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Review article

Breeder friendly phenotyping

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ABSTRACT

The word phenotyping can nowadays invoke visions of a drone or phenocart moving swiftly across research plots collecting high-resolution data sets on a wide array of traits. This has been made possible by recent advances in sensor technology and data processing. Nonetheless, more comprehensive often destructive phenotyping still has much to offer in breeding as well as research. This review considers the 'breeder friendliness' of phenotyping within three main domains: (i) the *'minimum data set'*, where being 'handy' or accessible and easy to collect and use is paramount, visual assessment often being preferred; (ii) the *high throughput phenotyping (HTP)*, relatively new for most breeders, and requiring significantly greater investment with technical hurdles for implementation and a steeper learning curve than the minimum data set; (iii) *detailed characterization or 'precision' phenotyping*, typically customized for a set of traits associated with a target environment and requiring significant time and resources. While having been the subject of debate in the past, extra investment for phenotyping is becoming more accepted to capitalize on recent developments in crop genomics and prediction models, that can be built from the high-throughput and detailed precision phenotypes. This review considers different contexts for phenotyping, including breeding, exploration of genetic resources, parent building and translational research to deliver other new breeding resources, and how the different categories of phenotyping listed above apply to each. Some of the same tools and rules of thumb apply equally well to phenotyping for genetic analysis of complex traits and gene discovery.

1. Introduction

Phenotyping remains a cornerstone of plant breeding. Despite advances in genetics and the application of molecular technologies in crop research [1], crop breeding still relies heavily on the expression of grain yield and a handful of agronomically important traits for making selections and defining commercial products. Where genes of major effect are concerned, some valuable markers can be applied routinely in breeding, including as part of genome wide selection schemes [2]. For complex traits, however, most of the promising genetic approaches must incorporate whole-genome information. These include genomic selection, that models all markers in a framework that does not identify marker-trait associations, but incorporates all individual marker effects to predict yield [3], and QTL or genome wide association studies (GWAS) that help to dissect complex physiological traits [4,5]. Gene editing also holds promise, relying mainly on targeted mutation of cloned genes with known effects on specific processes [6]. While impact of such technologies can only increase with better genome sequence and diversity information [7,8], developments in fields like epigenetics testify to the complexity of how genes interact with each other and their environment [9]. Nonetheless, there is an imperative to understand and exploit the genetic potential of crop adaptation to maintain food security, given that maximum day and night temperature records are now being broken routinely across continents, and episodes of drought linked to mass human migration [10]. Such understanding will be underpinned by rigorous phenotyping [5] if it is to have impact in crop improvement.

In field crops, grain yield is the most highly valued phenotypic trait for any breeder because it integrates all important traits and genes into a biologically and economically useful reference point. This is the case despite the large degree of interaction that cultivars show in terms of grain yield with management practice, variation in weather and soil

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properties, and seasonal effects including biotic and abiotic factors [11], not to mention the generally significant gap between experimental plots and farmers' actual yield. So far, no 'genetic index' has been able to replace grain yield as the driver of economic impact in breeding, notwithstanding the importance of genes of major effect and their markers [12], although, progress is being made [13].

In addition to yield, there is an array of so called secondary traits that have theoretical, and in several cases proven contribution to crop performance. While these traits are also subject to genotype by environment interaction (G × E), they can add value to breeding for targeted environments [14,15]. This is evident from the major investments that public and private breeding programs have made in high throughput phenotyping (HTP) with the expectation of increasing efficiency and selection accuracy [16]. The power of HTP is largely a function of proximal and remote sensing technologies which can measure crop characteristics throughout the season using spectral reflectance, in a non-obtrusive way and at a breeding scale [17,18].

However, precision phenotyping of traits -that cannot be estimated at high throughput- is also becoming more commonplace. This is because as the growing environment becomes more challenging in terms of adaptation, our physiological and genetic models will need to embrace new traits to achieve an understanding of the system as a whole. An example would be the need to consider the role of roots in transpiration and plant signaling [19] before gas exchange data at the leaf or canopy level can be properly interpreted. Such comprehensive crop models can better inform strategic crosses among groups of well characterized candidate parents in order to stack complementary alleles [15]. These considerations highlight the importance of translational research that ends in pre-breeding, such that commercially relevant discoveries in basic plant science are subject to reality checks in a mainstream crop improvement context [20–22].

Plant breeding performs an outstanding service in maintaining food security by not only achieving steady yield gains [23,24] but also in protecting crops from a continuous onslaught of rapidly evolving pests and pathogens [23], and maintaining high standards of end-use quality [26]. Withreason, breeders have been reluctant in the past to adopt physiological breeding approaches into already successful breeding pipelines, due in large part to their complexity, cost and relatively unproven status. However, accumulation of knowledge about physiological and genetic bases of yield and adaptation, as well as access to HTP methods are now facilitating their adoption by breeders. Wide scale adoption of sophisticated phenotyping methods will only happen if they add efficiency and effectiveness in terms of achieving targets. In this sense, 'breeder-friendly' phenotyping should complement breeding approaches by cost-effectively increasing throughput during segregant selection, and adding novel sources of validated complex traits to crossing blocks. In this regard, stringent criteria need to be applied before incorporating new traits or phenotyping protocols into mainstream breeding pipelines (Box 1).

'Breeder-friendly' is a somewhat plastic concept when it comes to

Box 1

Discovering and validating new traits and phenotyping protocols in a breeding context. Classes of Phenotyping.

In order to adopt new traits for strategic crosses or new phenotyping protocols into breeding pipelines, a series of criteria and validation steps are required to indicate their potential in crop improvement, most if not all criteria should be met to ensure practical value and cost-benefit in conventional breeding:

Prerequisites of new trait or selection protocol

- Trait shows association with one or more key performance characteristics (e.g. yield, yield component, lodging, disease or pest resistance, end use quality) in target environments, or have strong theoretical basis to do so (e.g., if a novel trait can only be found in an exotic background).
- Trait shows significant genetic variation in terms of its potential contribution to performance.
- Trait presents workable repeatability/heritability.
- Phenotyping methodology is able to discriminate different levels of trait expression with acceptable degree of repeatability across genetic backgrounds and environments.
- Trait or selection methodology is not coupled to detrimental traits that reduce commercial value (i.e. linkage drag).
- Marker-trait associations with significant marker effects are identified in appropriate populations/panels using GWAS and/or QTL analysis to establish genetic basis of a given trait.

Proof of concept through pre-breeding and trait stacking (traits, markers, selection protocol)

- New trait is crossed into agronomically acceptable backgrounds, and selected for at appropriate generations –depending on genetic complexity- to enrich for alleles associated with new trait.
- When trait is expressed in relatively homozygous backgrounds in lines (e.g. F5-F6 for in-bred crops) or hybrids (F1), pre-breeding populations are evaluated to measure association between trait expression and key performance characteristic(s).
- New selection protocol is applied at appropriate stage(s) of breeding pipeline to determine its impact on performance characteristics compared with a standard selection procedure.
- In the case of complex traits especially, the above criteria are also applied when additional trait(s) are combined in one or more genetic backgrounds, in order to evaluate interactions among stacked traits, genetic backgrounds and environment.

Test of trait/selection protocol robustness in target environments

- Lines expressing the new trait(s) are trialed across representative target environments to estimate interaction with environment and contribution to performance characteristics.
- New selection methodology tested across representative target environments to estimate its interaction with environment and robustness of its association with performance traits.

Development of markers (marker validation)

- If a phenotypic trait delivers proof of concept, close-linked genetic markers can be developed (based on preliminary marker-trait associations/QTL) with the view to improving the efficiency and heritability of selection within mainstream breeding pipelines.
- Markers will need to be validated in a similar way as described above for traits.

Box 2
Classes of Phenotyping.

Handy traits

"*Convenient to handle, useful, within reach*" are among the definitions of the word 'handy'. Such traits in the breeding context typically represent a minimum data set for agronomic evaluation plus a few easy to measure integrative physiological traits, indicating fitness when comparing genotypes in season. At the harvest ripe stage this includes direct measurement of the 'mission critical trait' grain yield. Selection of agronomic traits are essential for preliminary screening of large populations of uncharacterized lines such as segregating progeny or new genetic resources. These agronomic traits are also typically required in national evaluations to determine suitability for release of advanced lines as potential new varieties. For example, in Europe, new varieties are subject to DUS testing – Distinctiveness, Uniformity and Stability. Hence, apart from grain yield itself, the minimum data set usually includes plant type -including height, lodging tendency, and phenology (i.e. time to heading or flowering and physiological maturity), disease and pest resistance, seed characteristics and end-use quality. A few handy physiological screens exist that can help indicate the adaptive potential of a genotype. Some examples are: assessing above ground vigor visually, via imaging [33] or using the Normalized Difference Vegetation Index (NDVI), assessing leaf or canopy N status using SPAD meter or NDVI [16], and estimating root capacity or relative gas exchange rate using canopy temperature under stress [34–37]. These handy phenotyping tools have relatively low cost.

High throughput traits

Traits amenable to HTP are typically measured by some kind of vehicle or gantry that provides remotely-sensed data sets at orders of magnitude faster than possible by hand [33], on breeding plots that have likely already passed through a preliminary screen. This approach is also favored to collect phenotypic data sets under multiple environments for physiological and genetic studies, since a large number of lines can be characterized for a range of remotely sensed parameters throughout the growing season (Table 1) at relatively low cost. High-throughput measurements of NDVI and other spectral vegetation indices can detect differences in physiochemical and structural properties of the vegetation such as pigment content, hydration status, photosynthetic area and vegetative biomass (for details see Table 1). Similarly, estimation of canopy temperature using infrared thermography has been used to screen for water status and stomatal conductance [36–39]. Digital imaging using standard red-green-blue (RGB) cameras is being exploited for 3D surface reconstruction and image pattern recognition using sophisticated deep learning methods, which in turn provide estimations of traits such as plant height [40,41], tiller number [42], biomass [43–45] and disease detection [46]. Some measurement protocols have been established while intensive development of smaller, cheaper and more accurate sensors, especially of imaging systems, have facilitated their application on a wider range of vehicles including lightweight unmanned aerial vehicles (UAVs) [30,47–49].

Precision phenotyping traits

Precision or detailed phenotyping is likely to encompass intrusive (i.e. destructive) as well as HTP and handy approaches. Because of the greater time, detail and oftentimes specialized equipment needed for screening, it costs more, and it is typically limited to smaller panels of a hundred or so lines that have already passed through preliminary screening and represent candidate parents for breeding, pre-breeding, and to be used in genetic or mechanistic studies. Beyond those presented here (Table 1; Fig. 2), many other traits have been suggested as promising for achieving yield gains and climate resilience, and readers are referred to work referenced herein; for overviews see -under drought- [50]; -under heat stress- [51,52] and for yield potential [53], and works referenced therein too. Precision phenotyping is associated with higher human/capital investment and typically requires significant expertise and training, but the cost-benefit can be high where crosses result in the stacking of traits that significantly boost genetic gains [22] and in cases where the precision phenotyping can be used to understand the physiology and genetics of the breeding germplasm and then be developed in to handy and/or high-throughput phenotyping assays, and potentially molecular markers for rapid screening.

phenotyping. As well as throughput, other factors will determine the cost-benefit of a phenotyping protocol, including, the difficulty of achieving genetic gains in the target environment; the potential added-value of improving the trait(s); and the feasibility of applying the protocol effectively in the breeding pipeline. For the purposes of this review, three main classes of field based phenotyping will be considered (Box 2; Fig. 1) involving: 1) ***"Handy" phenotyping traits*** including those either routinely measured, or at least readily accessible for phenotyping at a breeding scale with relatively little capital investment; 2) "***High throughput (HTP)" phenotyping traits*** which require some training or specialization to measure and requires the construction or purchase of specialized equipment; such data may also provide derived traits via models; 3) "***Precision" phenotyping traits*** which are generally low throughput and/or expensive, but offer the potential for high pay-off in terms of opening current bottlenecks to yield improvement.

There have been numerous reviews of HTP methods in recent years [17,18,27–30] and the main purpose of this current review is to emphasize the current state of the art in 'breeder-friendly' phenotyping applications. Most of the examples will come from wheat, though the principles and technologies are broadly applicable to a wide range of field crops. Phenotyping interventions can be applied at different points in the crop breeding pipeline and their relative value to selection in the breeding pipeline will also depend on target traits and target environments (Table 1). Therefore, the degree of 'breeder-friendliness' is not absolute, but rather depends in part on the throughput required and cost-benefit for each individual crop and breeding program. A trait that takes several minutes or longer to measure would not be 'friendly' for measuring thousands of genetic resources or progeny plots. However, it may be useful and feasible when comparing dozens or even hundreds of potential parents with the view to stacking complementary traits through crossing, or for building physiological/genetic prediction models that can be applied to thousands of selection candidates. The traits presented (Table 1; Fig. 2), while varying in their level of throughput potential, have mostly been measured successfully in the field and have demonstrated association with yield or yield components. Many have also been put to use in pre-breeding [5,14,15,31] if not in a mainstream breeding context [32]. This review cannot be exhaustive in including all technologies available but focuses on some of the more promising and relatively breeder friendly technologies with broad application.

2. Phenotyping interventions at different stages of crop improvement

Crop improvement pipelines typically involve a range of environments, planting methods and objectives spread out over time. The relative merits of different phenotyping approaches will depend on all of these (Box 1) as well as the trait of interest (Table 1). In summary, the handy methods are best for single plant selections typically used for relatively heritable traits (e.g. phenology, height, foliar diseases) in early breeding generations or screening of genetic resources, while the high throughput approaches lend themselves to measuring canopies in yield plots. Precision approaches, being resource intensive, are usually reserved for characterizing parental lines as well as studies to elaborate the physiological and genetic bases of performance characteristics. However, end-use quality evaluation requires precision laboratory

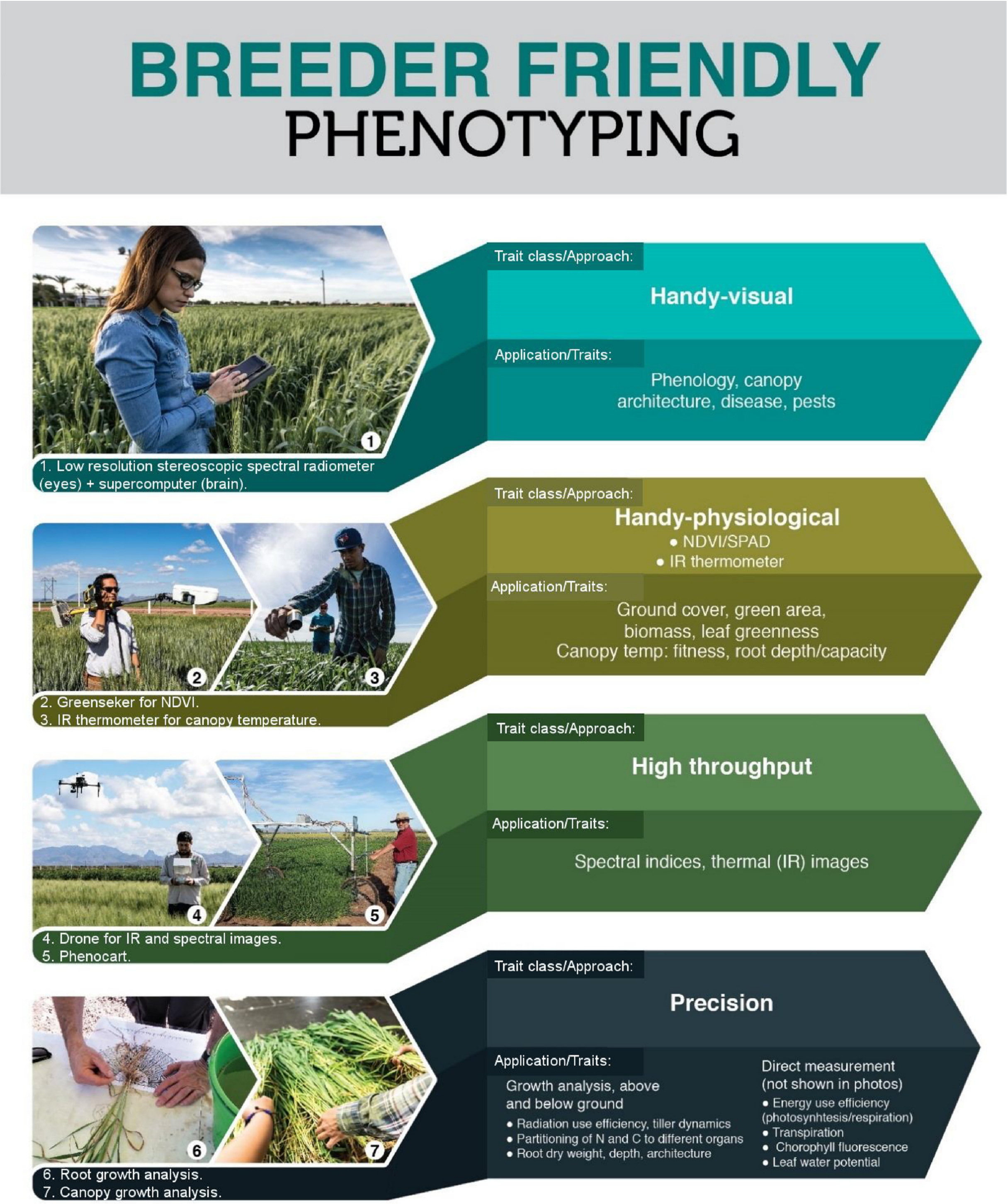

Fig. 1. Examples of different classes and applications of breeder friendly phenotyping.

protocols for selecting both parents and progeny.

Some phenotyping tools can be applied at relatively high throughput on single plants, such as the chlorophyll meter or the viscous flow porometer. The latter was associated with genetic gains in irrigated spring wheat [90], and shown to be cost effective according to economic analysis [91]. Nonetheless, given the numbers of plants typically involved at early generations in a full scale breeding program, the heterogeneity of the soil and unrepeatability of the plants inherent in spaced planted trials, as well as the heterozygosity typical of individuals at early breeding stages for inbred crops, low cost visual selection is normally favored.

Centralized breeding operations function if a range of targets can be simulated through the application of different management factors, such as irrigation, sowing dates, inoculation for disease, etc. These managed environments can be augmented through strategic use of remote phenotyping hubs (or ‘hotspots’) representing locations where strong selection pressure for a given trait can be guaranteed (Fig. 3).

3. Phenotyping for different targets

In conventional breeding, genetic gains are achieved generally through recombination of largely unspecified genes of minor effect by

Table 1
Applicability and value of phenotyping tools and traits at different stages in crop improvement in the field (see Pask et al. [48] for further details of protocols).

Traits	Value of trait	Tool/protocol/SRI/Related trait*	Throughput: H = high, M = medium, L = low	Precision: H = high, M = medium, L = low	Relevant target environment(s)	Large scale screening of genetic resources	Parental selection	Progeny selection in plots	Reference (value of trait and/or methodology)
MOST GROWTH STAGES									
In season biomass	Estimates radiation use efficiency (RUE)	Growth analysis (GA); Water Index (WI); LiDAR; digital RGB imaging (RGB)	L; M-H	H; M	All	?	+	+ (WI)	[44,45,55–57]
Tiller number	Excess tillers wasteful & provoke lodging	GA	L	H	All	?	+	?	[58,59]
Relative transpiration rate	Estimates access to water/gas exchange rate	Canopy temperature (CT); WI	H	M-H	All	+	+	+	[35,60,61]
Estimation of photosynthesis (PS) rate	Estimates photosynthetic potential	PS Index (spec); Chlorophyll Fluorescence	M-H	L-M	Yield potential	+ (spec)	+	?	[62,63]
Leaf/canopy pigments	Influence RUE and photoprotection	Spectral reflectance indices (SRI); SPAD	M-H	M	All	+	+	+ (SRI)	[29,64–67]
PRE-HEADING									
Crop emergence	Seed viability, sowing or soil problems	NDVI	H	H	All	+	+	+	[30]
Early vigor	Protect soil moisture; increase light interception	NDVI; RGB	H	H	Heat; Drought; Freezing	+	+	+	[68,69]
Light interception	Positive for biomass	NDVI; Ceptometer; RGB	H; L; M	M; H; M	Heat; Drought	+	+	+	[70–72]
Days to booting	Development pattern	Visual	M	M	All	?	+	+	[73]
CIRCA ANTHESIS									
Days to heading	Development pattern	Visual; RGB; SRI	H; M-H	H	All	+	+	+	[74,75]
Days to anthesis	Development pattern e.g. grain fill duration	Visual; RGB	H; M-H	H	All	?	+	+	[75]
Partitioning to organs	To optimize harvest index	GA	L	H	All	?	+	?	[76]
Crown roots; root angles	Lodging resistance; estimate root biomass	Shovelomics	L	M	Yield potential	?	+	?	[77]
Stem carbohydrates	Source of pre-anthesis assimilate	Near infrared reflectance (NIRs); Anthrone	M; L	M; H	Post anthesis stress	+ (NIRs)	+	?	[78,79]
GRAIN FILLING									
Canopy architecture	Affects radiation use efficiency	Visual; LiDAR, RGB	M-H	M-H	Yield potential	+	+	+	[80–82]
Canopy temperature	Predictive of root capacity under stress	Infrared thermometer; thermography	M; H	M-H	Heat; Drought	+	+	+	[34,35]
Stay-green	Prolongs photosynthesis	NDVI; SPAD; Visual score	M-H; L; L	H	Post anthesis stress	?	+	+	[83]
Lodging	Associated with yield loss	Visual; Lodging standard methods; Pushomics	H; M-H	H	Yield potential	?	+	+	[84,85]
Spike density	Useful if other yield components not known	GA; RGB; LiDAR	L; M-H	H; M	All	+	+	+ (RGB)	[86–88]
Days to physiological maturity	Maturity class; development pattern	Visual; SRI	H; M-H	M	All	?	?	?	[89]
Yield components	Informative on genetic yield strategy	GA	L	H	All	?	?	?	[56]
Disease detection	Selection for disease resistance	Visual; RGB; SRI, full spectrum analysis	M-H	L-M	All	+	+	+	[46]

SRI: Spectral reflectance indices.

* Related trait: trait that can be measured for indirect estimation of another trait.

+ = applicable.

? = potentially applicable.

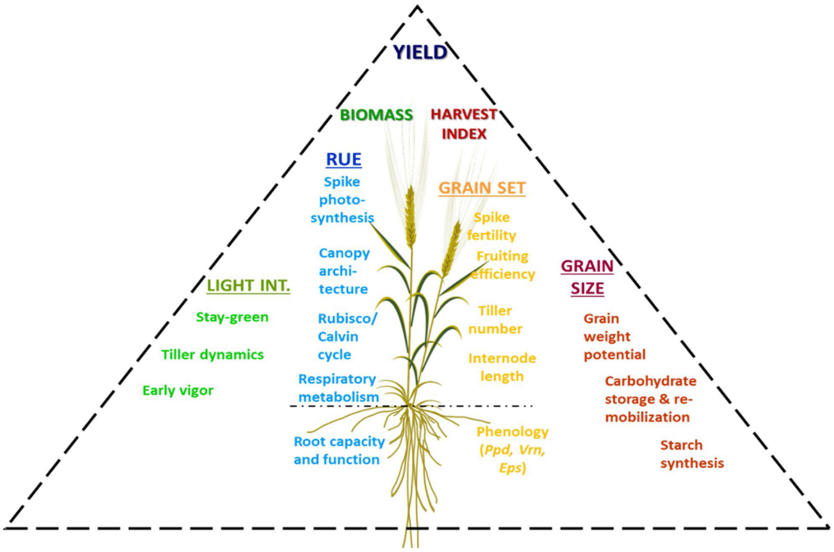

Fig. 2. Trait hierarchy in relation to approximate degree of integration, depicting some of the established drivers of biomass (source) on the left of the plant, and harvest index (sink) on the right side. Abbreviations: Int = interception.

intercrossing elite lines (“best with the best”), or introducing alien chromatin into elite backgrounds typically associated with disease resistance [92], and then selecting the best yielding progeny. Apart from yield testing *per se* and measurement of end-use quality traits, the intervention of phenotyping in the above has been largely restricted to ‘handy’ traits (Table 2) [26. The approach has been highly successful in wheat [23,24]. At CIMMYT and many large programs, breeding is conducted in relation to a range of target environments where typically, near optimal conditions are used to estimate yield potential, and a series of managed biotic or abiotic stress environments are also employed according to target profiles [93]. The target environment determines first which are the main traits of interest (based on trait models) and secondly, which classes of phenotyping are required, depending in part on urgency and cost-benefit (Box 1). Examples for a range of strategic breeding goals are presented in the next section.

3.1. *Yield potential*

While in crops like wheat, maintaining disease resistance can consume many of the resources for crop improvement, increasing the genetic yield potential of crops is essential since it is a key incentive for most farmers when it comes to variety replacement. Since genetic gains need to increase above current rates if global demands for cereals are to be met [94], attention has turned to yield potential related traits, especially radiation use efficiency (RUE) [95–99]. However, increased RUE alone does not guarantee increased yield unless additional assimilates result in more and/or larger grains, and increased RUE itself may require additional uptake efficiencies of water and nutrients. Experiments in various cereals have shown that a high demand for assimilates —determined by sink strength of the grains—can stimulate the supply of photo-assimilates, and vice-versa. The studies have demonstrated that well-managed wheat crops typically carry excess photosynthetic capacity, and as a

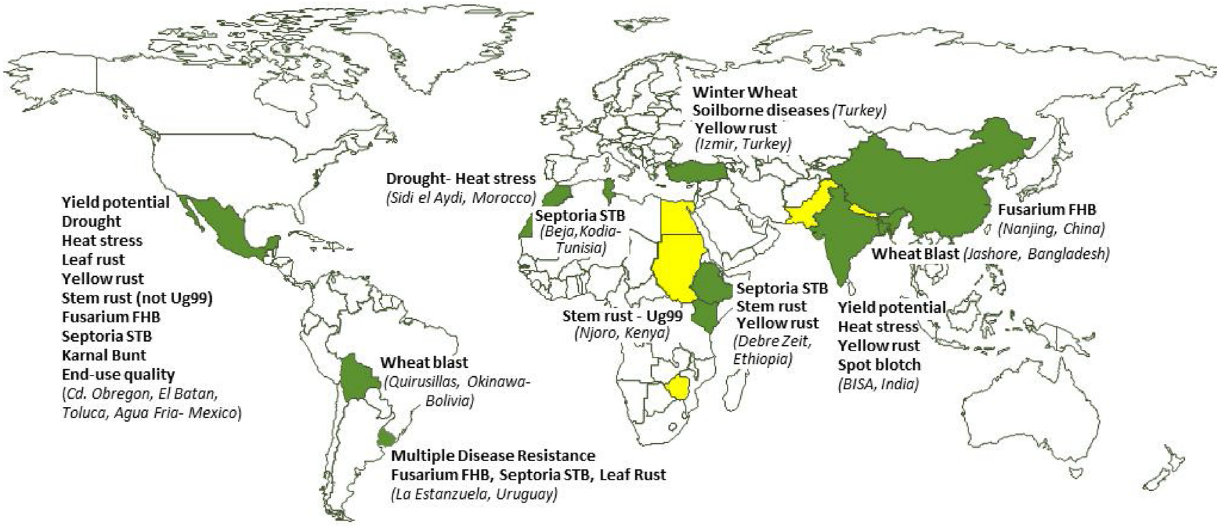

Fig. 3. Global network of precision field-based wheat phenotyping platforms of the CGIAR Program WHEAT (see http://wheat.org), developed with the support of co-investing national agricultural research institutes. The objective is to generate multi-location phenotypic data on prioritized traits, under defined good practices, and fostering germplasm exchange. The selected locations represent key environments, for example, hotspots for specific diseases and future-climate analogue sites. This model opens opportunities to increase coordination in wheat phenotyping, avoiding duplications, and building on efficiency and capacity for research. Green: functional platforms for particular traits, Yellow: planned platforms. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

Table 2

Classes of phenotyping traits accessible for breeding and translational research, and considerations for their application (see Deery et al. [82] and references in Table 1).

Tool	Use/Trait measured	Advantages	Disadvantages	Application
HANDY PHENOTYPING TOOLS				
Eyes	Visual traits like phenology, disease score, lodging	Fast	Subjective, potentially low repeatability across observers	Minimum data set for agronomic acceptability
Ruler	Plant height	Cheap, easy to use	Standardization	Minimum data set for agronomic acceptability
Mass balance	Grain or straw weight; average kernel weight	Easy to use	> $1000 (for reliability)	Minimum data set for agronomic acceptability
Plot Harvester	Yield (and therefore calculation of grains/m [2]); possibly straw weight	Precision, reliability, direct assessment of yield	> $100,000 + maintenance	Yield measurement
Hand held IR-thermometer	Canopy temperature indicating transpiration/vascular capacity of roots, etc.	Cheap, easy to use	Affected by weather conditions	Indicates effective root system and adaptation
Hand held NDVI meter	Vegetative index indicating canopy greenness/ground cover/stay green	Robust to weather	~$1,000	Indicates establishment, vigor, canopy N status
Chlorophyll meter (e.g. SPAD)	Leaf level of greenness	Robust to weather	> $1,000	Indicates leaf N status
HIGH THROUGHPUT PHENOTYPING TOOLS				
Vehicle:				
Drone	Spectral devices for range of traits including thermography (see below), RGB cameras, LiDAR	Non-invasive, fast	Low payload, regulation restrictions, windy conditions	Extensive trials, including irrigated or flooded fields
PhenoStick/Phenocart/Phenobot	Spectral devices for range of traits including thermography (see below), RGB cameras, LiDAR	High payload, no regulation restrictions	Access in wet soil, etc.	Relatively dry soil
Blimp	Spectral devices for range of traits including thermography (see below), RGB cameras, LiDAR	Mobile, high payload	Sensitive to wind	Low wind situations
Gantry	Spectral devices for range of traits including thermography (see below), RGB cameras, LiDAR	High payload	Relatively immobile	Intensive research areas
Aircrafts	Spectral devices for range of traits including thermography (see below), RGB cameras, LiDAR	High payload, fast	Low resolution, expensive (potentially) pilot training / license	Extensive trials and farms
Sensors:				
Infrared	Canopy temperature, root index, heat and drought adaptation	Fast	Low resolution, elevated cost, affected by weather	Indicates effective root system and adaptation
Multi- and Hyperspectral	Spectral indices, full spectrum analyses for range of traits	Fast, relatively cheap (multispec), easy to use (multispec)	Expensive (hyperspec), difficult to use (hyperspec), sensitive to movement (hyperspec), data size	Range of traits related to pigment composition, light absorption, water status, nitrogen status, structural properties, disease detection
Digital cameras (RGB)	Feature extraction (morphology), 3D reconstruction (canopy architecture), light interception, growth analysis	Fast, high resolution, cheap	Data size	Traits related to pigment composition, light absorption, structural properties, disease detection
LiDAR	Canopy architecture	Precision	Complex data processing	Canopy structure
IMAGE ANALYSIS/DATA PROCESSING:				
Spectral indices	Range of traits related to pigment composition, light absorption, water status, nitrogen status, structural properties, disease detection Simple growth analysis	Simple processing	Usually affected by view geometry	–
Full spectrum analysis	Range of traits related to pigment composition, light absorption, water status, nitrogen status, structural properties, disease detection	More information than spectral indices	Complex processing	–
Feature recognition	Spike counting, stand counting, disease detection, phenology	Allows to measure complex structural traits	Complex processing	–
3D reconstruction (LiDAR and digital imaging)	Canopy structure	Measurements are relatively easy to implement (RGB)	Complex processing, computing resources	–
PRECISION PHENOTYPING				
Full growth analysis	Integrated measure of growth, partitioning, RUE	Comprehensive	Slow, requires an oven	Selection of parents with RUE, WUE & partitioning traits
Fluorescence	Light and dark fluorescence of the chlorophylls	Clip to measure dark adapted leaves	> $15 K; spot measurement	Photoinhibition, physical damage in photosystems, recovery from shade
NIR Reflectance	Estimate of tissue water soluble CHO content in plant tissue (e.g. stems)	Inexpensive/sample	Capital investment, resolution	Pre-anthesis contribution under drought, photosynthetic capacity

(*continued on next page*)

Table 2 (*continued*)

Tool	Use/Trait measured	Advantages	Disadvantages	Application
Dynamometer, caliper, ruler + protractor	Stem and root lodging probability	Inexpensive/allows estimation in the absence of lodging events	Slow (~10 plots/day/person)	Lodging risk estimation after anthesis
Ceptometer	Light interception by the canopy or by *strata*	Estimation of LAI	Depends on clear skies and plot uniformity	Amount of light intercepted by the canopy, coefficient of extinction
IR gas analysis	Gas exchange (photosynthetic rate, stomatal conductance and transpiration)	Measures C fixation and transpiration	> $50 K; spot measurement, slow	Identify PS potential and adaptation to environment

result, increasing photosynthetic potential does not necessarily optimize grain number as shown by the negative association observed between harvest index and biomass [100]. Therefore, to achieve full expression of yield potential, it will be necessary to optimize the source:sink dynamic by ensuring that expression of grain set matches the photosynthetic potential of current and future genotypes.

Evidence for genetic variation in source:sink balance (SSB) and its importance in boosting yield and radiation use efficiency (RUE) in field grown plots has come from various sources, including studies with cytogenetic stocks (see [101]). More recently, a cross designed to combine different traits associated with high sink strength in high RUE backgrounds resulted in doubled haploid lines expressing exceptional yield and biomass in a high yielding environment in Southern Chile [234], further supporting the idea that the right combination of sink traits can permit increased expression of RUE. In addition, results of the Wheat Yield Collaboration Yield Trial (WYCYT) have shown significant increases in yield potential across international wheat targets in the selected progeny of crosses designed to combine favorable sources of source and sink traits with high RUE [31]. Subsequent rounds of pre-breeding have confirmed further yield progress [102,103].

Since stacking "source" and "sink" related traits (Fig. 2) via strategic crossing is gaining a body of evidence to support its efficacy – while at the same time involving intuitively valuable traits for increasing potential yield (source) and harvest index (sink), respectively-, the subsequent section will discuss the phenotyping approaches required to measure these traits in a mainstream breeding context.

3.1.1. Source: (Light interception and RUE)

Biomass of elite cultivars has increased modestly in recent years [100,104–107]. Although these changes have come about as a result of selecting for superior grain yield rather than for the physiological traits *per se*, it is feasible to select for them directly. Furthermore, there is clear evidence for expression of superior biomass and related-traits (such as light interception and RUE) in many genetic resources [5,108].

Greater total biomass can result from increasing crop light interception (LI) and radiation use efficiency (RUE) or their component traits (Fig. 2). Of the RUE related traits shown in Fig. 2, canopy architecture, and root capacity under abiotic stress [34] are the only ones that might be considered handy or high throughput. Canopy architecture is typically evaluated with a visual score which may be based on digital images, and root capacity can be estimated using CT, at least under stress [34,35]. The other traits depicted in Fig. 2 require more precision approaches.

For example, total canopy light interception is estimated relatively accurately with a light bar or ceptometer through comparing incident light above and below the canopy [109]. Since LI is not static, it is best measured at predetermined growth stages, and close to when the sun is at its zenith to maximize resolution between genotypes. Use of a ceptometer would certainly be considered a 'precision' approach. However, since LI is associated with ground cover, more 'handy' or HTP approaches include measuring NDVI either directly [29] or using proximal sensing tools like UAV carrying RGB or multi-spectral cameras [110]. The main restriction is that NDVI only shows good resolution between genotypes at relatively low canopy density (i.e. leaf area index < 3), and therefore has application either under abiotic stress when vegetation is reduced, or at early stages of canopy development under more favorable conditions [55]. Chlorosis or loss of green area is associated with reduced LI during the senescence stage of grain-filling (or earlier under biotic and abiotic stress), but cannot be estimated by measuring LI directly since chlorotic and dead leaves also intercept light. However, the 'stay-green' trait is well estimated using NDVI that provides an integrated greenness index of the whole canopy [83]. Flag leaf 'stay-green' can also be estimated from repeated SPAD measurements (every 4–7 days) in the same culm [54].

Reliable estimates of biomass and RUE require precision approaches, specifically growth analysis (i.e. the destructive sampling of plant organs over time). Biomass is sampled at different growth stages to measure changes in dry matter accumulation, which together with estimates of LI, enable RUE to be estimated at discrete growth stages. Genetic diversity has been identified for RUE at distinct growth stages [5] which may perhaps permit their alleles to be stacked through strategic crossing [5]. On this note, growth analysis is an integrative and fairly precise measure of net carbon assimilation and RUE compared with say measuring gas exchange, which requires expensive equipment and is much less integrative both in terms of duration (readings typically being snapshots in time) and the photosynthetic organs measured (usually just leaves fully exposed to light).

As described earlier, while remote sensing protocols to estimate in season biomass and LI exist (Table 2), currently the resolution between genotypes is more suitable for HTP than precision needs. Jin et al. [87] provide a methodology to estimate end-of-season biomass from maximum canopy height (around flowering) and stem count/diameter estimates using ground-imagery after harvest. However, they acknowledge that while this estimation of ‘bio-volume’ has a high correlation with end-of-season biomass, it is also well correlated with anthesis biomass as it is mostly a structural description, not accounting for sugars etc. However, Furbank et al. [28] outline examples of how HTP is beginning to deliver on the ability for breeders to estimate RUE.

While LI and RUE are the most integrative estimates of photosynthesis and can be used directly to boost yield through their combination with positive expression of HI, the principle of trait stacking requires that diversity for their component traits (Fig. 2) also be considered as part of a translational research approach to evaluate their potential to contribute to genetic gains. For example, favorable expression for the components of source traits can be crossed in order to stack such traits as part of a parent building exercise aimed at significantly boosting biomass. These could include spike and leaf photosynthesis, pigment composition and light reactions, the dark reactions of photosynthesis related to Rubisco and the Calvin cycle, as well as respiration costs for growth and maintenance [97]. These traits are generally low throughput which is why they can only realistically be considered in the context of parental selection and parent building.

For example, a study of diversity in Calvin cycle enzymes and Rubisco within the *Triticeae* demonstrated the potential benefit of replacing Rubisco of *T. aestivum* with Rubisco from *Hordeum vulgare* or the wild species *Aegilops cylindrica*, in terms of achieving higher assimilation rates [111]. Another photosynthetic trait recently identified which offers to significantly boost RUE, is related to the speed of induction of photosynthesis on shade to sun transitions [99]. Work under an International Wheat Yield Partnership (IWYP, https://iwyp.org/) research project is attempting to identify genetic diversity for this trait in wheat germplasm.

The main restriction to selecting for photosynthetic and respiratory traits even at low numbers is that many require expensive equipment and highly trained technicians. However, the use of spectral reflectance to estimate photosynthetic rate [62] and respiration [112] at leaf level have been reported as well as at canopy level [113]. In particular, the inversion of integrative canopy radiative transfer models and the estimation of sun-induced chlorophyll fluorescence have shown their potential to track dynamic changes of photosynthetic traits at canopy level. Chlorophyll fluorescence is directly link to the electron transport rate in the light reaction of photosynthesis, and its passive estimation using spectroscopy has been used to detect natural and stress induced variations in photosynthetic activity at canopy level [114–117]. All these approaches currently lack refinement for routine use in precision phenotyping for parental selection but have further potential for improvement.

3.1.2. Sink: (harvest index and related traits)

According to the majority of published studies, most historical genetic gains in cereals are related to increases in harvest index (HI) [23,118]. When combined with high-input agronomy, plant height reduction (*Rht)* genes in wheat and their equivalent in rice and other crops caused dramatic increases in HI and productivity in the 1960s and '70s [119]. However, subsequent increases in HI are less well understood and genetically complex. Therefore, HI still expresses large genetic variation –typically 0.40 to 0.55 in modern wheat- [100,118], depending on plastic response to environments as well as underlying genetic background effects, both of which are poorly understood. Expression of HI can be considered integrative since many physiological processes affect it (Fig. 2). Unfortunately, HI has not been amenable to high throughput phenotyping, and is rather estimated from the ratio of yield and above ground biomass at maturity. Using a growth analysis type approach at physiological maturity, the components of HI can also be calculated, including grain number, grain size, spike number and grain number/weight per spike. Other spike fertility and dry-matter partitioning traits can also be measured using more detailed growth analysis, including spike dry-matter to calculate, spike partitioning index at anthesis [76], number of grains per spikelet, and fruiting efficiency or grains per unit spike DM at anthesis [120].

Research has clearly linked these traits to yield but the lack of high throughput screens has limited their use in mainstream crossing. Recent advances based on digital RGB cameras or prototypes with threshers and line scan cameras offer some promise for automation, achieving 1000 plots/day [121,122]. The development of reliable markers is

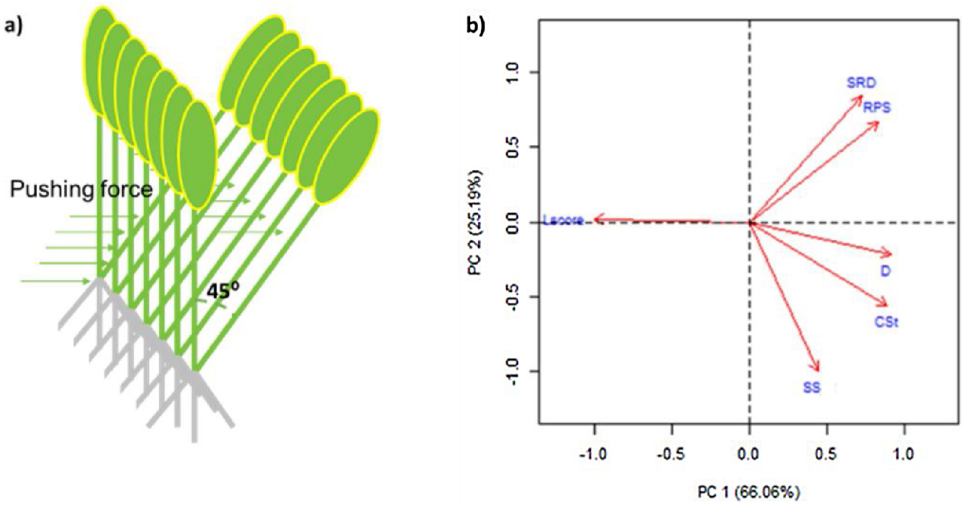

Fig. 4. **(a)** Diagram of applied pushing force at canopy level to measure Canopy Strength (CSt), and **(b)** biplot with correlation between CSt and lodging related traits.

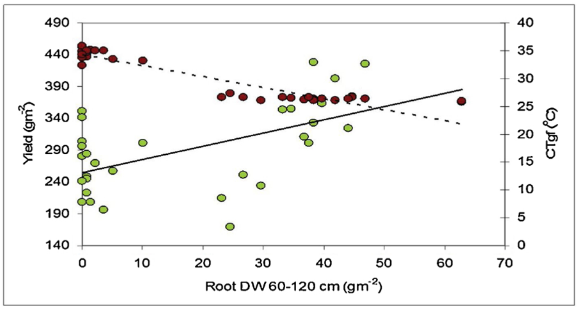

Fig. 5. Association of root dry weight below 60 cm with (i) yield (R [2] = 0.35) and (ii) canopy temperature (CT) (R [2] = 0.88) during grain filling (gf) for 16 wheat sister lines of Seri/babax under water-limited conditions, NW Mexico. Green circles represent yield; red circles represent canopy temperature. Data from [34]; figure published in Reynolds and Pinto [165] based on data from Lopes and Reynolds [34]. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

expected to help stack sink related traits such as grain number and weight [123], and in pre-breeding at the IWYP-Hub several trait and marker combinations are being tested through translational pre-breeding research approaches (https://iwyp.org/).

Crop phenology has a major influence on grain sink determination. To optimize seed set and grain weight potential, the timing of the sensitive reproductive growth stages has been genetically fixed largely to avoid periods of abiotic stress. The most sensitive developmental stages in cereals have been shown to be rapid spike-growth phase (from initiation of booting until heading), meiosis, and pollination [124,125]. Although these phenological stages can generally be observed by eye, sequential remote sensing has potential to score for ear emergence and possibly other stages at a breeding scale [126].

Better understanding of the physiological and genetic components of phenological development are expected to lead to more optimal and stable expression of HI across a wide range of environments and as a result of better targeted breeding. To achieve this, more detailed analysis of early phenological patterns (e.g. 107), will likely be needed for parental selection and/or in the development of reliable molecular markers, so that stacking of the appropriate alleles can be achieved.

Improvements in sink strength can imply changes in plant organ partitioning that potentially result in negative tradeoffs with the functionality of the plant as a whole. For example, little is known about possible tradeoffs with root growth when above ground biomass is increased, although studies of water uptake suggest that there has not been a negative consequence associated with increased yield and biomass in semi-dwarf wheat so far, even under reduced irrigation [128]. Other studies suggest that the *Rht* gene in wheat decreased root capacity [129]. While it is well known that the *Rht* gene also reduced investment in the stem mass, it did not compromise structural integrity in terms of lodging tendency as the reduction in height lowered the plants center of gravity. Nonetheless, increased partitioning to the spikes could at some point compromise investment in the root and stem strength necessary for a stable structure, especially given that further reduction in height is not compatible with higher yielding crops with heavier spikes [118]. Therefore, it is important to be able to phenotype and select for the traits associated with lodging resistance to protect genetic gains.

3.2. *Lodging*

Lodging is a persistent phenomenon affecting wheat and other crops that involves the interaction of plants with abiotic (wind, rain, soil) and biotic (e.g. diseases) factors and the crop management (e.g. fertilizers, irrigation schemes, plant growth regulators) [130]. Reductions of grain yield have been estimated from 7 to 80 % [130–137] together with reduced grain quality and greater drying costs [130,138,139]. Lodging has been reported to be a potential problem for wheat in the UK [138,140], Canada [141], China [142], India [143], Mexico [144], Western Europe [132] and Australia [137]. Plant breeders commonly classify wheat cultivars for lodging resistance only if a natural lodging event occurs. However, lodging events are not consistent in every crop cycle nor do the lodging factors affects fields uniformly. These aspects make difficult the continuous identification and removal of lodging susceptible genotypes throughout the breeding cycle [145].

A set of stem/root biophysical properties related to the stem and anchorage strength (lodging-related traits) [84,146] can be used to screen germplasm for lodging resistance, enabling breeders to classify genotypes by type of lodging (root/stem lodging) and more importantly, in the absence of natural lodging. Models indicate that increasing stem/anchorage strength would be necessary to improve stem/root lodging resistance in winter wheat [147] and spring wheat [148]. Previous work have shown wide genetic variation for these lodging-related traits [147,149,150]. Nevertheless, measuring these traits currently requires significant investment of time in the field and laboratory [147,150]. According to [85], optimizing lodging methods would be feasible to screen parental lines and small exploratory genetic diversity panels, but not sufficiently high throughput to screen very large numbers e. g. more than 1000. Optimized lodging methods are prerequisite to develop genetic markers for lodging resistance. Several promising quantitative trait loci QTL have been reported [151–161].

A ‘breeder friendly’ and faster phenotyping tool has been reported to assess lodging resistance directly in the field with positive results [145,151,162]. This instrument’s operational principle is to measure stem strength (single or multiple stems) when an external pushing forceis applied. A similar approach followed at CIMMYT wheat program has led to the testing of a new trait named Canopy Strength (CSt). This friendly phenotyping trait consisted of capturing the pushing force applied to bend the wheat canopy (stems in 0.3 – 0.5 m of the experimental plot) at 45° angle from its vertical position (Fig. 4a) (‘Pushomics’). Since it takes only a few seconds to measure this trait, it would be adequate for large scale screening of genetic resources. Biplot from a principal component analysis indicated that canopy strength was strongly positively correlated with stem diameter (D) and to a lesser degree with stem strength (SS). A weaker positive correlation was also found for root plate spread (RPS) and structural rooting depth (SRD). A key finding was the strong negative correlation between canopy strength and lodging score (Lscore) (Fig. 4b, unpublished data). Despite canopy strength still being a trait currently under testing, these results are highly promising.

3.3. *Abiotic stress*

Strategic crosses that combine parents with good expression of source and sink has also shown impact on breeding under abiotic stress [31,163] and have, for example, led to the release of three wheat varieties in Pakistan. This approach functions because when a genetic resource like a landrace, for example, shows good expression of biomass under drought, it can be concluded that it either expresses highly efficient water budgeting or has the root capacity to access subsoil water [108], either trait being potentially valuable. However, what a landrace typically lacks is good expression of HI. Therefore, crossing (and backcrossing) it with an elite line and selecting among progeny for handy traits like cool canopy and kernel size -as well as grain yield- is likely to facilitate the identification of segregants where the useful traits from both the landrace (biomass) and the elite line (HI) have been successfully stacked. Similarly under heat stress, a genetic resource with large biomass relative to check lines encompasses unspecified mechanisms of heat tolerance, even if poor local adaptation does not permit good expression of grain yield. Crossing with moderately heat tolerant lines that express high HI under the same stressful environment has been shown to produce some progeny with complementary alleles indicated by yield gains [31].

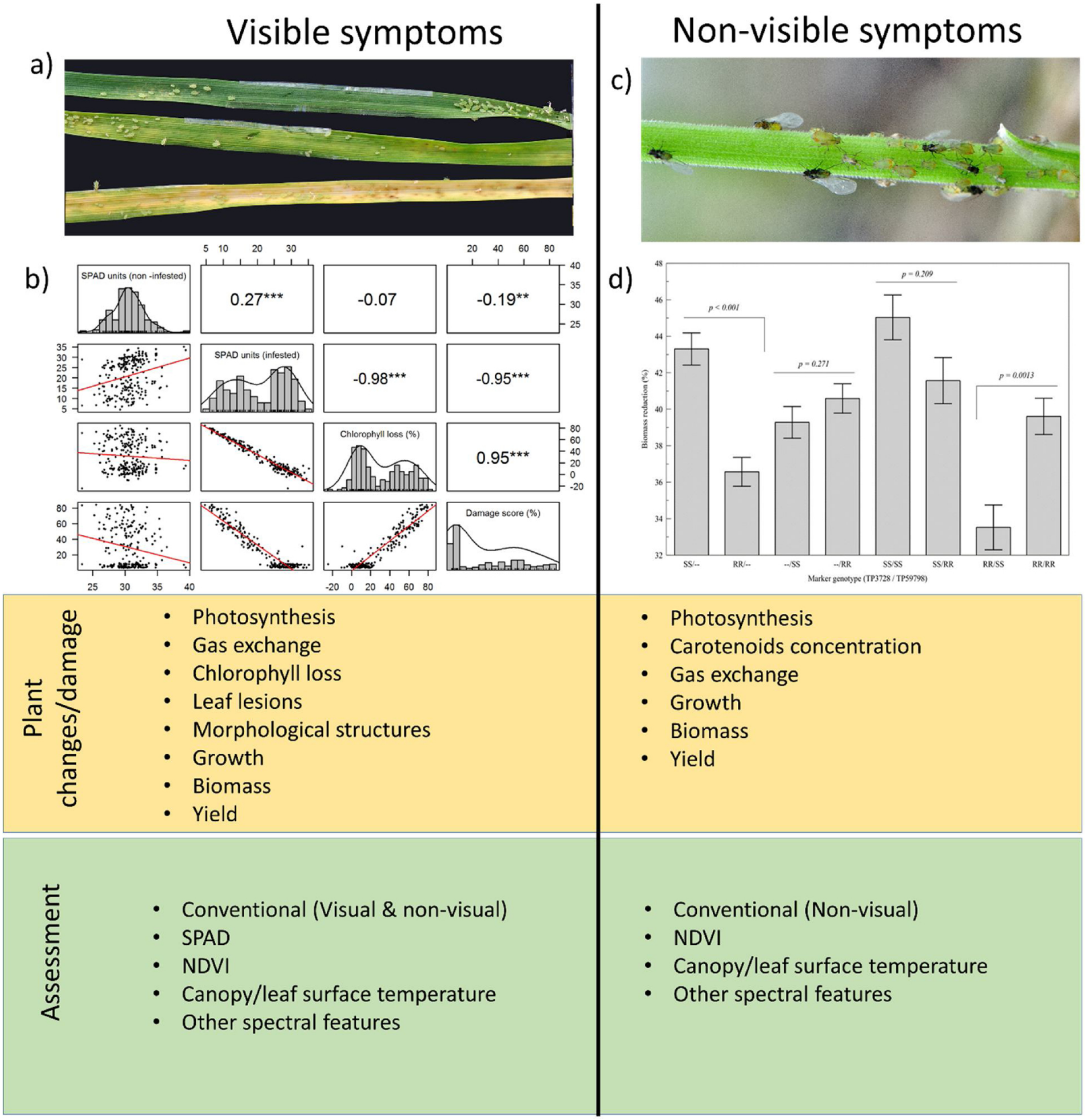

Fig. 6. Phenotyping options for arthropod resistance on possible plant responses to arthropod attack. a) Resistant and susceptible wheat genotypes to *S. graminum* responses after 14 days of exposure; b) Chlorophyll content relationships between resistant and susceptible plants under *S. graminum* infested and non-infested conditions [197]; c) Absence of visual symptoms upon feeding by *R. padi*; d) Biomass loss caused by *R. padi* in resistant and susceptible plants [200].

Most of the traits presented in Fig. 2 would have likely value under abiotic stress, even if the underlying mechanistic and genetic bases are not entirely the same among diverse environments. This highlights one of the advantages of the physiological breeding approach currently. Namely that since so few physiological traits have been applied in mainstream breeding, there is a significant opportunity to stack traits that have not been previously considered in a deterministic way [15] and for which large genetic variation is typically found even among relatively elite material [164], and more so in genetic resources [5]. A principal example mentioned already, is the selection for effective root systems to improve access to water. Extensive work in populations of random inbred lines –controlled for genes of major effect- has shown clear benefit of responsive root systems and even some common genetic basis under both heat and drought stress environments [35]. The trait is well estimated by canopy temperature (Fig. 5), one of the traits that are part of the breeders ‘handy tool kit’.

Many other traits have been proposed to improve source under abiotic stress. These include epicuticular wax, a handy trait being easy to observe by eye, associated with photo-protection since it can reduce radiation load on the leaf. Recent work showed it to be amenable to high throughput screening using SRIs [166] though it has not been systematically studied for its potential impact on genetic gains. On the other hand, the precision trait carbon isotope discrimination has been well researched from theory all the way to breeding for its impact on increasing transpiration-use efficiency, providing proof of concept for its value in water-limited environments in Australia [167].

In terms of sink traits specifically for abiotic stress, inadequate meiosis and pollination may reduce grain set [125], while remobilization of carbohydrates reserves in the stem can increase grain size [78,79]. The former can be observed relatively easily by examination of the spike in the field, while the latter requires a laboratory protocol. Work by crop physiologists at CSIRO in Australia have demonstrated

Table 3
Principal sources of within-site environmental variation that confound field-based research (adapted from Reynolds and Pinto [146]).

MAIN FACTOR	SUB FACTORS
Temperature	Day-day variation, extremes in max/min temperature; fluxes during data collection.
Light	Day-day variation in light due to cloud cover; time of year; fluxes during data collection.
Rain	Season to season, and within growth cycle variation in precipitation patterns.
RH/VPD*	Largely a function of all the above, these affect transpiration and canopy temperature.
Irrigation	Spatial and temporal variation in water application.
Nutrition	Non-uniform distribution/uneven access to nutrients.
Soil	Variation in: depth; moisture profile; physical & chemical properties of soil.
Wind	Fluxes of wind speed during data collection can affect some traits.
Pathogens	Genetic variation in susceptibility; soil pathogens hard to detect and control.
Pests	Timely detection is a challenge; genetic variation in susceptibility; birds and mammals especially hard to control.
(Diurnal cycles)	This source of variation is not directly related to environment *per se* but needs to be considered when developing measurement protocols.

* RH = relative humidity; VPD = vapor pressure deficit.

the breeding value of a number of other physiological traits for adapting to drought and heat, and the following reviews are recommended [14,50,52].

3.4. Biotic stress: phenotyping for resistance

The conventional selection for disease resistance is a labor-intensive activity that requires well trained eyes to identify pathogens and to score the level of infection. Clear guidelines and standardizations are well established in current protocols, but ultimately the quality of the evaluation still relies on the experience of the evaluator, making it prone to subjectivity. Several studies have shown how the use of sensor-based approaches can potentially overcome this subjectivity by ensuring accuracy and repeatability for disease detection, while increasing the capacity to evaluate larger populations in a shorter amount of time [46,168–172].

Pathogen infections would usually imply changes in plant optical properties by inducing alterations in the pigment composition, in the structural properties of the plant tissues or in metabolic processes. While evaluating these changes at leaf level can be relatively easy, at canopy level it can represent a challenge, first because only a fraction of the whole vegetation is visible to sensors, and secondly due to confounding effects such as the canopy structure, illumination conditions or similar symptoms produced by abiotic stresses [173]. The use of imaging systems helps to partly overcome this issue as they permit the evaluation of pathogenesis on individual leaves as well as integrative evaluations over the whole canopy. For instance, high-resolution digital RGB imaging has been used at canopy level to detect and quantify visual symptoms in individual leaves using analyses of spatial patterns, and changes in image color and texture [174–176]. The main limitation of RGB imagery is that it is restricted only to optical changes in the broad spectral ranges of red, green and blue.

Multi- and hyperspectral imaging systems are more powerful tools to detect specific changes in the spectral reflectance of the vegetation due to pathogenesis. Although they usually lack the spatial resolution of digital RGB cameras, their spectral range and spectral resolution make them more suitable to detect changes in leaf tissue reflectance in the visible (i.e. 400 – 700 nm) and in the near infrared (i.e. 700 – 1000 nm), which have been reported as the most sensitive to pathogen infections [177,178]. Spectral analysis for disease discrimination and quantification range from simple vegetation indices [179,180] to sophisticated statistical analysis that consider changes in the whole spectrum [181]. Alternative approaches to RGB and spectral imaging are thermography and fluorescence spectroscopy. The former has been used at plant and canopy level to detect changes in transpiration rate during early stages of disease infection [46,182], whereas the latter can be used to detect the accumulation of compounds in leaf tissues related to disease resistance [183] and changes in photosynthetic rate induced by pathogenesis [184].

Although the sensitivity of different imaging system to detect pathogens has been proved, there is still some way to go to have a fully functional approach for breeding. RGB imagery or multispectral imaging for vegetation indices can be easy to implement in the field on different moving platforms such as field carts or UAVs, but their use usually requires a minimization of possible confounding effects in the observed trials and they might not have the capability to discriminate between pathogen species. The information provided by hyperspectral imaging might be useful to discriminate between diseases and other abiotic stresses, but the analysis of this kind of data is more complex and at the moment its use relies mainly on empirical relationships that are not easy to understand, nor to apply generically. Consequently, further research is required to achieve easy-to-use but reliable tools for disease resistance selection under field conditions.

3.5. Biotic stress: phenotyping for disease resistance

Incorporation of insect resistance in crop cultivars is a genetically determined management method that 1) is environmentally friendly; 2) is readily available to farmers in the form of a new cultivar; 3) increases farmers profit, both directly via protecting yield and indirectly via reducing insecticide use; 4) limits the spread of yield-reducing insect-spread viral diseases, and 5) can be easily combined with different farming systems, including low input ones.

The most important factor that limits breeding for resistance to arthropods in general, is the difficulty of phenotyping large sets of germplasm. This reduces the possibility of finding new diverse resistance sources with adequate levels of protection. Furthermore, selection methods cannot be easily applied in established breeding pipelines, especially not in large breeding programs. These factors are most restraining in the case of certain insect pests that do not leave visible feeding symptoms on plants [185], thus making it most difficult to identify resistant germplasm and breeding in consequence.

Conventional aphid resistance screening is time consuming and difficult to apply in large germplasm sets. It frequently requires several replicates, destructive plant sampling methods, and is often problematic to conduct in the field. Under laboratory/greenhouse conditions is relatively easy to screen for resistance to feeding damage by symptomatic insect species compared with screening for resistance to those that fail to elicit symptoms. Damage to the plants caused by non-symptomatic pests is only evident once the plants are stunted because of high aphid population levels and the growth of sooty molds due to the presence of honey-dew on the plants.

Remote sensing can be used to effectively identify aphid damage in the field and distinguish it from other plant stresses in wheat (Fig. 6). For example, it is possible to differentiate between hot spots of damage caused by *Diuraphis noxia* (Mordvilko) and *Schizaphis graminum* (Rondani) both of which give rise to visible plant symptoms [186–190]. Furthermore, it may be possible to predict with high levels of confidence which plants are more prone to mite attack [191]. Furthermore, advances have been made with satellite imagery to identify at large

Table 4
Examples of traits affected differentially by environmental conditions at the time of measurement (from Reynolds and Pinto [146]).

SENSITIVE:	MAIN CONFOUNDING FACTOR(S)
Canopy temperature	Cloud, wind, temperature drift, irrigation status
IR-based spectral indices	Cloud, wind, temperature drift, irrigation status
Gas exchange	Irrigation status
Water relations	Cloud, wind, temperature drift, irrigation status
Lodging traits	Wind
Plant growth regulators	Cloud, temperature drift, irrigation status
Metabolites/enzymes/RNA	Cloud, temperature drift, irrigation status
NOT SENSITIVE:	
Yield and yield components	
Leaf pigments (like chlorophyll)	
Pigment based spectral indices	
Structural characteristics and partitioning (i.e. growth analysis including roots)	
Isotopic composition (e.g. stable carbon isotopes)	
Stored water-soluble carbohydrates (as far as we know)	
Genotype (DNA extraction)	

scale damage caused by aphids [192,193], which should help with modelling their epidemiology, virulence and response to control measures.

The implementation of remote sensing to screen for arthropod resistance is highly dependable on the physiological responses of the plants caused by pest species. Leaf surface temperature, photosynthetic activity, gas exchange, and carotenoid concentrations change upon the infestation of various phloem sap feeders [194–196]. All of these responses are associated with specific spectral features. However, the remaining question is if those responses are differential between potentially resistant and susceptible plant genotypes. It is obvious for some aphid species that these responses differ between resistant and susceptible germplasm, for instance, *Aphis glycines* Matsumura, *S. graminum* and *D. noxia* tolerance can be efficiently assessed using handy chlorophyll measuring devices, up to the level of using such measurements to identify resistance genes in mapping populations and screening breeding advanced lines [197–199]. Hence, remote sensing based measurements need to be further explored, particularly for the cases of insects that do not cause symptoms visible to the human eye, for instance in wheat, the aphids *Rhopalosiphum padi* L. and *Sitobion avenae* (Fabricius).

4. Phenotyping for genomic studies

Phenotyping for genomics studies is a key translational research activity if reliable markers are to be developed for molecular breeding approaches. The more accurately traits are phenotyped across large populations the more likely they will lead to gene discovery, thus, remote sensing tools must deliver both throughput and precision in this context. The upper limit of the maximum phenotypic variance that can be explained by a marker is limited by the heritability estimates of the trait. Though there generally remains missing heritability-unexplained percentage of phenotypic variation even after considering all major and minor effect QTLs/genes, the generally low heritability of many traits could be contributed by the error in phenotyping together with the genotype × environment interaction [201]. These constrains, when considered together makes accurate phenotyping using HTP a highly efficient tool, to avoid variation in the genotypic value due to temporal and spatial differences while field phenotyping. For example, it has been shown that HTP approaches using UAVs are more accurate when compared to ground based proximal sensing of CT and NDVI in large experimental fields [202]. Another example is the use of high throughput multispectral and hyperspectral indices from an aerial platformtaking non-destructive measurements and revealing gene expression patterns and drought responses to different levels of plant water status in field conditions. This study was on a single wheat genotype “Chinese spring”, but through HTP a large amount of phenotypic data was generated which was associated with the RNAseq data to identify gene clusters for drought tolerance in wheat [203].

Table 5
Examples of canopy level traits affected differentially by growth stages at the time of measurement.

SENSITIVE:	MAIN CONFOUNDING FACTOR(S)
Canopy temperature	Ground cover/tillering, spikes, chlorosis, height
Water relations	Leaf age
Infrared-based spectral indices (canopy)	Ground cover, canopy architecture, leaf age
Leaf pigments (like chlorophyll)	Leaf/canopy age
Pigment based spectral indices	Leaf/canopy age
Stored water-soluble carbohydrates	Organ, growth stage
Structural characteristics and partitioning	Stage of life cycle
Isotopic composition (e.g. stable carbon isotopes)	Organ, growth stage
Centre of gravity (for lodging)	Plant age and weight of spike
Gas exchange	Organ, organ age, source:sink status
Metabolites/enzyme activity	Diurnal cycle, organ, tissue, organ age
Plant growth regulators	Diurnal cycle, organ, tissue, organ age
RNA	Diurnal cycle, organ, tissue, organ age

In the context of precision phenotyping for genetic studies, the design of the experimental population and experimental conditions is a key and critical consideration to obtain meaningful phenotypic data. Confounding effects like phenology associated with genes of major effect can mask the identification of QTL [163]. Genetic mapping populations aimed at discovering minor gene effects can be designed explicitly to avoid such confounding factors [4] by using well-adapted common parents that match in terms of genes of major effects. For diverse panels of material as used for genome wide association studies (GWAS) [204,205] it is critical that genetic structure is accounted for as well to avoid other confounding effects [206].

While phenotyping for genotyping, it is important to consider the effects of already identified genes in the assembly of the population; in wheat this includes the major genes of vernalization (*VRN*), photoperiod (*Ppd*), and plant height (*Rht*) that can have profound effects on phenotypic data. For example, a huge variation in flowering time due to *Vrn* or *Ppd* genes can result in considerable variation for economically important traits like yield and grain quality. If canopy based phenotyping is conducted across an array of genotypes, plant height (*Rht* genes) in particular can confound phenotyping, especially when targeting high yield environments where plant height differences can be large and cause shading as well as differences in boundary air layers that impact on gas exchange.

An example of a population which was assembled to avoid the confounding effect of phenology in spring wheat is the Wheat Association Mapping Initiative (WAMI) population [83]. In addition, several recombinant inbred line populations were developed in spring wheat with narrow ranges of phenology [4,207]. Genetic mapping in these populations for yield potential, drought and heat stress have identified QTLs for grain yield independent of phenology and plant height effects. These studies on the populations are also able to identify pleotropic effect of genes (e.g. T*aGW2* genes in chromosome 6A affecting several traits). Interestingly, a QTL mapping population developed with a very narrow range of flowering time (3 days) did not identify any major genes for flowering time, but identified a novel region in chromosome 6D associated with yield and some yield components contributed by a synthetic derivative line [207].

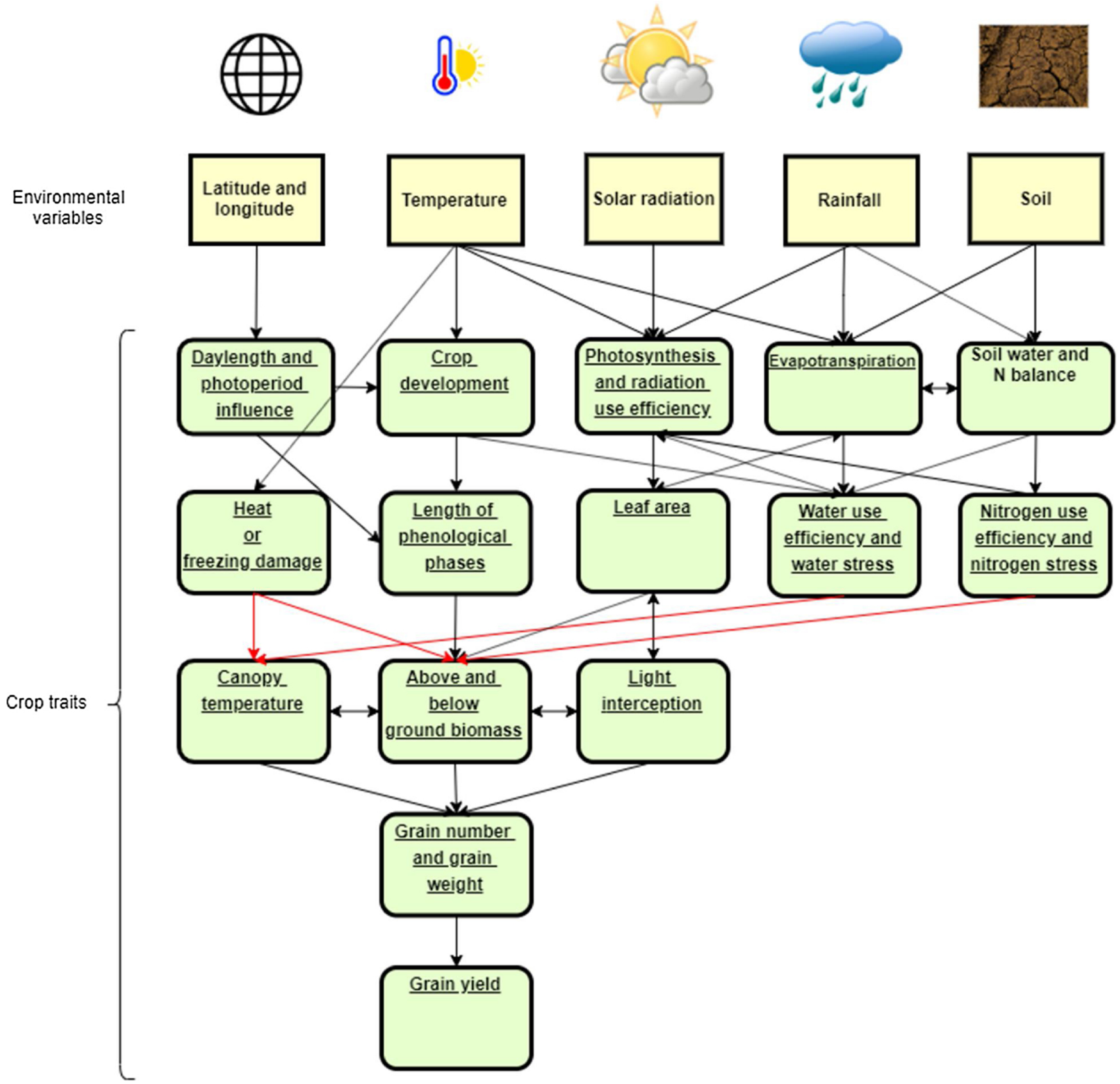

Fig. 7. Interaction among environmental factors and crop specific traits indicating how crop development, growth, and grain yield characteristics are influenced by one or multiple environmental factors. Yellow boxes correspond to environmental variables and green boxes correspond to affected crop trait. Black arrows indicate the direct or indirect influence of environmental variables on crop traits, and the influence of crop traits among themselves. Red arrows indicate possible damaging influences on crop traits. (Figure drawn by Diego Pequeno). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

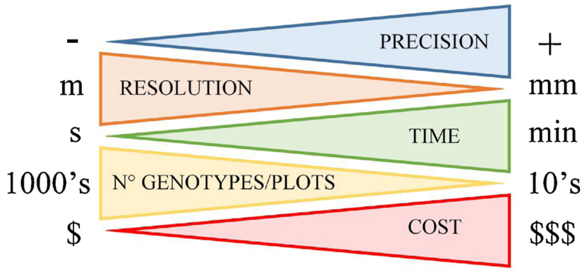

Fig. 8. Representation of the trade-off between the main factors to consider when choosing a protocol.

5. Overcoming confounding factors associated with field phenotyping

5.1. Environment

Crop scientists usually prefer to conduct phenotyping under field conditions where results can be more realistically extrapolated to target cropping systems. It has been shown that complex traits measured in controlled environments are not well related to expression in the field [208]. For example, soil temperature profiles in the field are very different to those seen in pots and have significant interaction with plant growth response [209]. However, since field conditions are inherently variable, repeatability or broad sense heritability of genetically complex traits can vary considerably due to interaction with environment, including weather as well as planting method and other aspects of crop management. Therefore, it is important to either measure or control these environmental factors as best as possible, so that heritability is maximized as traits move through a selection pipeline. Main sources of variation in the environment that should be measured or controlled are summarized below in Table 3.

All of the factors in Table 3 will have a cumulative effect on yield and on most other traits. However, in terms of phenotyping *per se,* the expression of some traits are quite sensitive to one or more environmental factors at the precise time of measurement. For example, the spectral water index or canopy temperature can be affected almost instantaneously by temperature, cloud cover, and wind, as well as being influenced on a day to day basis by irrigation status and diurnal cycles. For these kinds of traits, developing and applying well defined protocols (see Pask et al. [48]) can help minimize the confounding effects of environment, and improve heritability of their expression. Some of the main traits that are directly affected by such environmental factors are listed in Table 4. Though not well studied, traits that are affected by dynamic processes such as gas exchange may show diurnal rhythms that can confound data and should be considered in the experimental design of protocols. However, the sensitivity of traits to the environment can also be put to good use. For example, traits affected by water relations like canopy temperature or water index [61] when measured under hot, irrigated conditions reflect the ability of the vascular system to match evaporative demand in real time [35], while the same trait measured without irrigation has been shown to be associated with root depth [34].

5.2. Growth stage and growth habit

The expression of most traits interacts with growth stage. This is obvious when evaluating phenology or conducting growth analysis, for example. However, it can be less obvious for other traits where morphological or anatomical changes are not visible or quite subtle (Table 5). Taking again the example of canopy temperature, expression is affected at a number of factors; by ground cover due the warming effect of the soil, by the presence or absence of spikes which tend to be warmer than leaves, and by chlorosis as senescence will affect stomatal aperture. When measuring traits that are affected by height, ground cover, morphology and degree of development, it is crucial to design protocols that avoid these confounding effects. One of the easiest ways to achieve this is through experimental design where confounding factors like height and maturity class are contained within well bordered sub-blocks. Another alternative is to measure traits on different genotypes at comparable stages of development, however, this can introduce other confounding variables associated with weather and irrigation status that also vary over the cycle.

While growth stage can affect growth habit for any class of material, exotic materials like landraces and other non-adapted germplasm generally present a larger problem for phenotyping due to their more extreme growth habits and wide range of phenology. The most obvious are variation for height and phenology. When evaluating diverse materials in relatively small yield plots, taller lines will have an ‘unfair’ advantage in terms of intercepting more radiation. Similarly lines that are earlier maturing will experience the same advantage albeit temporarily. Tall lines can also express more gas exchange and cooler canopies than shorter neighbors simply due to being exposed to more air movement, while shorter lines, especially if boxed in by taller genotypes experience a boundary layer of relatively still air which reduces the opportunity for carbon fixation and evaporative cooling [210]. Confounding effects like these can also be at least partially mitigated through experimental design as described in the last paragraph, and by including checks that are within the same height and phenology range as the genetic resources being tested. Using nearest neighbor(s) height and/or phenology as covariates in the statistical analyses is also necessary to help compensate for these effects.

6. Integrating environmental data with trait expression at different growth stages

The need to consider ‘confounding factors’ in field trials is mainly because crop growth, development, and grain yield are results of the cumulative influence of complex interactions between environmental factors and crop traits, as well as crop management (Fig. 7). Accurate environmental data collection is crucial to understand differences among genotypes, management practices, and water and nutritional effects on crop response. Interpretation of experimental data will be limited without comprehensive environmental data, especially when field trial results are conducted over diverse locations and cropping systems.

7. Choice of measurement protocol: trade-offs between friendly and sophisticated

Nowadays breeders can choose from a wide range of protocols for field phenotyping. In general, the simpler the protocol, the cheaper and faster it will be to implement. However, even for HTP approaches it is becoming quite common to find solutions in the market that are user friendly and fast to implement, but they can have an elevated cost associated with the sophisticated algorithms used for the data processing or analysis. This can be the case, for example, with some image-based protocols, where sophisticated statistical and image analysis algorithms are used to extract useful information. The choice of the right approach would then depend on the necessities of the user, and it usually implies a trade-off between aspects such as spatial resolution, precision, throughput and costs. A representation of the trade-off between the main factors to consider when choosing a protocol is suggested in Fig. 8. For instance, it is very hard to avoid a coarser spatial resolution and lower precision if the objective is to measure a large number of genotypes in a short time. But on the other hand, such an approach would result in a reduction of costs estimated per plot or genotype. Terrestrial vehicles and unmanned aerial platforms (UAVs) have probably the best tradeoff between all these factors for breeding purposes. Terrestrial vehicles can provide a very high spatial resolution and data quality at a fairly high throughput to measure hundreds of plots in a short time. Additionally, they have the advantage that many sensors can be integrated on the same platform for simultaneous measurements.

On the other hand, the use of UAVs clearly increases throughput in comparison to terrestrial vehicles (from hundreds to thousands of plots) while decreasing confounding effects related to short-term variations of the environment such as changes in temperature or illumination conditions as well as impact on the field plots due to contact and soil compaction. Some drawback of UAVs, at the moment, are the loss of resolution and limited payload compared to ground vehicles or stationary gantries. However, this might be soon overcome since the technology is advancing very fast towards smaller sensors with higher resolution. It is worth noting that both, terrestrial vehicles and UAVs, are currently more recommended than manned aircrafts and satellite imagery for breeding purposes, given the reduced frequency of data collection and the coarser resolution of the latter, which is not optimal for the small plots typically found in genotypic screening [202].

The development of new indices and platforms usually requires specialists to process and interpret the data; for example, image analysis is one such specialization. However, more and more user-friendly software solutions are becoming available (even provided by the same sensors manufacturers) for the estimation and analysis of well-established remote sensing indices. This, together with an increasing choice of versatile and accessible ground and aerial vehicles, has resulted in an important number of breeding programs and research groups that are actively using these platforms, sensors and traits in their pipelines

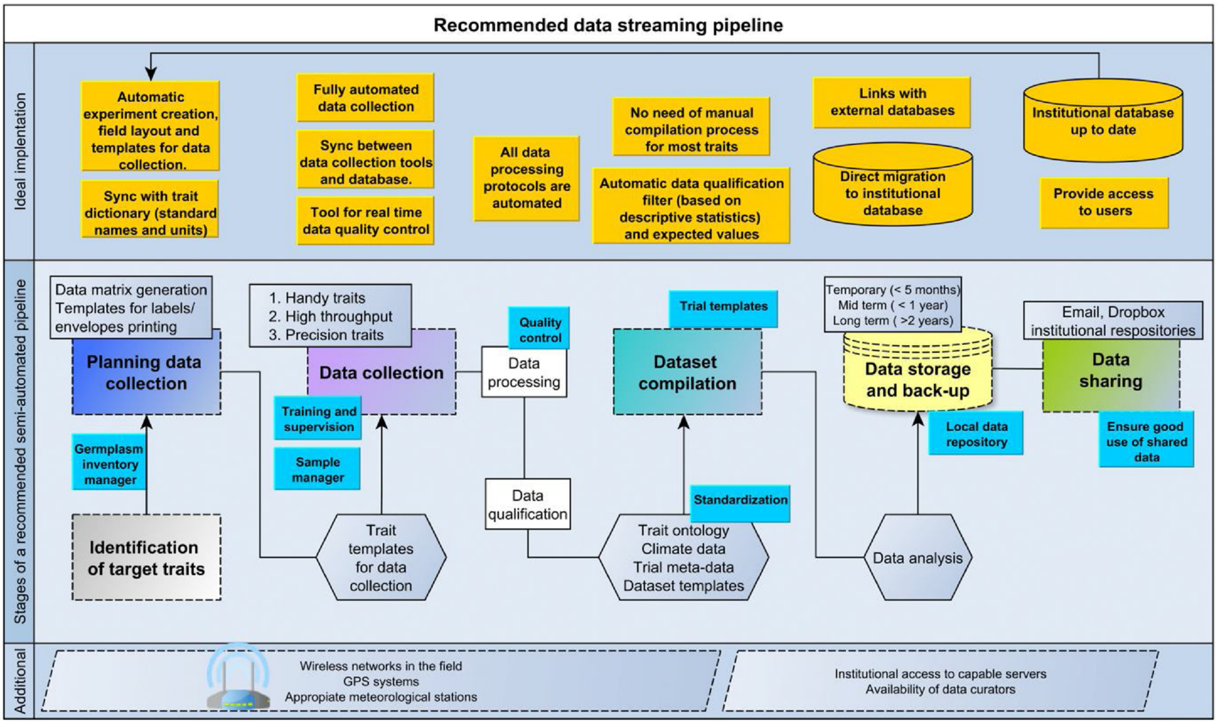

Fig. 9. A recommended flow diagram for a none to semi-automated phenotypic data streaming pipeline. The yellow text boxes suggest the ideal implementation in a nearly full-automated data workflow. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

8. Estimation of derivative traits for breeder friendly phenotyping technologies

Crop growth models (CGMs) have been used in many aspects of crop research and production, largely to support decision making at the field, farm or policy levels [211], with wheat having been a major focus for this work [212]. They have also contributed to plant breeding through 'environment-typing' of trials (understanding how well they represent the Target Population of Environments [TPE] for the breeding program [213]), in order to estimate environment co-variables that can be used in the statistical analysis of multi-location trials. A second major use in breeding has been in the exploration of ideotypes comprising different combinations of adaptive traits, i.e. to estimate the potential 'value' of traits or trait combinations using sets of locations and historical weather data to represent the TPE [214,215].

A more explicit use of CGMs is sometimes termed 'model-assisted phenotyping' [216], and capability in applying these approaches is now becoming practical and can be illustrated for traits related to estimation of canopy dynamics. Model-assisted phenotyping refers to the use of models to compute 'derived phenotypes' that may be difficult to measure directly, and Luquet et al. [216] argued that it is possible to estimate difficult-to-measure model parameters related to leaf growth by running the model through datasets of changes in observed leaf area. In the same vein [217], estimated glasshouse-derived genotype parameters can be obtained for leaf growth response to temperature, soil water deficit and vapor pressure deficit. These parameters were run through a cropping systems model (APSIM) to compute leaf area dynamics in field environments. By running simulations in multiple environments (i.e. historical weather records), this method allows breeders to assign a 'value' to adaptive traits, i.e. in which environments and conditions is a particular temperature or water deficit response likely to be of greatest advantage.

This same approach can be applied to single field experiments in order to estimate model parameters, but is challenged by the demands of such models for detailed parameterization. A pragmatic response to this parameterization challenge is that of Potgieter et al. [218] who used UAVs to calibrate vegetation indices against observed LAI for a small number of plots, and then extrapolated these relationships to large numbers of breeding plots. This approach uses no physiological modelling, but can derive information to calibrate models for estimating complex traits that are difficult to measure (e.g. precision traits), from handy and high-throughput measurements. The most recent and explicit evolution of combining UAV and models to monitor leaf area dynamics of maize is that of Blancon et al. [219]. This high-throughput method relies on a combination of physiological modelling and model inversion. A simple 5-parameter model of leaf appearance, leaf size and leaf death was used. The leaf appearance rate was measured on all genotypes (ca. 400), while parameters for maximum leaf size and a leaf death function were estimated after constructing a calibration (transfer function) between UAV multi-spectral images and LAI for a subset of genotypes. The advantage of this approach is that it uses a direct calibration between UAV data and a model to account for genotype x environment interaction effects on leaf growth dynamics. The model parameters were shown to have a higher heritability than LAI *per se*. A similar approach could be applied to models of canopy growth in wheat, using a modified model. The maize canopy / UAV methodology has also been developed further to design methods to rapidly characterize leaf rolling traits after a calibration step of under-canopy camera measurement [220].

Improvements in feature extraction from high-throughput field phenotyping methods are providing the potential to further utilize model-assisted phenotyping [221]. For example, if we can indirectly estimate biomass at different times of growth, in addition to the characterization of canopy dynamics, then it becomes possible to directly estimate radiation use efficiency of different genotypes [28]. The ability to accurately estimate plant [42] and ear population [88] using deep learning methods allow models to be parameterized with other information such as tillering propensity (ears per plant), which can further improve their performance in estimation of higher-heritability phenotypes.

9. Bringing it together: combining genomics and phenomics for breeding

The rapid advancement of phenomics approaches and methodologies outline here is joining an already steady stream of genomic information in the breeding programs. The low-cost high-throughput sequencing that is readily available is providing breeders with genome-wide information across breeding candidates that is being utilized in genomic prediction models for predicting target traits (e.g. yield) across the candidates and making selections based on genomic estimated breeding values (GEBV) [222,223]. These genomic predictions can be implemented at various stages in the breeding program to optimized the benefit of the selection gain and time savings relative to the expense of the genotyping [224]. Depending on the cost of phenotyping vs genotyping, however, the optimal implementation of genomic selection varies from program to program.

In this context the increasingly high-throughput (and low cost) phenotyping methods compliment and augment genomic selection in breeding programs. This has led to the concept of 'phenomic selection' and GS + HTP methodologies and prediction models for application in the breeding program [225,226]. These new approaches that simultaneously leverage available genomic and phenomics data are being demonstrated in breeding programs and show great promise for increasing prediction accuracy and/or increasing the throughput for selection (via prediction) in early stages of the breeding program [32,227–229].

Taken together, the value and implementation of both genomic information and high-throughput phenotyping data in the breeding pipeline and a tool for selection increases as the relative cost decreases and throughput can increase. These new modeling approaches show great promise to accelerate the genetic gain in breeding programs through 1) increasing the (prediction) accuracy of early generation selection, 2) increase the population sizes that can be effectively evaluated and 3) providing complementary information that will augment the genomic predictions, providing both better genomic prediction models and more accurate selection of advanced breeding lines. As with any new breeding methodology, however, the breeder is the benchmark. A useful breeding tool that can be implemented in the program will save on time and effort or effectively provide better selections (and preferably both), under the constraints of a fixed overall budget for the breeding program. Time and effort that is shifted from current breeding methodologies (i.e. visual selection by the breeder) must be able to offset this benchmark.

10. Improving data streaming

Regardless of the phenotyping approach that breeders choose (see Box 1), a breeding program would more likely succeed if it can handle data in an efficient way. As the size and cost of data increases with high-throughput and precision phenotyping, this is a critical consideration in the implementation of these approaches. The appropriate design and implementation of a data streaming pipeline plays a crucial role in assuring good data quality, straightforward analytics, good timing for lines selection, data access by collaborators and safe mid to long term data storage. Moreover, it can facilitate analysis of complex traits that require the integration of different data sources, as well as physiological, environmental, management and other metadata for interpretation [16]. Currently, most breeding public organizations function under manual data collection and management operations, and continue to rely on paper and pen and subsequently transcribe data [230,231]. These practices entail a considerable amount of human resources and limit the efficiency in terms of time as well as errors.

Opportunities for improving data streaming pipelines will go hand in hand with the automation of phenotyping protocols and will depend on the data source (e.g. direct field assessments, imaging, ground base instruments, etc.), the intensity of measurements, resources available and capacity building. The latter point is crucial, since a key requirement in automation is to provide operators relative independence from system administrators. In Fig. 9, we suggest a semi-automated data streaming pipeline, identifying five main areas: 1) identification of target traits, 2) planning the data collection campaign, 3) data collection, 4) dataset compilation and curation, 5) storage and sharing.

Handling data from image analyses has a different aspect when it comes to data processing complexity; even single values per plot can be the result of laborious protocols. Nowadays, there are platforms and service providers that assist breeders in storing, managing and processing imaging data using cloud services, thus reducing cost for phenotyping compared to building up such a capacity in-house. In general, the speed and capacity to process imaging data is given by the platform and algorithm used. However, the organization and the access to the data could also be considered as critical factors for assuring a flawless imaging data streaming and easy association to geospatial and meteorological metadata.

11. Conclusions

A number of factors currently underscore the value of investing in phenotyping for crop improvement. One relates to the advances that have been made in recent decades in both phenotyping and the understanding of physiological processes in crops that could lead to significant breakthroughs in their adaptation, with appropriate investment in translational research. Another relates to opportunities for genetic dissection of physiological processes resulting from massive investments in genomics that can lead to precise application of markers in selection. Lastly, the imperative to breed crops to warmer and generally harsher climates, demands a better understanding of adaptation, and innovative breeding technologies. 'Breeder friendliness' is a key criterion when considering scaling out, because highly complex or unproven phenotyping methods are likely to be counterproductive. Nonetheless, the different contexts for phenotyping, including, parent building, screening of progeny and other genetic resources, translational research to deliver breeding innovations, and the challenge represented by the breeding target scenario, will ultimately determine the cost-benefit of increased sophistication.

Declaration of Competing Interest

No conflict of interest.

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Further reading

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