

Plant Disease Phenomics to Support Breeding of Robust Crops

Jonas Andereg^{1,2,*}, Andreas Hund³, Juan M. Herrera¹, Joaquin Gajardo³, Thomas Cherico Wanger^{1, 4}, Bruce A. McDonald²

¹Production Technology & Diversified Cropping Systems Group, Agroscope, Route de Duillier 60, Nyon, 1260, Switzerland

²Plant Pathology Group, Institute of Integrative Biology, ETH Zurich, Universitätsstrasse 2, Zürich, 8092, Switzerland

³Crop Science Group, Institute of Agricultural Sciences, ETH Zurich, Universitätsstrasse 2, Zürich, 8092 Switzerland

⁴Academy of Global Food Economics & Policy, China Agricultural University, Beijing, China

*Corresponding author: Jonas Andereg; E-mail: jonas.andereg@agroscope.admin.ch

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ABSTRACT

Phenotyping of plant disease remains a major bottleneck for breeding, variety testing, and crop management. While visual scoring has long been standard, advances in high-resolution imaging and computer vision offer great potential for more scalable and standardized quantification of disease under field conditions. This review synthesizes progress in image-based phenotyping of visible disease to support breeding of robust crop varieties. We frame robustness through the complementary mechanisms of resistance, escape, and tolerance, and we discuss how image-based phenomics can contribute to their quantitative assessment in the field. We focus on the challenges of scalable field deployment, including contact-free imaging, symptom diagnosis and localization, and canopy-level quantification under complex field scenarios. We highlight the importance of integrating disease phenotyping with phenology monitoring, 3D canopy reconstruction, and epidemiological and functional–structural plant modelling to move from descriptive disease quantification toward a mechanistic understanding of seasonal epidemics and their effects on yield.

INTRODUCTION

Background

Deploying robust crop varieties that maintain yield and quality under disease pressure is widely considered the most durable, cost-effective, and environmentally safe approach to disease mitigation. However, identifying robust genotypes remains a major bottleneck as it requires extensive field testing (92, 93, 141), making it difficult to collect phenotypic data with the detail, precision, accuracy, and throughput needed to support comprehensive selection decisions. While genotyping has become affordable, comparable gains in phenotyping remain far behind, leaving genomic information underutilized for breeding (12, 49, 137).

To overcome this bottleneck, rapid, non-invasive sensing techniques for disease detection, diagnosis, and quantification have been developed. Different sensor modalities including RGB (Red, Green, Blue), multi- or hyperspectral, thermal, and chlorophyll fluorescence imaging have been applied at scales from individual lesions to field canopies, with each sensor modality targeting specific aspects of a host's response to infection (129).

Non-RGB approaches often focus on pre-visual detection (23, 114, 149), characterization of symptom-level host-pathogen interactions (71, 86), and assessment of distinctive host responses to infection to support diagnosis (30, 85). In contrast, RGB-based approaches are limited to visible signs of disease but offer the major advantage of producing inexpensive, high-resolution images which can be directly interpreted by plant pathologists. Consumer-grade cameras and smartphones now routinely provide 20 to 100 megapixels, facilitating the collection of large high-quality image data sets at low cost.

End-to-end trainable deep learning (DL) models have played a critical role in RGB image interpretation by enabling the extraction of complex, multiscale disease-relevant visual features beyond simple color cues. In pioneering work, Mohanty et al. (90) demonstrated their potential to identify crops and associated diseases from RGB images of diseased leaves. Since then, DL based on expert-annotated imagery has enabled the localization, diagnosis, quantification, and phenotypic characterization of plant disease symptoms in RGB images that align closely with traditional visual assessments (65, 102, 152). This technology holds substantial promise for enabling precise, standardized, and high-throughput quantitative disease assessment under field conditions, with direct relevance for breeding, variety testing, and crop management.

Motivation and scope of the review

Numerous studies have addressed pre-visual detection, employing diverse sensors and analytical approaches, as summarized elsewhere (20, 24, 81, 83, 129). In practice, breeders

typically seek to track disease progression, producers rely on visual symptom-based thresholds to guide interventions, and epidemiologists aim to model and predict epidemics. Within these contexts, pre-visual detection often provides limited actionable insight. We therefore focus on quantifying visible symptoms. Important exceptions where pre-visual detection can directly inform management decisions include quarantine pathogens (149) or pathogens threatening food safety (82).

Substantial work has sought to optimize DL models, typically through architectural modifications or training strategies such as transfer learning and data augmentation. Yet, increasingly powerful and general-purpose models for image interpretation are emerging at a rapid pace, suggesting that hand-engineering neural network architectures for optimal performance on small, task-specific datasets may be of limited long-term value (132). We therefore focus instead on applications and challenges specific to disease phenotyping, highlighting key opportunities and challenges along the entire workflow, from raw data acquisition to comprehensive genotype characterization.

The review is grounded in three concurrent developments:

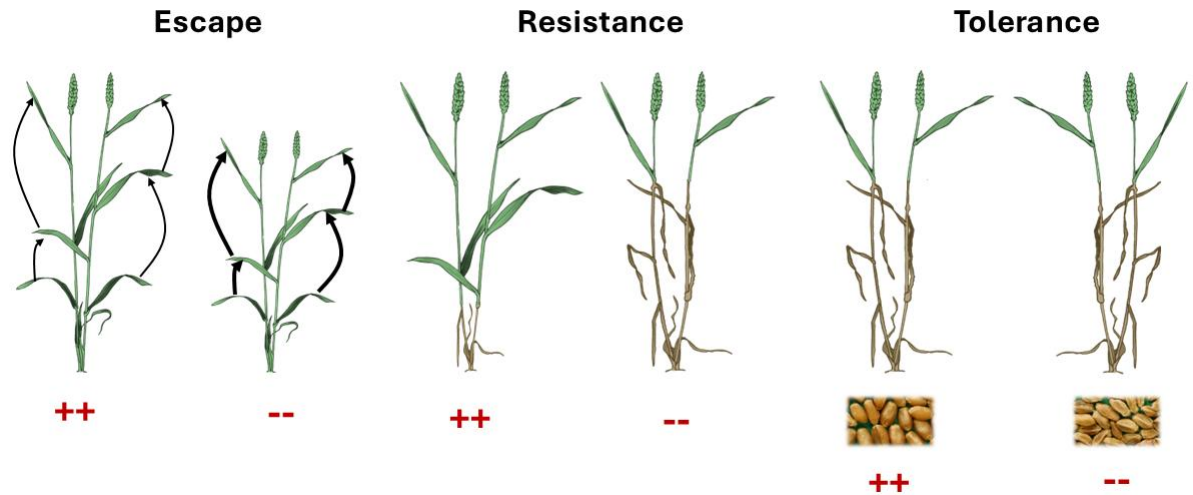
- (i) **From controlled-environment screening to in-field evaluation.** Image-based disease phenotyping is evolving from tissue- and organ-level assessments under controlled conditions toward canopy-level measurements in the field. While laboratory and field approaches sometimes target the same traits, they are not interchangeable. The choice of a phenotyping strategy must be guided by the target traits and pathosystem characteristics, with the biological interpretation of results depending critically on experimental context.
- (ii) **From diagnosis to large-scale quantitative disease assessments.** Recent work has largely emphasized disease diagnosis, yet in agronomic practice, the primary bottleneck lies in robust and scalable quantitative assessment. Despite its central importance for resistance breeding, precision agriculture, and epidemiology (27, 28, 83), the potential of RGB imaging for this purpose remains underexplored.
- (iii) **From single-disease phenotyping to a holistic field phenomics approach.** Parallel advances in RGB-based crop phenotyping increasingly enable dynamic monitoring of growth and phenology, plant morphology and canopy architecture, as well as yield component formation under field conditions (11, 113, 115, 154). Integrating such contextual information with spatially and temporally explicit disease assessments represents a major opportunity to improve our understanding of canopy-level host-

pathogen interactions that determine the trajectory of seasonal epidemics and the impact of diseases on crop performance.

Our review first outlines a conceptual ideotype of genotype robustness under disease pressure that serves as a unifying framework, then examines which phenotypic information is required to characterize specific components of disease robustness. By synthesizing recent advances across scales and experimental settings, we highlight key conceptual and methodological gaps and propose directions to align disease phenotyping with practical decision-making in breeding, variety testing, and commercial crop production.

THREE PILLARS OF DISEASE ROBUSTNESS

Factors determining the robustness of a genotype under disease pressure may be broadly classified into three categories (Supplementary Figure 1; 94, 99, 103). **Disease escape** enables a host to avoid pathogen infection because genetically encoded factors prevent the pathogen from coming into direct physical contact with susceptible host tissues. **Disease resistance** increases the host's ability to restrict pathogen establishment, development, and reproduction once the pathogen has come into direct physical contact with host tissues. **Disease tolerance** minimizes yield and quality losses resulting from disease. We note that neither these categorizations nor these definitions are universally accepted (e.g., 94, 105, 143). However, these common definitions provide a useful conceptual framework, because the underlying candidate traits and mechanisms differ fundamentally among categories, leading to distinct phenotyping requirements.



Supplementary Figure 1 Graphical representation of particular forms of escape, resistance, and tolerance. ‘++’ and ‘--’ denote high level and low level of expression, respectively. Escape: Larger distances between leaves reduce spore dispersal (arrows) in the vertical canopy, reducing contact of upper leaves with pathogen spores. Resistance: With all else equal, disease-related damage is reduced. Tolerance: The impact of a given intensity of disease on yield and quality (here thousand kernel weight) is reduced. Illustrations of wheat plants were modified from Schürch et al. (118).

Disease resistance is essential for the development of robust cultivars and has received by far the most attention. Ideally, however, breeding strategies should aim to integrate escape and tolerance with resistance, as these mechanisms act largely independently, complement one another, and provide insurance when any single strategy fails (77, 92, 97, 98, 101). Their overall impacts are optimized when combined: for example, escape characteristics are particularly effective under low to moderate epidemics, but may be overcome by strong epidemics (1, 44). Each strategy offers specific advantages that can mitigate disadvantages of another. For example, while genetic resistance is easier to assess and has more predictable effects, it can lose its effectiveness due to pathogen evolution, and is often specific to certain diseases. In contrast, disease escape and tolerance are less predictable, but are also less prone to pathogen adaptation and are more likely to be broadly effective against multiple diseases (26, 141). Thus, combining resistance with escape and tolerance traits can enhance the overall robustness of a crop genotype, helping it maintain performance across diverse environments and against rapidly evolving pathogen populations. Separate assessments are needed to maximize progress for each mechanism individually: for example, without accounting for the effects of escape, estimates of resistance can be significantly biased (74, 110).

The remainder of this review follows this conceptual framework. For each disease mitigation strategy (escape, resistance, and tolerance), we summarize the current knowledge of its genetic, molecular, physiological, and mechanistic basis and outline the associated phenotyping requirements, with a particular focus on the extent to which RGB imaging can address these needs.

RESISTANCE

Genetic, molecular, and physiological basis

Plant disease resistance is commonly categorized into major-gene resistance (MGR) and quantitative resistance (QR). Major resistance genes against biotrophic pathogens typically encode proteins that trigger a localized hypersensitive response upon detection of a pathogen effector. Similar mechanisms underlie strong single-gene mediated defense reactions against necrotrophic pathogens, primarily by limiting stomatal penetration rather than inducing hypersensitivity (22), which can result in slower and more quantitative resistance reactions (88, 126). While MGR is highly effective, it is often isolate-specific and, like fungicides, exerts strong directional selection that can rapidly diminish its effectiveness (38).

In contrast, QR usually arises from the combined action of many genes with small additive effects (93, 99, 100, 120). QR does not prevent infection but slows epidemic development, for

example by reducing infection frequency, lesion expansion, spore production, or by extending the latency period (62, 70, 99, 120). Collectively, these ‘components of QR’ (141) decrease the pathogen’s multiplication rate and increase the time required by the pathogen to complete its lifecycle. Therefore, QR is also referred to as rate-reducing resistance.

In many pathosystems, MGR and QR are not strictly separable. For example, resistance to *Septoria tritici* blotch in wheat is highly quantitative at the field level (67), reflecting the genetic diversity of natural pathogen field populations, the strain-specific partial effectiveness of individual major resistance genes (88), and the deployment of multiple resistance genes within cultivars (32). These factors contribute to complex, polygenic resistance phenotypes, even when individual components follow a gene-for-gene model.

Whether MGR or QR dominates pathogen-plant interactions depends largely on scale and context. Seedling assays using single pathogen strains under highly conducive greenhouse conditions mainly expose the effects of major resistance genes, obscuring weaker components of resistance. In contrast, field evaluations with diverse pathogen populations across several growth stages and under fluctuating environmental conditions typically reveal more complex, quantitative, and dynamic outcomes. These approaches provide complementary insights, but are not interchangeable. Accordingly, we review disease phenotyping across scales and contexts of observation, contrasting organ- or symptom-level assessments under highly controlled conditions with field evaluations representative of the target environment.

Controlled-environment phenotyping of pathogen-plant interactions

Resistance or susceptibility reactions following the gene-for-gene model often result in a bimodal distribution of phenotypes, reflecting pronounced susceptibility or near-complete immunity. End-point visual assessment of symptom presence or absence is fast and provides a straightforward and objective readout of pathogen-plant compatibility. Nevertheless, limitations in throughput, phenotypic detail captured, the ability to understand temporal dynamics through repeated assessments, and in precision and accuracy have been noted. These can be addressed using image-based phenotyping, as described next.

Throughput. Limitations in throughput are often noted (i) in quantitative genetics studies that evaluate large panels of host and pathogen genotypes, (ii) when tracking disease development through repeated measurements over time, and (iii) when aiming for detailed symptom characterization. In these cases, the volume, frequency, and precision requirements can exceed what can be achieved by manual scoring.

Attempts to increase throughput have focused on image acquisition and trait extraction from images. One notable attempt is a robotic system proposed by Lück et al. (78) which automates

the repeated imaging of inoculated leaf segments. On a larger scale, conveyor-belt phenotyping systems may facilitate whole-plant monitoring (4). A system proposed by Thomas et al. (131) enables automated imaging of field-like canopies under controlled conditions, using an automatic sensor positioning system. Beyond these examples, most efforts have focused on incremental improvements in image acquisition and processing by relaxing standardization requirements and enabling parallel imaging of more samples (41, 45, 78, 87, 152).

Though essential, these advances are insufficient on their own to enable high-throughput assessments of pathogen-plant interactions. Throughput in phenotyping is commonly defined as the number of experimental units that can be processed per working hour (58), with the most important objective being to match the scale at which germplasm can be genotyped (12, 49, 137). In that respect, gains obtained by the aforementioned systems remain elusive, because the primary bottlenecks lie not in image capture and analysis, but in the labor-intensive steps of growing plants and pathogens, performing inoculations, tracking inoculated material, and preparing it for standardized imaging. We argue that these approaches should be consistently referred to as precision phenotyping rather than high-throughput phenotyping systems (87, 147, 152). No systems providing true end-to-end high throughput along the entire phenotyping workflow are currently available. Given the complexity and diversity of the operations involved, breakthroughs cannot be expected soon.

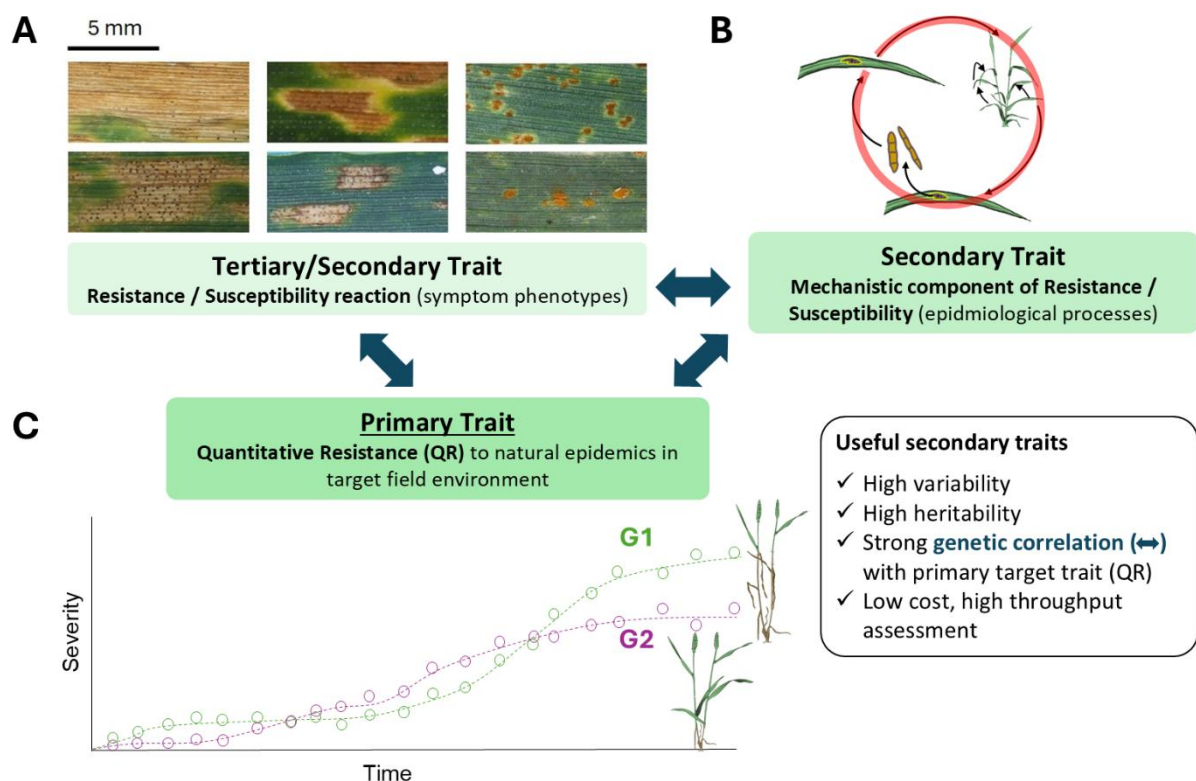


Figure 1 Conceptual framework for phenomics-enabled decomposition of quantitative resistance (QR) into component traits for trait-based selection. Field-expressed QR is a complex, canopy-level dynamic trait reflected in a reduced rate of epidemic development (C). Linking this target trait to underlying component traits could improve breeding efficiency. Static traits

measurable from single snapshots, such as lesion phenotypes indicating resistance or susceptibility reactions (A), may serve as practical selection criteria. Alternatively, epidemiological processes that determine the speed and multiplication factor per infection cycle (B) can be measured through repeated imaging. The effectiveness of this approach depends on the strength and robustness of the genetic correlation between QR and its component traits (blue arrows). Illustrations of wheat plants were modified from Schürch et al. (118).

Phenotypic detail. Sensor-based phenotyping can generate insights into aspects of disease that are impractical to obtain manually. A simple binary classification of host-pathogen interactions overlooks that hypersensitive responses and other resistance or susceptibility reactions are rarely uniform (94). A prominent example is tan spot of wheat, where different isolates induce necrosis, chlorosis, or both depending on the combination of effectors and susceptibility factors involved (48). Other examples include rice blast, where symptoms vary from small necrotic spots to rapidly expanding lesions (86); wheat septoria tritici blotch, where necrotic lesions can be surrounded by diffuse yellow halos or clearly delimited by dark brown borders (7, 147), and fruiting body size and density can differ markedly (67, 110, 125) (Figure 1A); wheat brown rust, where pustules are sometimes surrounded by chlorosis, sometimes not (Figure 1A); leaf spot on sugar beet, where lesions differ in the relative sizes of differently colored sub-areas (71, 72); and Northern leaf blight on maize, where lesions display a variety of shapes, sizes, and colors (91). A substantial genetic component is often evident (86, 91, 147), indicating that detailed symptom analysis can provide valuable insights into the nature and intensity of resistance or susceptibility reactions (7, 45, 72, 86).

Most studies of symptom phenotype focus on visible traits. While hyperspectral imaging can enhance contrast, detect pre-visual symptoms, and detect subtle structural or biochemical changes, its added value over RGB for characterizing host-pathogen interactions remains unclear. Many hyperspectral studies rely on visible traits for model training (71, 72, 86), and spectral signatures often reflect broad stress responses rather than specific host-pathogen processes (e.g., 71, 86). Multi-modal benchmarking at identical resolution is needed to quantify potential advantages, but the difficulty of generating an objective ‘ground truth’ and the different amenability of types of sensor data to different data processing workflows (21) complicate a direct comparison. The added value of higher spectral resolution for symptom diagnosis and characterization must be clarified to guide future research.

Temporal integration. Repeated phenotyping facilitates monitoring of symptom development over time, which is particularly useful in pathosystems involving apoplastic, necrotrophic pathogens, where host responses to infection can be slower and more quantitative (126). A well-studied case is the wheat resistance gene *Stb7*, which confers variable levels of resistance to *Z. tritici* isolates carrying different variants of the matching effector (88). Although this variation was uncovered using single end-point measurements, dynamic analyses could

help reveal underlying mechanisms. For example, lesion development rates have been linked to resistance gene expression levels (19); end-point severity has been decomposed into contributions from infection frequency, lesion expansion, and latency period duration (41) or pustule number and pustule size (96); and the contribution of lesion expansion rates to field epidemics has been quantified (9). Such studies often highlight how dynamic assessments can uncover ‘more complex quantitative forms of resistance’ (41) beyond gene-for-gene interactions. Yet, variation is sometimes traced back to major resistance genes (19, 88). Many key variables influencing field-level QR are not present in controlled-environment assays (92, 93, 141). How QR traits measured under such conditions relate to the same traits in variable field environments is often unclear, as is the relationship between specific QR components and overall QR (9).

Organ-level monitoring of disease development under field conditions is technically challenging due to greater scene variability (e.g., dynamic lighting) and complexity (e.g., multiple disorders), and because fixed imaging setups that ensure consistent positioning and orientation of samples cannot be employed. Nevertheless, some reports of image-based in-field dynamic assessments are available (9, 10). Improving robustness and throughput remain key challenges and depend on the availability of benchmark datasets (8).

Precision and accuracy. Limitations of visual scorings in terms of accuracy and precision have been extensively documented (28). Image processing algorithms, by applying a fixed set of decision rules, act as fully objective evaluators, avoiding reproducibility issues (28). However, this does not guarantee precision nor accuracy of the assessment. The risk of systematic bias may exceed that of visual assessments unless algorithm performance has been thoroughly validated across the full range of relevant scenarios (10, 67, 152). This is an achievable objective under controlled conditions, provided clear boundary conditions are defined. Still, algorithm development and validation are time-consuming, and gains in precision and accuracy must clearly outweigh limitations imposed by other steps of the experimental workflow, such as the inoculation procedure (57, 93).

Perspectives for application. Organ-level disease phenotyping enables characterization of symptoms at a fine scale, allowing capture of both ‘static traits’ such as lesion shape, colour, size, or edge properties, and ‘dynamic traits’ derived from time-series data, including lesion expansion rates. However, concrete applications of such image-derived traits in breeding remain poorly defined. One possibility is to exploit cases where symptom-level phenotypes are strongly correlated with overall disease resistance (86). In such cases, easily scored lesion traits could serve as secondary traits for indirect selection of QR (Figure 1A, 1C), avoiding challenges

associated with dynamic assessment of canopy-level QR (Figure 1C). This strategy is particularly attractive in pathosystems where diverse gene-for-gene interactions converge on a limited set of resistance or susceptibility reactions that produce characteristic symptom phenotypes while strongly influencing overall disease resistance. Where static lesion traits strongly correlate with dynamic traits, they could replace more costly time series measurements (Figure 1A, 1B). This approach can be tested for lesion traits already known or newly discovered from image-based phenotyping (9, 146).

Decomposing QR into mechanistic components (i.e., dynamic traits) and measuring their responses to environmental factors such as relative humidity and temperature would improve understanding of genotype-by-environment interactions in QR, aiding epidemiological modelling and supporting management decisions through better predictions of seasonal epidemics (3, 9). This is because components of QR that represent epidemiological processes are at the bottom of the trait hierarchy, representing basic biological processes. Accordingly, in analogy with a widely accepted paradigm in crop growth modelling (34), their dependency on environmental variables can be assumed constant across environments.

Mechanistically deciphered components of resistance would also provide a basis for pyramiding of functionally complementary resistance mechanisms (e.g., reduced infection frequency with increased latency period and reduced lesion growth rate).

The effectiveness of indirect selection can be evaluated using the breeder's equation, and this should be done early: Secondary traits for disease resistance are most useful when the germplasm to select from is variable, trait heritability is high, genetic correlations with overall resistance are strong, and assessment costs are low enough to support large-scale screening and a high selection intensity (60, 134). In addition, secondary traits would be useful in pathosystems characterized by diverse and fast-evolving pathogen populations and highly polygenic host-pathogen interactions, but less useful where less diversity is present and relatively few genes dominate interactions. In the latter pathosystems, development of molecular markers is preferable. At present, these ideas remain largely aspirational, and visual field scoring remains the dominant practice.

Field-based phenotyping of pathogen-plant interactions

Measurement strategies. Field evaluations are required for reliable assessment of canopy-level QR, as polycyclic epidemics and their drivers cannot be adequately reproduced under controlled conditions (93, 94, 141). Field evaluations usually follow two complementary approaches. Under artificial inoculation, the targeted disease typically dominates, producing characteristic symptoms and synchronized disease development that is comparably easy to

score. Such trials provide a robust estimate of genetic resistance if the inoculum is representative of natural pathogen populations. In contrast, natural infections are often characterized by more subtle differences between genotypes, asynchronous and spatially heterogeneous disease development, and co-occurrence of multiple diseases at comparable intensities. In natural infections, disease expression is influenced significantly by escape mechanisms and genotype-by-environment interactions. These conditions require more sensitive, specific, and robust assessment methods, as well as spatially and temporally explicit quantification of disease to capture relevant variation in disease progression.

Although visual scoring remains widely used, it faces even greater limitations in accuracy, precision, and throughput at the plot scale than at the single organ scale. Implicit integration across multiple biological scales (from symptoms to organs, plants, vegetation fractions, and plots) introduces subjectivity, while limited throughput reduces the number of candidate genotypes that can be evaluated. Together with the lack of standardization that complicates estimation of genotypic value across environments, these factors reduce genetic gain for QR (13, 117). Repeated assessments are typically required to achieve a satisfactory level of precision and capture important rank changes over time. These challenges motivate the need for high-throughput, season-long, canopy-level assessments, which entails numerous additional challenges discussed below and illustrated in Figure 2.

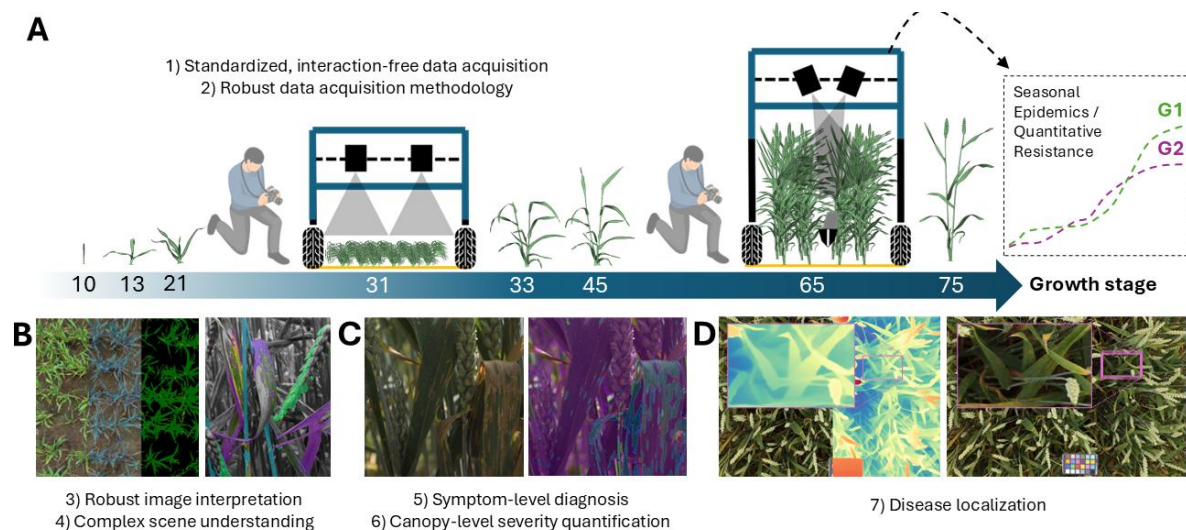


Figure 2 Seven key challenges in high-throughput image-based disease diagnosis and quantification in the field. (A) Many diseases develop gradually as a function of genotypic and environmental factors, and epidemic development is closely related to quantitative resistance (QR). Data acquisition must be interaction-free and compatible with evolving canopies. Manual image acquisition protocols can support method development, but must allow transfer to autonomous platforms. (B) Data processing must be robust across growth stages and scene complexity, enabling reliable background removal and extraction of relevant organs. (C) Images must balance resolution for symptom-level diagnosis with adequate sampling area for canopy-level severity estimation. (D) Localizing symptoms within the three-dimensional canopy (e.g., leveraging co-registered depth maps) increases value for downstream analyses. Illustrations of wheat plants were modified from Schürch et al. (118).

Interaction-free data acquisition. To achieve high throughput, disease severity must be assessed directly at the canopy level, avoiding destructive sampling or similar labour-intensive

measurements. Therefore, remote sensing approaches capturing canopy-level signals have been widely proposed (5, 29). These methods generally work satisfactorily in simplified scenarios (e.g., detection of MGR with a few diagnostic inoculated strains), but extending them to field evaluations of QR under natural infection is highly challenging due to morphological, structural, and phenological diversity of cereal canopies, co-occurrence of other stresses, and varying agronomic practices which confound disease-related signals (5, 89).

High-resolution RGB imaging of sampled plant material can facilitate reliable disease diagnosis and measurement of field-level QR, but is labor-intensive and has required stringent image standardization until recently. The advent of DL has relaxed many of these requirements (65, 75, 152), speeding up data acquisition, and even enabling repeated assessment of the same leaves in situ (9, 10). However, a clear separation between foreground and background is typically required, meaning that single organs have to be properly exposed and oriented with respect to the imaging device. This introduces subjectivity and represents a complex and time-consuming operation that contradicts throughput requirements.

Segmentation of individual plants or organs without direct interaction is feasible in crops such as sugar beet (54) but is difficult in dense cereal canopies. For many applications, a severity metric at the vegetation fraction level is sufficient, though this still requires plant-background and organ segmentation as well as identification of the image area suitable for analysis to relate detected symptoms to the total visible susceptible tissue (11, 59, 153). Prompt-based approaches have been proposed (128, 143), but human-computer interaction during inference is impractical for large datasets, and proposed work-arounds are not applicable for images of dense canopies that rarely allow reliable foreground-background separation. Zenkl et al. (153) addressed this by combining texture analysis with depth estimation to identify in-focus image regions, coupled with organ segmentation to quantify susceptible tissue. This approach enabled interaction-free severity estimation much faster than leaf-by-leaf approaches (153). Focus-bracketing can further increase the leaf area analyzed without a corresponding increase in time used for data acquisition (151).

Scene variability and complexity. Time-resolved phenotyping to capture epidemics requires robust data acquisition and processing (Figure 2A-C). Robustness in this context requires (i) flexible adjustment of sensor position, orientation, and exposure to ensure consistent imaging of comparable vegetation elements despite variation in canopy height and three-dimensional structure (Figure 2A); (ii) sufficient scene understanding to reliably identify plants and their organs across growth stages and distinguish them from background elements such as soil, sky, or residues (Figure 2B), and (iii) the ability to detect and segment disease symptoms

in images captured under variable and complex illumination (Figure 2C). Meeting these requirements depends critically on the availability of training data with balanced sampling across growth stages, lighting conditions, genotypes, and environments.

The need for such training data has been widely recognized for tasks such as plant-background segmentation (79) and organ segmentation (139). While the need for comparable datasets in disease phenotyping is increasingly recognized, most currently available large datasets span multiple crops, encompass diverse imaging scenarios, and show substantial variability in image and annotation quality and detail (e.g., 142). To maximize the usefulness of models for quantitative disease assessments, focus should be placed on generating diverse but crop-specific datasets with comprehensive, highly precise symptom-level annotations. It is critical that failure cases are detected, curated, and iteratively incorporated into such data sets to sustain robustness as models are deployed beyond their calibration domains. This continuous effort is expensive, while plant phenotyping is a small market and each disease within each crop represents an even smaller market share.

Data scarcity is a pervasive issue in DL for plant phenotyping, and reducing the need for manually curated training data at minimal performance loss is an active field of research (132). Proposed solutions include synthetic data generation, domain adaptation, and, more recently, the leveraging of foundation models for vision tasks (132). A wheat-specific foundation model pre-trained with 2.5 million high-resolution images consistently outperformed models pre-trained on general-domain data sets when fine-tuned on comparably small data sets for specific vision tasks typical of field-phenotyping (55). Whether these approaches will similarly benefit disease phenotyping at the macro-scale remains to be explored.

Multiple disorders and symptom variability. Biotic and abiotic stresses commonly co-occur, creating multiple visible disorders. To avoid systematic bias in the assessment of one disease due to the presence of other disorders, individual symptoms must be reliably diagnosed, and this diagnosis must be achieved based on single-shot images, as tracking individual lesions over time in an interaction-free manner remains largely unavailable.

RGB-based diagnosis is feasible when an expert can confidently diagnose symptoms through visual inspection, provided images capture the visual cues with sufficient quality and context (20). However, image-based diagnosis is often evaluated on datasets with a single disease per image, at stages when symptoms are very prominent, typical, and visible on specific photographed organs (63, 102, 104, 119, 130). This can lead to an overestimation of the technology's readiness for practical field application. In reality, multiple disorders often co-occur in the same images, and symptoms display a wide range of appearances related to their

age, host and pathogen genotypes, spatial context, and environmental conditions. Based on our own experience (10, 152), mixed infections can be handled by computer vision algorithms in cereal pathosystems, but symptom appearance can vary largely according to symptom age, particularly in rusts, where emerging pustules progress from pre-rupture to ruptured and sporulating, to discharged uredinia or telia. Since different diseases can be prevalent at different times and new symptoms can appear continuously, the full range of symptom stages can be present at any time and must be accurately diagnosed. Generating the necessary training data could benefit from image time series with symptom tracking (8).

In these complex scenarios, diagnosis must be achieved at the symptom-level, including for disorders not caused by pathogens. A prime example is leaf tip necrosis associated with the quantitative resistance gene *Lr34* in wheat. Mis-diagnosing this host-driven necrosis as a biotic stress symptom represents a worst-case scenario, because it would lead to selection against a valuable source of resistance. This adds complexity for both models and human annotators, making symptom-level diagnosis far more challenging than image-level classification. It requires a multi-level decision within the diagnostic image processing workflow and a data-centric rather than a model-centric approach with high-quality training data (109).

Diseases with systemic symptoms require capturing broader spatial contexts for correct diagnosis. Examples include viral infections causing general yellowing and stunted or delayed growth, or root pathogens such as *Gaeumannomyces graminis tritici* causing dead wheat culms but distinguishable from fusarium head blight if the entire plant is imaged to reveal that stems and leaves are necrotic as well. Similarly, detection and segmentation of wilted sorghum leaves, and correct damage attribution to sorghum charcoal root rot requires images with sufficient spatial context (52).

A central open question is whether a higher spectral resolution could significantly improve single-shot symptom diagnosis in cases where neither color nor spatial context from RGB imagery is sufficient. In theory, hyperspectral imaging could provide additional discriminatory power (81). Systematic evaluation of which spectral ranges or derived indices offer consistent gains in diagnostic accuracy, and whether these can be translated into practical protocols for breeding likely depends on simultaneous imaging using different sensor modalities and co-registration of the resulting images as a basis for conducting such comparisons (37, 59).

Data aggregation. Symptom-level diagnosis in many cereal pathosystems requires very high spatial resolution. For example, reliable detection of *Septoria tritici* blotch fruiting bodies requires ~0.03 mm per pixel (125, 152). At this scale, each image captures only a small portion of an experimental unit and many single-image-based measurements must be aggregated to

obtain precise phenotype estimates, similar to traditional leaf sampling. Aggregation is especially important in pathosystems with unevenly distributed symptoms (e.g., splash- or smear-dispersed infections), but is complicated by auto-correlation across repeated measurements (151) and the need to assign values to different parts of plants or canopies to account for their variable importance for yield formation (e.g., vertical leaf layers (33); Figure 2D).

ESCAPE

Candidate traits and measurement strategies

Disease escape occurs when plants avoid infection not through resistance, but via genetically determined traits that reduce direct physical contact between the pathogen and susceptible host tissues (100, 103, 141). Common escape traits include plant morphology and the resulting canopy architecture, leaf surface traits, and phenology (94, 103, 106, 141). Despite their importance, sometimes explaining 50% of the genotypic variance in disease severity (74), these mechanisms remain poorly characterized overall (103, 141), limiting ideotype development.

Many morphological, structural, leaf surface, and phenological traits are highly heritable in cereals and have been exploited by breeders. This indicates potential for further improvements, though modifications may involve important trade-offs with other agronomic constraints (32).

Plant morphology and canopy architecture influence epidemics by altering microclimate and spore deposition, dispersal, and interception within the canopy (94, 106). A common example is the association between plant height and disease: for splash-dispersed pathogens this mainly reflects effects on spore movement and interception (1, 14, 106), whereas for wind-dispersed pathogens it largely reflects height-induced microclimatic changes affecting infection and disease development (93). Plant height may also be a proxy for other architectural traits such as canopy density and vertical leaf layering and overlap that interact with other traits such as leaf insertion angle, curvature, and length to determine the distance between infectious lesions and new leaves, influencing the vertical spread of secondary inoculum (77, 107) while shaping the penetration of light, rain drops, and air flow within the canopy, which in turn affects pathogen survival, growth, and infection success.

Phenology also strongly interacts with disease. Late-maturing genotypes are often more resistant than early-maturing ones (110, 133). However, it is often unclear whether observed associations arise from genetic linkage, pleiotropy, or represent true phenological escape. Sometimes, they may simply reflect biases introduced by assessing disease severity at a fixed point in time without accounting for differences in crop developmental stage (14, 42, 66, 133).

A direct assessment of escape and its separation from genetic resistance can be impractical, as it would require quantifying both the number of spore penetration attempts (reduced by escape) and their success rate (reduced by resistance). As an alternative, some studies corrected disease severity for the effect of already known escape traits related to phenology, plant height, and vertical leaf layering (14). To estimate the relative contributions of resistance and escape, variance in disease severity explained by possible escape traits was compared with variance explained by the presence of major resistance genes. A more holistic estimate of escape, agnostic both to specific escape traits and the genetic architecture of resistance, could be obtained by comparing a genotype's performance under natural epidemics with its level of genetic resistance estimated under artificial inoculations that minimize the influence of escape traits (110, 124).

Assessing escape and unravelling underlying mechanisms requires specific phenotypic data. First, contrasting management and environmental conditions must be included, emphasizing the importance of measurement throughput to enable this expansion in scope. Second, many observed or postulated escape effects are spatial; accordingly, their validation requires spatially explicit measurement of disease, e.g., across different leaf layers in a canopy. Third, phenotyping should simultaneously capture disease and candidate escape traits related to morphology, architecture, and phenology (14). Fourth, both escape and disease-related traits should be evaluated dynamically rather than as end-point values. For example, stem or internode elongation may be more relevant to disease escape than final plant height and vertical leaf layering in the fully established canopy (76, 77, 106). Finally, measurements must span extended periods and be robust to associated variability.

Phenotyping of candidate escape-related traits and spatial disease occurrence

Quantitative characterization of canopy architecture and plant morphology relies on accurate three-dimensional representations of organs, plants, and canopies, typically derived from depth maps, or explicitly represented as point clouds, voxels, or surface meshes. Such representations provide the basis for estimating structural traits at plot-level (e.g., canopy height, volume, or leaf angle distribution), and at plant- and organ-level (e.g., leaf shape, size, curvature, and insertion angle, internode length, or ear volume, shape, and orientation). Extracting meaningful traits from raw 3D data typically requires point cloud segmentation for plant and organ identification, geometric fitting, and surface reconstruction (15, 17, 56, 61, 150, 154), with methods often tailored to crop architecture and phenotyping goals (56, 105, 148).

Field-based 3D phenotyping presents a series of specific technical challenges: dense canopies cause occlusion and self-shading; uniform canopies present few visually distinctive

features that can be used as tie points for 3D reconstruction; variable ambient illumination, wind-induced motion, and the need for high throughput constrains sensor options. When high-quality 3D data are obtained, trait extraction remains challenging due primarily to overlap, incomplete visibility of plants and organs, and a lack of annotated data sets that can be used for method development (18, 150).

Despite these challenges, significant progress has been made for several major field crops. A pragmatic approach is to estimate canopy cover, above-ground biomass, and plant height using Light Detection and Ranging (LiDAR) (64). RGB-based structure from motion and multi-view stereo approaches are particularly well suited for large-scale application under field conditions due to their robustness to ambient illumination and ability to generate highly detailed, texturized 3D reconstructions (17, 39, 43, 61, 142, 154). Structure-from-motion approaches based on UAV RGB imagery have been extensively validated across diverse environments and crop species, demonstrating high accuracy and robustness in tracking canopy height development (25, 111, 113), allowing an effective capture of this important dynamic component of spatial escape. A robotic system equipped with multiple 2-camera stereo vision setups allowed extraction of plot-level architectural traits such as canopy volume and plant surface area, as well as plant level traits such as leaf angle, in sorghum and maize (17, 142).

Dense 3D reconstruction of crop canopies based on multi-view imaging has advanced considerably by complementing traditional approaches based on key point matching and triangulation with learned 3D representations (15, 43, 61, 145, 154). Some of these new approaches learn to estimate depth from a single image (144), while others can jointly predict all geometric aspects of a scene (including camera positions, depth, and 3D structure) without relying on explicit feature matching (138). These developments significantly improve reconstruction accuracy in complex crop canopies where repetitive textures and occlusions often limit traditional methods, but these outputs eventually have to be converted to explicit 3D representations such as point clouds or meshes for trait extraction. Extracting high-precision plant-level morphological traits, particularly for deeper canopy layers, remains challenging in dense stands and may require physical interaction to open crop rows and thin plants within rows at image acquisition.

Similar datasets can support tracking of phenological development. For example, the beginning and end of stem elongation can be estimated based on direct measurements of canopy height (68, 113) or indirectly via multi-view ground cover estimates (112); heading and flowering stages can be estimated based on inflorescence detection in a timeseries of high-resolution RGB images (115); senescence and ripening can be estimated based on color

properties of plant organs and their dynamics (11). The combination of structural features such as height and high-resolution RGB imagery may further improve phenology inference (112). However, these approaches primarily capture biophysical growth or major, visually discernable morphological or biochemical changes in plants, which serve as proxies for phenological transitions rather than providing a direct measurement (40).

Precisely localizing disease in 3D canopies involves mapping detected lesions onto 3D canopy representations. Ideally, each symptom would be assigned to a specific leaf on a specific plant, capturing both its vertical position in the canopy profile and its position within the plant's hierarchical structure (76, 77, 106). This can be done by segmenting lesions directly in 3D models (108) or by projecting lesions detected in 2D views onto reconstructed 3D canopies (135, 154). However, this requires identifying all organs, assigning them to a specific individual plant (topology) and determining their arrangement within that plant (phyllotaxy). This is particularly difficult in dense canopies and would require the entire plant to be fully represented, which is in conflict with the high spatial resolution imaging needed to support symptom diagnosis.

A pragmatic approach could combine disease phenotyping from appropriate view angles with co-registered depth information to enable approximation of the affected leaf layer and the position of detected symptoms relative to the soil, the top leaf, and, potentially, the canopy light penetration gradient. A proof-of-concept of such an approach was demonstrated by Zenkl et al. (153), who combined monocular depth estimation with image texture analysis to identify focused regions in images with a very shallow depth of field. Although their side-view imaging setup did not allow estimation of the vertical position of detected symptoms within the canopy, this limitation could be addressed by adopting a nadir or an oblique top-down imaging geometry in combination with methods to expose lower canopy layers (c.f. Figure 2A).

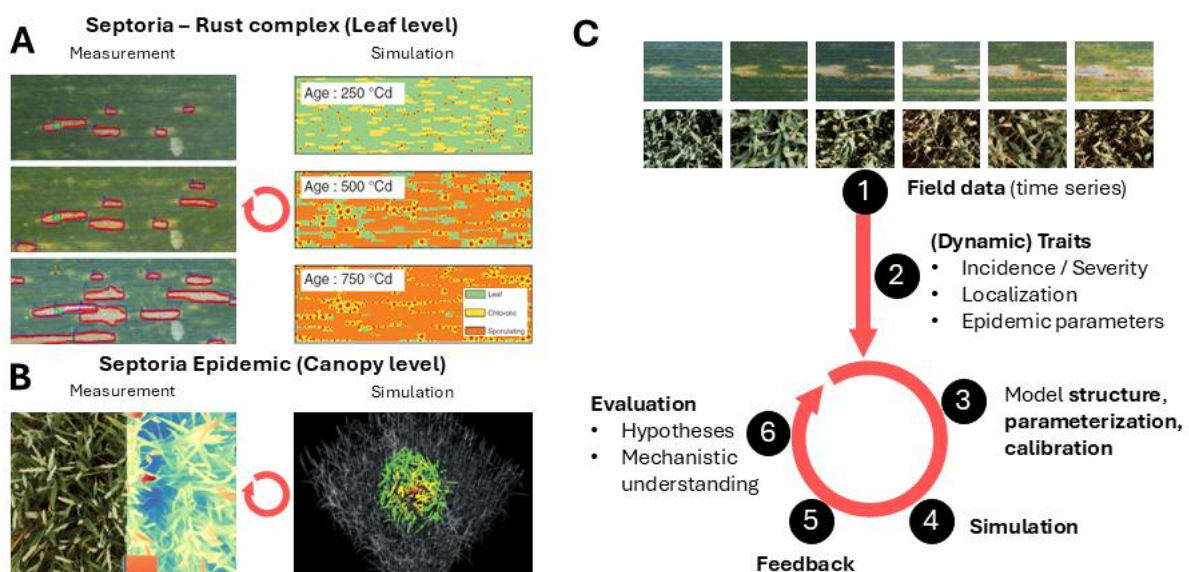
From candidate traits to mechanistic understanding

The outcome of pathogen-plant interactions emerges from complex, dynamic interactions between a changing canopy, a pathogen population, and a fluctuating environment (50, 121). As pointed out by Simko et al. (121), modelling is essential to 'sieve through' this complexity, as measurement alone can be insufficient. For example, identifying genotypes with strong escape characteristics is of limited value if the underlying mechanisms cannot be identified to derive ideotypes. Functional-structural plant models, originally developed to study light interception and canopy-level photosynthesis resulting from the dynamic interaction between the canopy and its environment (47), offer a powerful framework to mechanistically link plant morphology, canopy architecture, microclimate, and disease development. Some studies have

employed them to simulate key spatial-temporal processes involved in canopy-level epidemics, such as spore dispersal within the canopy (50, 51, 106, 136). These approaches have demonstrated potential for investigating the role of cultivar morphology and canopy architecture in determining the course of an epidemic (106, 121, 123). Unfortunately, the availability of ‘real data’ from field experiments that can be used to structure, parameterize, and validate such models has been extremely limited.

Field phenomics has been proposed as a natural complement to epidemiological modelling to address this limitation (121). Data collected at high spatial and temporal resolution at the leaf and canopy levels could help define the structure of simulation models in a more data-driven way, as has been done for the 3D plant models themselves (2) (Supplementary Figure 2). For example, non-destructive, dynamic estimates of height, leaf area index, leaf angles, leaf layering, and senescence patterns can be obtained, while spatially explicit disease maps would enable capture of lateral and vertical progression of disease, as outlined above.

Thus, combining these datasets could guide the development of models by (i) identifying which variables and interactions should be considered in modelling disease progression, (ii) providing biologically meaningful parameter values, and (iii) enabling model calibration and validation on a broad data basis to better reflect observed reality (Supplementary Figure 2). Bridging the gap between models and phenomics should support a paradigm shift from a gradual stochastic to a more ideotype-driven approach based on detailed, mechanistic understanding of pathosystems.



Supplementary Figure 2 Potential synergies between field phenomics and functional-structural plant modelling for advancing mechanistic understanding of disease epidemics in the field. (A) Image sequence of a diseased leaf showing detected and segmented symptoms alongside model-simulated progression for the same pathosystems. (B) High-resolution RGB image and corresponding monocular depth estimation from a state-of-the-art model. Integrating such depth maps with symptom detection and segmentation enables spatially explicit characterization of disease within the three-dimensional canopy. (C) Time-resolved phenotypic data at the organ- or canopy-level can inform the structure, parameterization, calibration, and validation of

epidemiological models. Iterative feedback (circular red arrows) between field observations and model simulations will refine model accuracy and support the development of an accurate and detailed mechanistic understanding of observed disease phenotypes. Right-hand panels of Figures (A) and (B) were adapted from Garin et al. (50, 51), *Annals of Botany*, by permission of Oxford University Press.

TOLERANCE

Candidate traits and measurement strategies

Tolerance reflects both constitutive and adaptive traits that help maintain source capacity under infection. Adaptive mechanisms include an upregulation of photosynthesis in healthy tissue, re-growth, enhanced remobilization, and delayed senescence (26, 92). Constitutive traits include a large canopy ensuring a high initial source:sink ratio, larger stem reserves, and canopy architectures that provide favorable light distribution and a high radiation interception efficiency (26, 92).

Dynamic compensation is central to yield formation and stability in cereals, as losses in one yield component can be offset by adjustments in others throughout much of the growing season. Taking the example of wheat, poor plant emergence can be compensated by more fertile tillers, fewer tillers by more grains per ear, and fewer grains by higher individual grain weight (122). Depending on their timing and severity, diseases can impair any yield formation process, thereby impacting any yield component (Figure 3A, 3B). Despite this, studies on tolerance rarely link disease intensity to phenology and individual yield components; instead, seasonal integrals of disease severity are typically linked to end-of-season grain yield (26, 98). This is notable given the large differences in how different yield formation processes, occurring at different developmental stages, respond to reductions in resource availability, and the varying potential to subsequently compensate these losses (26, 31, 35, 116). A mechanistic understanding of tolerance, which is necessary for its targeted optimization, requires temporally resolved data on disease intensity, crop phenology, and yield components (Figure 3A, 3B).

Empirical evidence for constitutive and adaptive traits that influence yield response to disease and could serve as selection criteria remains scarce. Few studies linked tolerance to candidate constitutive canopy or plant traits (36, 46) and even fewer to adaptive traits such as leaf senescence dynamics (11, 16). This gap likely reflects the prohibitive effort associated with detailed, season-long field phenotyping of disease, phenology, yield components, and candidate tolerance-conferring traits using traditional methods.

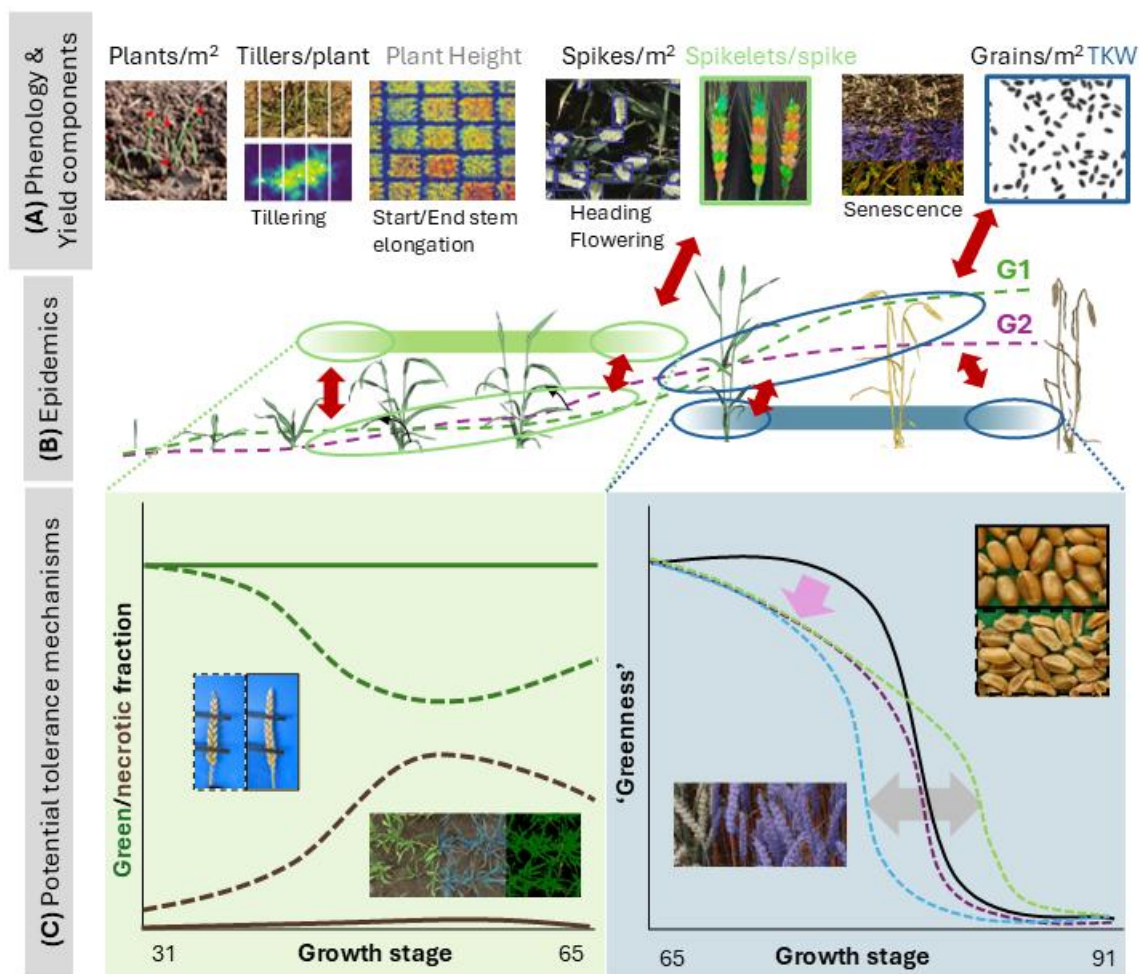


Figure 3 Tolerance characterization should combine growth-stage specific measurement of disease with monitoring of yield formation and phenology. (A) Examples of phenology and yield components estimated using field phenomics. (B) Epidemics for two contrasting genotypes (G1 and G2; dashed lines) measured from emergence to maturity. Phenology and coincidence of certain growth stages and yield formation processes with disease may differ across genotypes, resulting in different yield components being affected to varying degrees (circles and arrows). (C) Two example concepts for a phenomics-enabled search strategy for growth-stage specific tolerance, with images illustrating the nature of the required phenotypic data. Left: In spring, healthy plots maintain full greenness (solid lines), whereas diseased plots show necrosis (dashed lines). These differences affect ear fertility (i.e., grains per ear), as exemplified by ear images. The degree of impact reflects phase-specific tolerance. The mechanistic determinant of tolerance is elusive in this example, but could result from a large leaf area index or high biomass to maintain source capacity. Right: Between flowering and harvest, disease reduces the integral under the greenness curve (dashed lines) compared to a healthy plot (solid black line), affecting grain filling. The degree of impact reflects phase-specific tolerance. Greenness dynamics are influenced in two ways: i) a direct effect reducing canopy greenness during the stay-green phase (pink arrow); and ii) an interaction between disease and senescence. Disease may accelerate (blue dashed line), not affect (purple dashed line), or delay (green dashed line) senescence, within the leaf fraction and in other organ fractions (stems, ears). In this model, accelerated senescence is a mechanistic determinant of sensitivity, whereas delayed senescence is a mechanistic determinant of tolerance, if associated with increased rate or duration of grain filling. Illustrations of wheat plants were modified from Schürch et al. (118).

Tolerance is commonly quantified as the slope of the relationship between disease intensity and yield, where disease intensity is typically expressed as area under the disease progress curve. Variation needed to estimate this relationship is often obtained by pooling data across sites and years, particularly when the absolute size of healthy and diseased leaf area is used to estimate tolerance (98). However, because environmental factors are typically confounded with disease occurrence and severity, a gradient of damage within a specific environment may

ultimately be required to isolate disease-related effects. For example, septoria epidemics are more common under conditions of low light, excess rainfall, and low temperatures, which reduce crop performance even in the absence of disease (127).

Some authors have proposed estimating tolerance based on traits measured in healthy crops (i.e., constitutive traits) (16, 36), or through controlled manipulations of the source-sink balance which mimic disease effects, such as partial defoliation. Indeed, such experimental approaches have long been used to better understand sink- or source-related constraints at various growth stages (31). We believe that disease gradients, generated through differential inoculation or fungicide treatments, can become a practical approach for source:sink manipulation, as in-field quantitative and spatially explicit measurements of disease become more accurate, high-throughput, and scalable.

Phenotyping concepts for capturing tolerance and identifying tolerance-conferring traits

Based on the above considerations, we propose a two-tiered phenotyping strategy for tolerance, where the primary objective is to implement high-throughput disease progression monitoring along with phenology tracking (Figure 3A, 3B). In combination with an end-of-season assessment of yield components and in-season monitoring of yield formation processes (Figure 3A), such data will allow season-level aggregate measures of tolerance to be decomposed into sub-components that reveal how productivity is affected at specific growth stages. Once this has been achieved, the secondary objective should be to identify both constitutive and adaptive traits as mechanistic determinants of phase-specific tolerance in support of trait-based selection. Two example concepts implementing this proposed strategy for wheat are illustrated in Figure 3C.

Disease phenotyping. Tolerance characterization may allow certain relaxations compared with phenotyping for QR and escape. First, symptom-level diagnosis may be less critical, as tolerance to foliar diseases represents primarily a plant's ability to maintain productivity under a given level of damage in terms of the loss of photosynthetic capacity (26, 141). A broad differentiation among damage types may remain necessary, however: biotrophic and necrotrophic pathogens affect plant metabolism and canopy function in distinct ways, and abiotic stress and physiological symptoms must still be discriminated from pathogen-induced damage. Second, the spatial resolution and damage attribution to plant organs in the 3D canopy is less stringent, as the primary interest lies in quantifying overall damage to the crop, e.g., the total plant photosynthetic area as seen from outside of the plot.

In contrast, relative assessments of healthy and diseased area as typically used for resistance characterization deliver an incomplete picture. An exact, high-throughput measurement of leaf area index (LAI) in dense canopies is likely to remain a significant challenge due primarily to occlusion, even given further progress in 3D reconstruction of dense canopies. A precise, intermediate-throughput assessment of LAI could be achieved by combining non-destructive in-field leaf area measurements based on RGB images of single leaves (10) with image-based plot-level tiller or ear counts.

Yield component phenotyping. Plant density estimates are readily achievable in crops with larger inter-plant distances and precise placement of single seeds, such as maize or sugar beet. In wheat and other crops with a similar growth habit and canopy structure, plant density estimates may be based on leaf-tip detection at emergence (73), but this approach is complicated by the fact that emergence of second leaves on some plants may overlap with emergence of first leaves on later-germinating plants. Evaluation of greenness maxima in multi-view images may provide an alternative approach applicable at later growth stages (112), which may be useful especially in winter cereals to correct for differences in winter survival. Fertile tiller density can be estimated by detecting spikes visible in 2D canopy images (80), but accuracy can be improved using multi-view information aggregated through explicit 3D reconstruction (154). Several yield components such as average grain weight and grains per planted area can be determined at plot-level after harvest by combining simple image analysis with total grain weight. The average number of grains per spike, and the average number of spikes per plant can then be derived.

The most difficult yield components to assess are the number of spikelets per spike and the number of grains per spikelet. Some works have successfully segmented spikelets in ear images captured under controlled conditions (95). In principle, the same can be achieved directly from high-resolution RGB imagery captured under field conditions. A complicating factor is that spikes must be fully visible and properly oriented toward the camera, which may introduce sampling bias. This bias may be alleviated if multi-view approaches are adopted to reduce occlusion (154) and increase the portion of ears meeting these criteria. A direct image-based assessment of the number of grains per spikelet is not possible as grains remain enclosed within the glumes, lemmas, and paleae of the spikelets.

Where a ‘stress free’ reference treatment or a gradient in disease is available for each genotype under study, the combination of in-field and post-harvest assessment of yield components and their comparison across treatments can reveal the effect of a stressor on different yield formation processes for that genotype.

Phenotyping candidate tolerance traits. Most amenable to high-throughput phenotyping are constitutive or adaptive traits related to biophysical growth and phenological plasticity. Although traits that can be directly and mechanistically linked with tolerance can be difficult to measure, reasonable proxies are readily accessible. For example, early vigour can be approximated by canopy cover growth or canopy height development (53). This can be a proxy for the timing of leaf emergence, leaf elongation rate, phyllochron, and tillering which can impact the relationship between the growth of the canopy and the development of the epidemic (107). Compensation via plasticity in yield component formation can also be quantified (see above). This would be useful in cases where disease is more prominent during a specific growth stage, impairing a specific yield formation process. Potential passive effects of diseases or actively regulated adjustments of senescence in response to disease can be readily observed based on colour properties of plant organs and their dynamics (6, 11). Compensation may occur through modified senescence dynamics in disease-affected organs (leaves; organ-level compensation) as well as in non-affected organs (e.g., stems, ears; plant-level compensation).

CONCLUSIONS AND THE WAY FORWARD

Image-based phenomics can support mechanistic understanding of a crop's robustness to disease by enabling quantitative assessment of resistance, escape, and tolerance in relation to canopy structure, growth, phenology, and yield formation. Organ- and symptom-level assessments provide mechanistic insights and may yield useful secondary traits for indirect selection, while canopy-level evaluations under field conditions directly capture overall performance in realistic environments. Challenges include robust imaging across variable canopy architectures and illumination, symptom-level diagnosis under heterogeneous conditions, and biologically meaningful aggregation of high-resolution measurements to experimental units. Gaps persist in creation of broad training datasets, standardization of acquisition protocols, and integration of disease data with complementary crop phenotyping and modeling to link disease development to yield and quality.

To make image-based phenotyping actionable for breeding, variety testing, and crop management, research should focus on developing scalable, interaction-free data acquisition protocols, high-quality annotated datasets, and robust methods for symptom detection, segmentation, and aggregation. Integrating disease phenotyping with 3D canopy reconstruction, phenology monitoring, and epidemiological and functional-structural plant modeling will enable mechanistic interpretation of epidemics and prediction of their impact on

yield and quality. This approach can provide the mechanistic understanding required for data-driven ideotype design and trait-based selection.

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