques on the electromagnetic spectrum in order to observe and measure plant traits.

Outdoor phenotyping: phenotyping undertaken outdoors, usually on farm fields or natural ecosystems, using only a natural light source. Typically, imaging is undertaken by ground-based vehicles, drones, aircraft, and satellites.

Spectral features: arising from the emission or absorption of a photon with energy corresponding to the difference between initial and final states of the transition. In the instance of phenotyping images, a spectral feature refers to an observable change in the electromagnetic signature corresponding to one or more pixels. A spectral feature may indicate an area of interest such as the disease or abiotic/biotic stress.

of biochemical molecules within an organism's cells and tissues. However, Raman spectroscopy is most often used in combination with other methods, as Raman scattering is very weak, making it difficult to distinguish it from stray light [28]. Raman and IR spectroscopy have been used in plant biology to confirm evidence of incorporated cinnamaldehyde into the lignin of transgenic tobacco plants [31].

NMR functions by applying an external magnetic field to objects, which causes the spin of constituent nuclei to change and results in the emission of radiofrequency energy. The nuclei are affected by their chemical environment, so they will emit various radiofrequency energies, which generates data for analysis. An extension of the use of NMR is magnetic resonance imaging (MRI), which provides spatial information of the nuclei [28]. NMR has been used to determine metabolite composition in plant cells [32]. However, such instruments can only be operated in a laboratory setting, and no portable devices for in-field plant phenotyping are available [33].

HSI is a promising new technology for plant phenotyping that incorporates many of the individual capabilities of the technologies described previously. For example, HSI collects both spatial and spectral information, whilst NMR only collects spatial information and IR and Raman spectroscopy only collect spectral information. HSI, IR, and Raman spectroscopy provide multicomponent information that can be compared with NMR data to overcome the low sensitivity of that technology. Furthermore, HSI and Raman spectroscopy are sufficiently sensitive for detection of minor components [28]. Disadvantages of Raman spectroscopy are the high cost of the instrument and the strong interference caused by biological fluorescence signals in the background [34]. The cost of NMR spectroscopy instruments is also high, and they suffer from lengthy time of data acquisition [28,35].

Indoor phenotyping (controlled environment rooms, laboratories, greenhouses) mostly uses handheld HSI devices and fixed systems, which are suitable to phenotype limited numbers of plants. Example applications of indoor facilities include plant growth rate, crop stress detection, biomass estimation, studying the viability of tree seeds, characterising root systems, and physiological and biochemical trait measurement [36–39]. The concept of physiological trait measurement has been demonstrated by measuring the physiological reflectance index in sunflower canopies. This study used narrow waveband spectral measurements to quantify differences in abundance of xanthophyll cycle pigments and the efficacy of photosynthesis under different nitrogen fertiliser regimes. The findings of this study demonstrate the possibility of combining HSI technology with other methods to improve the ground-based estimation of canopy photosynthetic function [40].

Outdoor phenotyping (field-based) HSI platforms mounted on push carts, drones, fixed-wing aircraft, and vehicles are used to phenotype large surface areas. Mobile motorised vehicles with hyperspectral sensors and Global Positioning System instrumentation have been used to estimate nitrogen uptake, plant dry weight, and grain yield of barley and wheat [41–44]. Aerial platforms offer remote sensing to monitor growing crops and estimate crop yield over large geographic areas [45,46]. However, large-scale field applications using airborne platforms have problems with unstable solar radiation due to the constantly changing quality of solar illumination, clouds, and shadows [46].

The four primary HSI data capture principles are point scanning (whiskbroom), line scanning (push broom), area scanning (plant scanning), and snapshot, each of which has advantages and limitations (Figure 2A). Those four principles are described in a paper by Hagen and Kudenov [47]. Unlike 2D images, HSI generates data cubes capturing large amounts of information in a 3D matrix (Figure 2B). A 3D **HSI data cube** consists of 2D of spatial information plus one spectral

Vegetation/spectral indices: a number that quantifies vegetation biomass or plant vigour presented in a single pixel.
Wavebands: a range of wavelengths falling between two given limits in the electromagnetic spectrum corresponding to an HSI system.

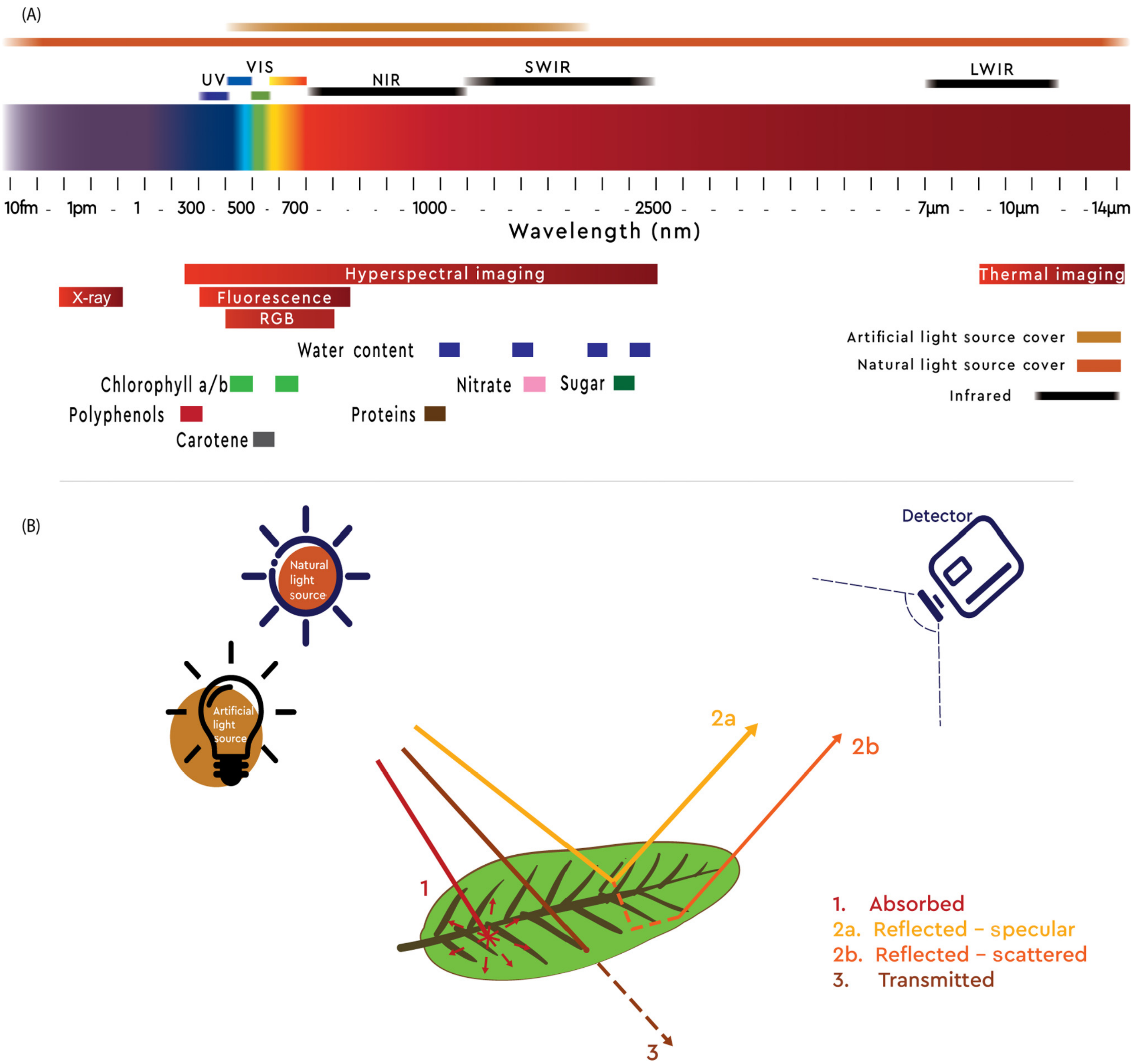


Figure 1. Imaging approaches in plant phenotyping with corresponding electromagnetic spectrum and component interaction. (A) Electromagnetic spectrum depicting all wavebands of interest in imaging techniques for plant phenotyping, and an example of sensitivity bands used in the detection of biochemical components and nutrients [15]. (B) Depiction of plant tissue interaction with electromagnetic radiation and measurement principles. Light in the form of photons (natural or artificial) is emitted with a specific energy and trajectory, interacting with the molecules that the sample contains. The energy and trajectory will be affected by the interaction with the sample (1–3). Molecules absorb (1) a certain amount of energy from the photon, allowing the remaining energy to arrive to the detector (2a and 2b). The energy will decrease, depending mostly on the chemical properties of the molecules of the sample that the photon is hitting. The photon arrives with reduced energy at the detector, creating the spectral bands characteristic of the molecules it interacted with at the sample. Prior to arriving at the detector, the photons can be absorbed completely (and therefore are converted into heat energy), reflected (2a and 2b), or transmitted (3). Reflection can occur in specular mode (2a) (reflected with the same angle as the incident) or in a scattered mode (2b) (reflected with a different angle from the incident) [106]. LWIR, long-wave IR; NIR, near-IR; RGB, red, green, blue; SWIR, short-wave IR.

dimension that contains information for hundreds of spectral bands [48]. Unlike red, green, blue (RGB), fluorescence, and thermal imaging techniques, which operate within a significantly narrower spectral bandwidth with less robust data, HSI nominally operates across a very broad

Box 1. Primary components of noninvasive imaging approaches for plants

Visible light (RGB) (multispectral imaging with three bands): The accuracy of visible light imaging is limited by inherent size distortions in the 2D image plane related to the morphology of the structure imaged [98]. This is due to the different distances between plants or field plots and cameras. The applications of visible imaging in the field are limited due to requirements of downstream image processing, such as minimising the difference in brightness and colour between background and object (e.g., plant, leaf), removing or avoiding canopy shadows, and the influence of light on automatic image processing [4]. The different spectrum of the light (sunlight) in the canopy because of angle, absorption by cloud, shading, and so forth act to filter the spectrum and thus limit accuracy.

Thermal and NIR imaging (VNIR and NIR) use IR wavelengths and may assist in measuring the functionality of turgid cell structure [99]. These enable phenotyping of roots in darkness, as well as sensing tissue moisture and water stress responses [100]. Thermal and NIR imaging measure specific radiation (range of wavelengths) coming from the object.

Fluorescence imaging largely uses the optical properties of chlorophyll for measurements and enables early detection of some stress symptoms. The fluorescence signal in relation to photosynthesis and very sensitive signal monitor abiotic or biotic stress. However, it is not specific (i.e., difficult to distinguish) which effect (e.g., temperature, light) generates changes in the signal, especially in field conditions where the environment is not controlled [4,101].

Laser scanning and other 3D mapping techniques are tools to study the growth and development of plants by assessing plant dimensions and morphology. Processing the cloud point data generated by these methods consumes time and computing resources. They also have low accuracy when phenotyping on a large scale as a result of scanning noise from interference (e.g., wind and rain) [50].

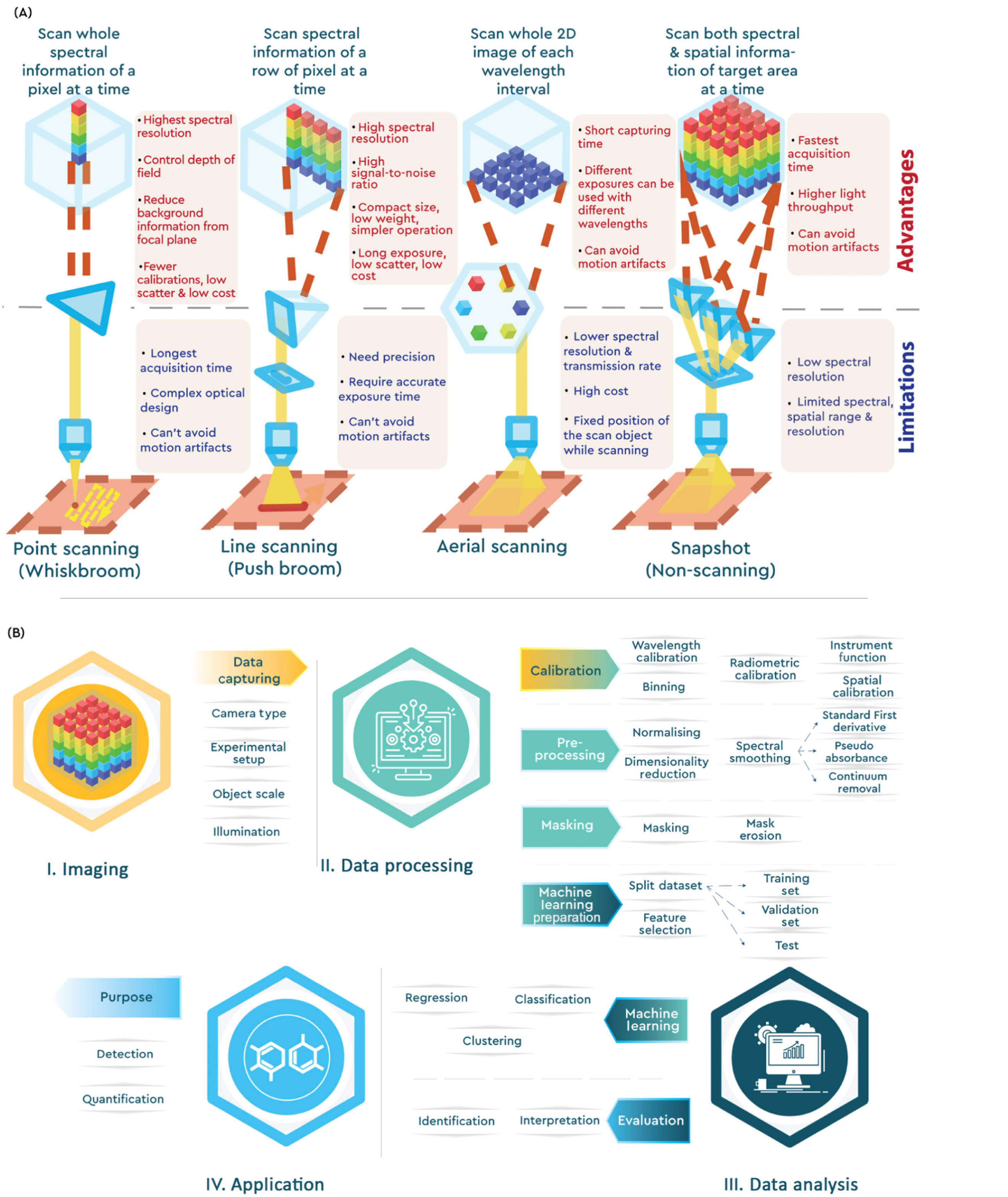
Tomographic imaging delivers high-resolution phenotyping of single plants but has the limitation that acquisition of MRI, positron emission tomography, and CT data takes a long time, which limits throughput [4,50]. Moreover, tomographic imaging techniques are not usable on aerial platforms due to the size and weight of the equipment.

Multispectral imaging (MSI) and HSI work based on the same principle. While MSI works on discrete spectral bands, normally from three to a number of bands or a set of custom wavelength bands [50,102], HSI offers continuous spectral measurement and therefore greater ability to detect phenotypic parameters [103,104]. Contrastingly, MSI can provide higher spatial resolution than HSI because the latter sacrifices spatial resolution to maintain a high signal-to-noise ratio [105]. Therefore, direct comparison of HSI and MSI data is difficult due to their differing spectral resolutions. HSI is able to detect stress at early stages of plant development and is less affected by external factors such as illumination conditions [104].

range of wavelengths and can therefore provide nondestructive quantification with individual identification of substances [4,47].

An HSI data cube can be combined with data from other noninvasive technologies, enabling researchers to capture and quantify undetected phenotypic traits. Five high-throughput phenotyping datasets were collected from multiple published papers with diverse imaging sensor types, multiple phenotyping platforms, and environmental conditions. These high-throughput datasets were classified into five separate categories that include datasets for crop yield prediction, abiotic stress phenotyping, disease and pest detection, and root phenotyping [49].

Data processing and mining tools are still evolving, with **machine learning** and **deep learning** algorithms being used to assist scientists in predicting trait parameters (Figure 2B) [50]. Data processing usually includes creating a smaller subset of data (data sampling), feature extraction, selection, and transformation. In most cases, removing the less informative features boosts the accuracy of the data model [51]. Although machine learning and statistics share considerable overlap, statistics are related to data inference, while machine learning encompasses prediction. In analytical statistics, **univariate, bivariate, and multivariate methods** are three common approaches. The univariate approach deals with only one variable in the dataset, whereas bivariate data analysis tends to find a relationship between two variables. Analysis of more than two



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variables is established using multivariate data analysis [52]. All these methods use different techniques to analyse, visualise, and study data relationships (e.g., histograms, charts, hypothesis testing, cluster analysis, principal component analysis (PCA), and other relevant techniques.

Univariate and multivariate statistical approaches have been applied to remote sensing (i.e., processing and analysis of HSI data). These statistical approaches tend to create an empirical relationship or regressive analysis between spectral data or **spectral features** and thereby report certain vegetation characteristics. **Vegetation indices** (VIs) can be computed by combining two or more spectral bands from HSI data [53]. Univariate statistical models are based on VIs created by selecting narrow hyperspectral wavebands (mostly in VIS spectra) associated with the parameter of interest. The major advantage of vegetation indices is the possibility to decrease the inconsistency of spectral reflectance caused by various indoor or outdoor factors such as scene illumination, soil background reflectance, canopy structure, and so forth [54]. Owing to that, multivariate statistical approaches, where the full wavelength spectra of HSI data are scrutinised instead, show significant application. The goal of multivariate statistical analysis is to link collected spectral data into significant chemical or physical traits. The primary challenge in multivariate HSI data analysis is that it aims to represent a large number of wavebands, which drastically increases the dimensionality of the data. Thus, it is necessary to perform HSI data dimension reduction to remove data redundancy and extract unique vegetation information. Some of the optimal or whole-spectrum analysis multivariate statistical models are partial least squares regression, stepwise multiple linear regression, PCA, and other similar methods [55,56].

Generally speaking, **data mining** is applied using state-of-the-art machine learning algorithms to discover specific data patterns and derive useful knowledge. The two most common predictive modelling problems in machine learning are classification and clustering. The main concern of classification, on the one hand, is to predict certain data value (e.g., applying regression analysis). On the other hand, clustering focuses on finding 'clusters' (i.e., grouping the relevant data instances) [57].

Machine learning algorithms find increasing application in the processing of HSI data due to their nonparametric nature as well as strong flexibility to deal with the nonlinear relationship between hyperspectral reflectance and target parameters [58–60]. Supervised machine learning methods require a reference dataset with known values and user correction to improve the predictive accuracy of the algorithm until the desired or acceptable level of performance is achieved [61]. Unsupervised methods attempt to automatically detect patterns without labelled training data [62]. Deep learning, being a subset of biologically inspired artificial neural networks, and at the same time machine learning, is entirely based on neural network architectures that include a large collection of image data. Valuable patterns can be automatically identified using raw data [50]. Machine learning algorithms overpowered traditional statistical methods, since they do not require any predefined condition regarding data distribution. For example, random forest is a common machine learning algorithm applied in spectroscopic calibration as well as a classification task using remote sensing techniques [63].

Benchmarking datasets are an essential tool to assess performance of a new phenotyping data analysis method and determine its pros and cons. They permit comparison of performance between computer-based analysis methods so that the most effective analysis method for the

Figure 2. Hyperspectral imaging approaches and data analytic workflow. (A) Hyperspectral imaging (HSI) approaches with advantages and limitations [107]. (B) Generalisation workflow of HSI [108]. A typical workflow consists of four parts: (i) image capture, (ii) data processing, (iii) data mining, and (iv) application. At each stage, there is a variety of parameters that need to be defined, which makes the comparison of different studies difficult to evaluate, as changing these parameters based on end use will mean that direct comparisons are not valid.

given experiment can be selected [49,64]. Benchmarking datasets are ideally large sets of real-life data, which should be relevant to the purposes of the method. The dataset should cover most common use: cases and targets/objects likely to be observed whilst performing the real analysis. Furthermore, the benchmarking dataset should contain meaningful metadata, including the data collection procedure and biological information condition of experiments [49].

Applications of HSI in plant phenotyping

Detection of biotic stress and interactions with micro-organisms

Due to its spectral and temporal characteristics, HSI is used to determine early phases of plant disease in both indoor and outdoor cultivation systems. Examples can be found for many different host plant species and types of pathogens (Table 1; Table S1 in the supplemental information online). For example, HSI has been used to determine *Septoria tritici* blotch (STB), a foliar disease caused by the fungal pathogen *Zymoseptoria tritici*, during the winter wheat growing season. HSI canopy data were used, on the one hand, to determine the normalised difference water index as an indicator of STB-induced water loss. Canopy reflectance and **spectral indices**, on the other hand, proved to be useful in quantifying STB. The early-stage detection of healthy and damaged leaves was determined by using a normalised difference water index and statistical analysis. The findings of this research indicate that canopy hyperspectral measurements have great potential to facilitate high-throughput plant phenotyping for disease resistance breeding [65]. Förster *et al*. used a 420–830-nm hyperspectral microscope to investigate the spread of powdery mildew disease on barley leaves. A deep learning algorithm was used to examine the temporal progression of disease in the hyperspectral spectra [66]. For the same pathosystem, the early onset and severity were detected by a highly automated HSI system [67].

Zhu *et al*. [68] assessed several machine learning algorithms suitable for managing high-dimensional features of HSI data to quantitatively and rapidly identify progress of tobacco mosaic virus. They used biophysical (textural) spectral features of tobacco leaves**.** HSI demonstrated a clear visible difference between the infected and noninfected leaves in a very short period of time (i.e., 48 h) in comparison with reference images used (based on the appearance of visual symptoms), found 5 days after inoculation. The results were compelling evidence for the pre-symptomatic detection of disease, which provides guidance for crop disease diagnosis and field management [68]. Other examples of HSI application for disease detection are summarised in Table 1 and in Table S1 in the supplemental information online. Combined, these studies show that while HSI imaging provides high sensitivity for early detection of disease, the parameters to carry out such HSI measurements are highly dependent on the disease symptoms and are thus likely specific for each plant–pathogen interaction. Although this can be an obstacle for a wide application of HSI to plant protection, the substantial crop losses caused by pathogens of up to 20% worldwide and cost for chemical protection reaching billions of dollars make HSI a promising additional technology that could contribute to sustainable agriculture [69].

Detection of plant responses to abiotic stress

Detecting plant abiotic stress responses earlier than is currently achieved may enable rapid intervention to ameliorate the stress and reduce yield losses. Examples have begun to emerge of HSI being applied during field cultivation and in the lab to achieve this. An example is the application of HSI to the detection of salt stress in wheat [70]. Also, wheat grain yield and specific metabolite profiles were predicted nondestructively using in-field HSI sensors [71]. In another example, HSI was used to predict stem water potential in a commercial California vineyard to help manage water stress. Five vegetation indices determined from HSI analyses were efficient in stem water potential prediction (photochemical reflectance index, green–red ratio index, ratio vegetation index, simple ratio index, and greenness index), with photochemical reflectance index achieving

Table 1. Examples of Hyperspectral Imaging Applied to Detection of Plant Traits[a]

Species	Aim	Wavelength (nm)	Data Modelling/Analysis	Vegetation Index	Data Modelling Accuracy	Refs
Biotic						
Wheat (*Triticum* spp.)	Disease detection	Variable	PLSR	NDVI	92.88%	[65]
	Metabolite prediction	Variable	PCA LASSO	N/A	Variable: 61–82%	[71]
Maize (*Zea mays*)	Leaf acid content prediction	Variable	Various	N/A	Variable	[77]
Mango (*Mangifera indica*)	Estimation of maturity	VNIR (390–890)	SVM LR GA	N/A	R^2 = 0.69	[82]
Potato (*Solanum tubersum*)	Biomass estimation	VNIR (400–1000)	Various	Various	R^2 = 0.35–0.88	[83]
Tobacco (*Nicotiana tabacum*)	Disease detection	VNIR (380–1023)	Various	N/A	Variable	[68]
Barley (*Hordeum vulgare*)	Disease detection	VNIR (420–830)	GAN-dCNN	N/A	N/A	[66]
	Disease detection	VIS (400–700) NIR (700–1000)	SiVM SVM	N/A	94.83%	[67]
Abiotic						
Wheat (*Triticum* spp.)	Salt tolerance evaluation	Various	PLSR SMLR	NDSI	Variable	[70]
Grapevine (*Vitis vinifera*)	Water stress detection	VNIR (400–1000)	LR	Various	R^2 = 0.3199	[72]
Arabidopsis thaliana	Early detection of drought stress	VNIR (400–1000)	*k*-means	NDVI	N/A	[73]
	New function of STP1/STP4 detection in glucose uptake to *A. thaliana* guard cells	Various	ANOVA	NDVI	N/A	[74]
Buckwheat	Correlations between nondestructive detection and biochemical quantification	VNIR (340–900) SWIR (1100–1700)	ANOVA	Various	N/A	[75]
Quality						
Rice (*Oryza sativa*)	Quality classification	Various	PLS-DA PCA GWAS	N/A	Variable	[78]
	Biochemical trait detection	VIS-SWIR (350–2500)	GWAS PCA	NDSI DSI SRI	R^2 = 0.31–0.68	[79]

Abbreviations: ANOVA, analysis of variance; DSI, digital sequence information; GA, genetic algorithm; GAN-dCNN, generative adversarial network – deep convolutional neural networks; GWAS, genome-wide association study; LASSO, least absolute shrinkage and selection operator; LR, linear regression; N/A, not available; NDSI, normalised difference spectral index; NDVI, normalised difference vegetation index; NIR, near-IR; PCA, principal component analysis; PLS-DA, partial least-squares discriminant analysis; PLSR, partial least squares regression; SiVM, simplex volume maximisation; SMLR, stepwise multiple linear regression; SRI, Simple Ratio Index; SVM, support vector machine; SWIR, short-wave IR; VIS, visible light; VNIR, visible to near-IR.

the best performance [72]. In *Arabidopsis thaliana*, a portable and high-throughput HSI setup with a spectral range of 400–1000 nm was applied to study drought stress using an unsupervised *k*-means clustering algorithm. This indicated that HSI is able to detect drought stress earlier than conventional normalised difference vegetation index (NDVI) measurements [73]. VIS to NIR (VNIR) HSI has been used to characterise the physiological properties of mutant plants with altered sugar transporters for transport of sucrose from mesophyll to stomatal cells [74,75].

HSI has also been applied to better understand the effects of deliberately imposed chemical stresses upon plants. Glyphosate is a broad-spectrum herbicide used in many cropping systems [76]. It is not, however, fully understood what effects glyphosate treatment has on resistant crops.

Feng *et al*. [77] applied HSI in the VNIR spectrum to assess glyphosate tolerance between a transgenic, resistant maize line and its parental wild type. It was possible to differentiate between glyphosate-treated and nontreated plants and build a correlation to shikimic acid concentration in maize leaves by applying machine learning algorithms to collected HSI data [77]. Similar to disease detection, application of HSI to screen plants for abiotic stress has high promise, but for now, a wider application is hindered by the specificity of parameters that depend on the specific combination of plant species and stress.

Yield and quality evaluation

Destructive quantification of grain properties in cereals such as wheat or rice often lacks the ability to determine useful parameters such as metabolite and micronutrient profiles due to the difficulty in measuring these parameters across sufficiently large sample sizes. HSI may provide the ability to take these measurements in high-throughput and consequently develop relevant predictive models. Applying the VNIR spectrum to evaluate the quality of whole rice grains grown in multiple field locations identified 24 predictive wavelengths. For this, selected wavelengths were used as inputs to a linear discriminant analysis model to classify rice subpopulations based on grain traits, including fat, starch, protein, moisture, colour, and other physicochemical properties. A subsequent genome-wide association study (GWAS) identified known and new candidate genes related to rice grain quality traits [78]. A second field study of rice determined the optimal wavelengths to predict grain quality traits using the normalised spectral index, simple ratio index, and differential spectral index. A GWAS analysis demonstrated the efficiency of using features of the stated spectral index by detecting SNPs in 43 genes with known relationships to grain quality [79].

Optimal harvesting time is important for the quality of produce and is determined in commercial orchards by monitoring fruit maturity. Farmers are targeting a balance between on-tree ripening and transport/shelf-life, known as 'harvest maturity,' which should include both physiological maturity and accumulation of desired nutrients [80]. Dry matter content in certain fruits (e.g., mangoes and bananas) represents a reliable indicator for fruit maturity associated with sugar and starch contents [81]. HSI has been applied to estimate dry matter content *in situ*. It was shown that by combining four optical filters to remove HSI wavelength redundancies, it was possible to use a reduced HSI spectrum to determine fruit maturity results accurately [82].

In some situations, HSI data may serve as a useful complement to traditional RGB phenotyping data. Above-ground biomass is a useful predictor of yield in some crops and can be investigated by applying HSI. Analysis of six potato cultivars using an unmanned hex-copter drone equipped with HSI and RGB imaging equipment determined that while RGB data alone were sufficient to estimate yield at 90 days after planting, the application of a model using full wavelength spectra from HSI data significantly improved prediction accuracy [83]. A variety of imaging techniques, including HSI, have been assessed in examining the effects of biostimulants in both indoor and outdoor facilities to improve management and production [84].

Use of HSI to measure root traits and physiology

Roots are the hidden half of plants and have been underserved by plant phenotyping methods. Their position in the soil or growing medium creates significant technical challenges that limit *in situ* measurement of root traits. However, roots contribute to plant physiology and ecosystem functioning as much as any other plant organ, so there is a significant need to develop better root phenotyping tools. For instance, more complex information, such as water content and root age, can be determined using HSI. Bodner *et al*. [85] implemented an HSI root imaging system to scan the growth of durum wheat in soil-filled rhizoboxes (containers for investigating root growth over longer time series placed in a natural soil structure) using a limited number of wavebands

(222 bands) between 1000 and 1700 nm. Promising topsoil and subsoil segmentation results were obtained with a fuzzy clustering method performed on dimensionality reduced images using PCA. Segmented root axes combined with a chemometric classification model, based on the decision tree algorithm, allowed determination of the radial composition of root axes and monitoring of their decomposition [85]. HSI is a relatively new approach for root phenotyping of soil-grown plants. Although acquisition and processing time limit throughput compared with RGB imaging, spectral signatures provide potential added value by encoding physiochemical root/soil constituents. HSI thus bridges high-throughput RGB and computed tomography (CT)/MRI deep root phenotyping technologies.

Development of portable HSI devices for rapid in-field analysis

Noise introduced during scanning of plants in the field or greenhouse is a common problem in HSI systems. Scanning of crop canopies (indoor or outdoor) can be compromised by fluctuations in daylight and weather conditions. Greenhouse lighting conditions are similarly challenging with the interaction of artificial light, ambient light, and disruption of overhead illumination by the imaging equipment. The result is nonuniform lighting intensities on the leaf surface, which makes the calibration process challenging [86]. Wang *et al*. [87] developed a portable and low-cost HSI handheld device intended for real-time leaf phenotyping in the wavelength range 400–900 nm. The device uploads raw HSI data and image-processing results to a smartphone app that can perform on-the-spot prediction. The device was able to distinguish different genotypes of corn plants and whether they were under high or low nitrogen treatments in the field using NDVI [87]. Unlike during imaging of crop canopies using large and sophisticated instruments, the hand-held device is designed for single-leaf imaging and only requires the user to be in direct contact with the leaf. Widespread use of such equipment has the potential to allow farmers to determine nutrient limitations or diseases early and take preventative steps.

Critical narrative of current HSI applications

Environmental factors and genome content radically affect plant growth, quality, and yield. Performance metrics can in part be monitored using modern high-throughput imaging systems. These systems are composed primarily of noninvasive imaging technologies used to collect complex plant trait data and perform analysis, as well as to undertake the evaluation. The most common noninvasive instruments include RGB imaging, hyperspectral or multispectral remote sensing, thermal imaging, fluorescence imaging, 3D imaging, and tomographic imaging. Owing to a large range of wavelengths in the spectral domain, HSI leads in the effective monitoring and analysis of plant morphology and physiology. The possibility to collect and extract more information places hyperspectral technologies beyond visible-band imaging (RGB), thermal imaging, and 3D imaging for the examination of plants under different stress conditions in both indoor and outdoor experiments. HSI has been proved to enable superior yield prediction and novel gene identification; however, X-ray CT and 3D laser scanning are more suitable for 3D representation of plant surface, tissue, and organs [88,89]. Fluorescence imaging goes beyond HSI in characterising photosynthetic activities at the microscale [90].

Accurate detection of plant disease can be incredibly helpful in choosing the most appropriate chemical application or other effective practices. Noninvasive hyperspectral scanning demonstrates considerable potential for early detection of crop disease severity in both field and controlled environment conditions, though there is still vast room for improvement of specificity and robustness. Much of the published literature addresses the deficiency of specificity to disease symptoms and tends to increase sensitivity and specificity mostly through various customised VI-based models created using an effective selection of disease wavebands [67,68]. Additionally, insufficient robustness of multivariate data analysis techniques is evident due to the variations in spectral data. These statistical approaches require separate evaluation due to the inevitably high data dimensionality and redundancy that complicate disease detection. Therefore, robustness is the ongoing research problem, since a majority of the models are unreliable during application on unknown plants/mutants as well as different environmental conditions. This was evident in the data collection using the HSI platforms to detect the two most common wheat diseases, such as STB [65,91] and yellow rust [92], including the identification of grapevine leafroll disease in a vineyard [93]. However, deep convolutional neural networks may have high detection accuracy, achieved by combining spectral-spatial information extracted from high-resolution HSI data. Deep learning models of high accuracy have also been generated when using ground-based or unmanned aerial vehicles to collect spectral data. The only limitation of these models is the requirement of extremely large volumes of unprocessed data to attain crop disease detection and diagnostic accuracy, comparable to human expertise.

Nondestructive HSI screening has shown great potential in examining plant phenotypes under diverse environmental conditions (simulated or realistic), applied to produce more climate change–resilient and high-yielding crop varieties. Simplified univariate and multivariate statistical models provide excellent results in extracting sensitive spectral signatures for the assessment or prediction of many traits, including salt tolerance based on growth, water relations, and ion content of leaves; grain yield and metabolite profiles; potato yield; stem water potential in vineyards; novel plant functionalities, different acid concentrations, and glyphosate tolerance based on shikimic acid concentration; and water levels, nitrogen content, and other physiological and biochemical plant traits [22,70–73,75,77,82]. However, the accurate prediction of certain plant traits and metabolites related to optimal yield production is not possible by considering only the VNIR spectral region in canopy reflectance. One current challenge in HSI is to achieve optimal extraction of spatial features to monitor leaf nitrogen content [94]. Broader information about generic nutrients such as protein, nitrogen, and sugars can be extracted from the VIS-SWIR region. The VIS-SWIR region was mostly applied for the analysis of dry matter content in fruits such as banana and mango in field conditions [80,81]. Overall, models that use full spectra of collected HSI data have proved their superiority in the evaluation of important parameters under different stress conditions.

Plant breeding efficiency can be improved by reducing the gap between plant phenomics and genetics, combining hyperspectral technology with genomic selection. Biochemical and biophysical plant traits extracted from hyperspectral data can be used in GWASs to identify various gene candidates, pathways, and markers. The VNIR spectral region is the most effective in selecting novel candidate genes influencing rice grain quality and chalkiness and chlorophyll content together with the prediction of protein content [78,79,95]. Similarly, deriving genomic markers and pedigrees from wavelength relationship matrices available in high-dimensional HSI data can permit optimal prediction accuracy of grain yield [96]. High-throughput HSI data collection associated with GWAS and genome modification technologies (e.g., CRISPR/Cas9) has facilitated crop breeding programs by identifying more candidate genes than traditional time-consuming phenotypic tools [97].

Concluding remarks and future perspectives

While HSI has great potential, there are still numerous challenges surrounding its application. The high cost of large and mobile instruments inhibits widespread use in agricultural settings. The processing and interpretation of large volumes of data are limited to computational scientists, and development of easy-to-use instruments suitable for famers and horticulturists in the field is in its infancy. Thus, the production of low-cost instruments and data processing systems for specific applications should be a priority. New artificial intelligence and data mining techniques

Outstanding questions

How can HSI approaches be more widely standardised for specific plant trait studies to improve multistudy comparisons?

How can the calibration of outdoor HSI instruments be improved to reduce noise/error and increase crop canopy scanning throughput?

How can deep learning algorithms find more widespread adaptation among plant biologists and geneticists in working with HSI data to accelerate plant trait discovery?

Can HSI analysis pipelines be trained to apply widely across plant species and their specific biotic or abiotic combinations without individual parameter determination?

The future plant biologist will need to be trained to apply HSI approaches with genetics and environment to fully realise the potential of both genomics and HSI for crop improvement.

may help optimise and develop such low-cost systems. Data selection and optimisation will enable engineers to develop cheaper sensors. The design of new statistical models to examine correlations between different biochemical components and biotic and abiotic stress will also reduce data processing complexity. Additionally, the extent of technical variation and errors in datasets is not yet fully understood. Given that variation exists with the light source (angle, intensity, interference) and that object (shape, size, angle) will influence the data collected, approaches must be developed to understand how this can introduce errors and how it can be corrected. As in other 'omic' approaches, internal standards can be introduced, so, in this instance, 2D and 3D objects with known optical properties may be deployed to account for variation and standardise data. The use of standards would help integrate studies and account for errors (see Outstanding questions).

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Declaration of interests

Martin Trtílek is chief executive officer of Photon Systems Instruments. The other authors declare no conflicts of interest.

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