Bottlenecks and opportunities in field-based high-throughput phenotyping for heat and drought stress

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Highlight – This review focuses on developing high-throughput phenotyping approaches to quantitfy key physiological traits at high temporal frequency, involving diverse germplasm to incorporate greater heat and drought stress resilience in crops.
Abstract

Flowering and grain-filling stages are highly sensitive to heat and drought stress exposure, leading to significant loss in crop yields. Therefore, phenotyping to enhance resilience to these abiotic stresses is critical for sustaining genetic gains in crop improvement programs. However, traditional methods for screening traits related to these stresses are slow, laborious, and often expensive. Remote sensing provides opportunities to introduce low-cost, less-biased, high-throughput phenotyping methods to capture large genetic diversity to facilitate enhancement of stress resilience in crops. This review focuses on four key physiological traits or processes that are critical in understanding crop responses to drought and heat stress during reproductive and grain-filling periods. Specifically, these traits include: i) time-of-day of flowering, to escape these stresses during flowering, ii) optimizing photosynthetic efficiency, iii) storage and translocation of water-soluble carbohydrates, and iv) yield and yield components to provide in-season yield estimates. An overview of current advances in remote sensing in capturing these traits, limitations with existing technology and future direction of research to develop high-throughput phenotyping approaches for these traits are discussed in this review. In the future, phenotyping these complex traits will require sensor advancement, high-quality imagery combined with machine learning methods, and efforts in transdisciplinary science to foster integration across disciplines.

Keywords
Remote sensing, Field-based high-throughput phenotyping, Heat stress, Drought stress, Time-of-day of flowering, Photosynthetic efficiency, Water-soluble carbohydrates, Yield estimation
Abbreviations

CNN - Convolutional Neural Network
LIFT - Laser Induced Fluorescence Transient
NDVI – Normalized Difference Vegetation Index
NIRS – Near-infrared Spectroscopy
PLSR – Partial Least Squares Regression
PRI – Photochemical Reflectance Index
TOF – Time-of-Day of Flowering
UAVs – Unmanned Aerial Vehicles
QY – Quantum Yield
WSC – Water-soluble Carbohydrates
Introduction

Advancements in quantifying abiotic stress impact on the productivity of field crops have become more important than ever in order to breed for heat and drought stress resilience or to understand the ability of a plant to maintain yield under abiotic stresses. In order to meet the future global food demand, global agriculture production must be doubled by 2050 as compared to 2012 (Food and Agriculture Organization [FAO], 2017; 2019). As of 2008, it has been shown that yields in major crops such as maize (Zea mays L.), rice (Oryza sativa L.), and wheat (Triticum aestivum L.) are increasing at an annual rate of 1.6%, 1.0%, and 0.9%, respectively (Ray et al., 2013). If the same rate of increase is sustained, maize, rice, and wheat would see an increase in production of 67%, 42%, and 38%, respectively, by 2050. This rate of increase, obtained largely through advances in breeding aided by high technology management, has mitigated the negative effects due to a challenging and damaging climate until now, but, as demand grows and climate instability continues to increase, these negative effects could pose a threat to global food security in the future.

The Intergovernmental Panel on Climate Change (IPCC) has predicted that heat waves in the future will occur at a more frequent rate and with increases in both duration and intensity (IPCC, 2014). The increase in global mean temperature and the expected instability in precipitation creates a potential major risk to global food security. Gourdji et al. (2013) have predicted that, by 2030, 31% of maize, 16% of rice, and 11% of wheat growing areas will record over five reproductive days with temperatures above their respective critical threshold, in any given year. This increase in temperature coinciding with sensitive developmental stages, such as flowering, will have detrimental impacts on yield (Jagadish, 2020). Empirically, heat stress during the booting and flowering stages in rice reduced yield by as much as 28.5% depending on the timing and duration of heat stress (Aghamolki et al., 2013). Similarly, a significant reduction in winter wheat yield was recorded with heat stress.
coinciding with heading and lasting for 15 days, even though a stress period of five days was sufficient to induce yield loss (Balla et al., 2019). In addition, it is predicted that with every degree centigrade increase in mean temperature, the global wheat production will be reduced by 6% (Asseng et al., 2015).

Drought reduced yield in about 75% of all globally harvested areas of maize, rice, wheat, and soybeans (Glycine max L.) between 1983 and 2009 (Kim et al., 2019). The IPCC has also predicted a shift in the water cycle where the higher latitudes will receive increased precipitation while the mid-latitudes and those areas already prone to drought will encounter a more substantial decrease in water supply (IPCC, 2014). Daryanto et al. (2016) synthesized 144 studies between 1980 and 2015, and reported an average yield reduction of about 21% for wheat and 39% for maize due to drought. Zhang et al. (2018), using a meta-analysis approach including over 110 independent studies, recorded a 28% and 25% yield reduction due to drought in wheat and rice, respectively, with the largest reduction associated with stress during grain-filling. Similarly, Sehgal et al. (2018) reported that the most critical growth stages with significant reductions in yield due to drought and/or heat stress were the reproductive and grain-filling stages. Hence, a better understanding of plant’s responses to both heat and drought stresses during reproductive and grain-filling stages is crucial to provide new opportunities for breeding programs to enhance the rate of success in developing stress-tolerant genotypes.

Remote sensing approaches allow for data collection on much larger studies encompassing a wide genetic diversity in order to phenotype for abiotic stress resilience. Remote sensing has been utilized for a variety of purposes such as measuring canopy height (Varela et al., 2017; Thompson et al., 2018; Thompson et al., 2020; Zhou et al., 2020), biomass (Neumann et al., 2015; Padilla-Chacón et al., 2019), canopy temperature (Romano et al., 2011; Pauli et al., 2016; Graß et al., 2020), leaf area (Neilson et al., 2015; Zhang et al.,
2019), and predicting yield (Rischbeck et al., 2016; Becker and Schmidhalter, 2017; El-Hendawy et al., 2017; Zhou et al., 2020). Through the use of specialized vegetation indices (VIs) or spectral bands alone, remote sensing can quickly and efficiently collect data on different traits simultaneously, non-destructively, and with a high spatio-temporal frequency. In addition, remote sensing presents the opportunity of correlating an index with the trait of interest, without being confounded by a differential time-stamp, unlike manual measurements (Janse, 2017; Xue and Su, 2017).

In order to effectively utilize remote sensing for the diagnosis of drought and heat stress impacts on crops, the data obtained should help in understanding complex physiological processes that determine yield, at a scale that cannot be achieved by manual methods. Recently, there have been attempts to review advances in sensor technology and estimation of agronomic traits such as plant height, biomass or greenness (Araus et al., 2018; Chawade et al., 2019). Hence, to avoid duplication, this review utilizes the progress achieved in the realm of sensor technology and focuses on quantifying key physiological traits or processes that are critical in understanding crop resilience to drought and heat stress during the reproductive period, but more specifically with focus on the grain-filling period. These specific traits include phenotyping for i) time-of-day of flowering (TOF), as a means to escape heat stress during flowering, ii) enhance photosynthetic efficiency by optimizing stay-green versus senescence, iii) water-soluble carbohydrates translocation and contribution to yield under stress, and iv) yield components i.e., grain number and grain size determination to provide in-season (and before harvest) yield estimates. These traits define major physiological and agronomic aspects related to heat and drought stress resilience in crops and are complex, labor-intensive, time-consuming to measure, and change dynamically over time to be effectively captured through traditional methods. Opportunities exist with each trait to increase the throughput and accuracy of trait determination via remote sensing. This review
aims to identify ways to utilize advances in remote sensing and to strengthen efforts towards developing heat and drought tolerant crops for the future. Finally, the review identifies limitations and bottlenecks in remote sensing methods and provides recommendations for future research in order to overcome these limitations.

**Time-of-day of flowering (TOF) – A route to escape heat stress**

Historically, adaption to abiotic stresses has been acquired naturally in crops through evolution, but crops are not equipped to deal with significant intra- and inter-annual climate variability faced under current and predicted future climate. Traits that induce heat stress resilience can be classified into three categories: tolerance, avoidance, and escape. Tolerance is defined by the ability of the plants to continue operating their physiological processes under stressful conditions (Khan *et al.*, 2014). Traits that define avoidance allow normal processes to continue by creating a more favorable microclimate. An excellent example for heat stress avoidance is transpirational cooling, wherein canopy temperature is decreased to optimal levels even under severe ambient hotter environments (Lin *et al.*, 2017). This trait, however, is highly beneficial under sufficient water supply (Julia and Dingkuhn, 2013) but not beneficial under combined drought and heat stresses, as the competition to conserve water to survive drought is prioritized (Lin *et al.*, 2017). Escape on the other hand, provides the opportunity for sensitive physiological processes to occur during favorable times of the season (macro-escape) or the day (micro-escape).

Shortening crop growth duration in order to complete their life cycle or to prevent exposure to severe hot and dry summers would be an example for macro-escape (Stone, 2001; Barnabás *et al.*, 2008), while adjusting their sensitive flowering time to cooler hours with more favorable vapor pressure deficit (VPD) conditions is an example for micro-escape (Sheehy *et al.*, 2005; Jagadish, 2020). Heat stress and higher VPD during flowering leads to
significant yield reductions in a large variety of crops and the inclusion (naturally or through genetic improvement) of an early morning flowering trait has been shown to significantly reduce spikelet sterility and yield losses in rice (Ishimaru et al., 2010; Hirabayashi et al., 2015; Bheemanahalli et al., 2017) and sorghum (Chiluwal et al., 2020). Although crops can employ tolerance, avoidance, or escape independently or in combination, this section focuses on advancing methods to phenotype for TOF as an effective means to minimize crop damage from heat and drought stresses (Jung and Müller, 2009; Jagadish et al., 2015). Currently, the TOF is manually phenotyped, which is tedious, prone to human error (subjective to bias), confounded by spatio-temporal variability of measurements, and can only be measured on a limited number of genotypes (Ishimaru et al., 2010; Aiqing et al., 2018; Chiluwal et al., 2020; Pokharel et al., 2020) (Fig. 1A). Traditionally, researchers have identified the flowering pattern in crops by counting the number of opened flowers at specific time increments or by marking opened flowers by fine-tipped pens (Hirabayashi et al., 2015), but this can lead to confounding results as any physical stimuli can alter the flowering pattern (Kobayasi et al., 2010).

Steps toward optimizing this methodology to reduce temporal variability with manual measurements and to overcome physical stimuli induced by human touch have been proposed. For rice, Kobayasi et al. (2010) utilized digital cameras to determine the flower opening time. This allowed for more frequent measurements (10 minute intervals), created a physical representation of the inflorescence at the specified time point so it could be evaluated, repeatedly if necessary, at a later date. This approach also enhanced accuracy by utilizing a tripod and a timer to initiate the data collection. Significant steps have been made in the last few years, which have allowed to increase the number of genotypes phenotyped, and reduced the variability in measurements. The first step forward came via utilizing fixed field-based phenotyping systems such as the Field Scanalyzer phenotyping platform. The unit
contains multiple sensors including high resolution digital cameras which, when combined with machine learning, can positively identify flowering in wheat (Sadeghi-Tehran et al., 2017). This methodology has an accuracy ranging from 76 to 92% and its imprecisions are linked to the size and color of the anthers as they can vary amongst genotypes (Sadeghi-Tehran et al., 2017) (Table 1). A significantly greater challenge in determining the flowering opening time was observed in *Setaria viridis*, wherein the flower opening was predominant during the night in all three tested accessions (Desai et al., 2018). A Raspberry Pi system equipped with infrared imaging allowed the authors to correlate the flower opening time of the night with the movement in floral bristles, coinciding with extrusion of anthers (Desai et al., 2018) (Table 1). The ability to capture the night-time flower opening is important to quantify the trait in some wild species known to predominantly flower during night (rice; Sheehy et al., 2007) or for capturing late evening flowering as seen in wheat (Aiqing et al., 2018).

A mobile methodology has been developed by utilizing a high-clearance field-based high-throughput mobile phenotyping platform outfitted with multiple high resolution digital cameras which collected geo-referenced images with the help of a built-in RTK GPS system (Barker et al., 2016; Wang et al., 2019). Utilizing deep learning tools, this methodology is able to correctly identify plant phenology and growth stages and the system was utilized to identify flowering dates, which were associated with plot-based breeder’s score (Wang et al., 2019) (Table 1). The system, however, was not employed to identify TOF due to lack of high temporal measurements on a single day. The success of the system in identifying heading and flowering dates indicates that the system is sensitive enough to be modified to capture images at a high temporal setting to explore the flowering pattern in different crops.

The success of utilizing both fixed field-based phenotyping systems and ground-based mobile phenotyping platforms indicates that aerial high-throughput phenotyping for capturing
TOF in crops is achievable. Unmanned aerial vehicles (UAVs) are capable of carrying extremely high resolution red-green-blue (RGB) digital cameras and as cameras have gotten smaller, this has allowed even smaller UAVs to carry them (Colomina and Molina, 2014) (Fig. 1B). Low altitude flights will allow capturing extremely high resolution images of the canopy in order to quantify the TOF. Two examples for the TOF phenomenon are presented wherein sorghum and rice genotypes vary in the proportion of flowers that open at different times of the day (Fig. 1C, D). The extremely short window (minutes after dawn) in sorghum and a much longer flowering window (hours after dawn) in rice provides the diversity in the scale of operation in crops with TOF, and the efficiency and accuracy required to capture the genetic diversity for this trait. The difference in color between the green leaf background with a contrasting yellow by the anthers provides the opportunity to establish a phenotyping approach that can employ an area- and color-based detection method to define the temporal magnitude of flowering (Fig. 1 C, D). Employing this method will allow for screening a large number of genotypes, at high spatio-temporal frequency, and with increased effectiveness thereby facilitating integration of this trait into abiotic stress breeding programs.

**Photosynthetic Efficiency – capturing stay-green versus senescence dynamics**

Photosynthesis is one of the key physiological processes which can be optimized for achieving maximum yield potential in crops, with abiotic stresses negatively impacting photosynthetic efficiency which can significantly reduce grain yields (Crafts-Brandner and Salvucci, 2002; Long et al., 2006; Feng et al., 2013; Ambavaram et al., 2014). Attainable maximum yield can be determined by analyzing the amount of light captured, the ability of the plant to convert this energy into biomass, and the proportion of biomass partitioned to grain (Muchow et al., 1990). Improvements in the amount of radiation captured, increases in the partitioning of biomass into grain have been achieved through plant breeding, however,
there is room for further improvement in efficiency in translating intercepted radiation into biomass. Theoretically, maximum potential photosynthetic efficiencies are indicated to be 0.051 for C3 and 0.060 for C4 crops (Long et al., 2005). The maximum short term rates of photosynthetic efficiency recorded reached around 70% of this potential in both C3 and C4 plants while the maximum season long measured efficiencies was about 47% of the maximum for C3 and 57% of the maximum for C4 crops (Monteith, 1977; Beadle and Long, 1985; Piedade et al., 1991; Beale and Long, 1995). Thus, increasing yields to meet the future global demand will rely on the further improvement of photosynthetic efficiency or crops ability to convert captured light energy into biomass.

Possible developments to improve photosynthetic efficiency for heat and drought stress resilience include introducing the C4 photosynthetic pathway into C3 plants, improving Rubisco kinetic properties, and increased photoprotection to reduce high levels of reactive oxygen species (Gowik and Westhoff, 2011; Whitney et al., 2011; Murchie and Niyogi, 2011). Heat and drought stress can increase the oxygenation reaction of Rubisco, which can result in a direct loss of up to 30% of fixed carbon (Raines, 2011). This degradation of fixed C is extremely influential on potential yield when drought or heat stress occur during flowering or grain-filling. In addition, the early onset of senescence due to abiotic stresses is characterized by accelerated chlorophyll degradation and severely reduced photosynthetic efficiency (Hörtensteiner and Feller, 2002; Woo et al., 2018). These negative effects can be reduced through functional stay-green phenotypes, by extending the activity of the photosynthetic machinery (Thomas and Ougham, 2014). Functional stay-green phenotypes are shown to have a positive effect on either yield, heat or drought stress tolerance in sorghum (Sorghum bicolor L.) (Borrell et al., 2014), wheat (Spano et al., 2003; Pinto et al., 2016), barley (Hordeum vulgare L.) (Seiler et al., 2014; Gous et al., 2015), maize (Cairns et al., 2012), and rice (Fu et al., 2011).
Traditional measurements of photosynthetic efficiency are laborious, destructive and fail to detect the subtle changes that occur at the inception of senescence (Šebela et al., 2020). Sequential biomass harvests have been proposed to capture the photosynthetic efficiency for the entire growing season (Zhu et al., 2010), which is highly cumbersome to achieve with large breeding populations. A major milestone in addressing the above limitation was reached through the creation of the laser induced fluorescence transient (LIFT) method for remotely measuring this plant trait (Raesch et al., 2014) (Table 1). The LIFT technique uses a laser at 665 nm to excite the leaves and the fluorescent emission at 690 nm by the plant is collected by a reflective telescope and processed (Kolber et al., 2005, Pieruschka et al., 2012).

Advancements have been made in the mobility of this system to be utilized with highly precise global positioning systems in a field setting; however, it is still quite bulky and requires a large cart or all-terrain vehicle for its operation (Muller et al., 2018). Another limitation of the system is that it can measure an area larger than the targeted leaf, which can confound conclusions due to overlap of multiple layers of leaves within the canopy (Raesch et al., 2014).

A study using hyperspectral imaging on evergreen tree leaves exposed to a simulated short term drought stress, revealed a reduction in photosynthetic efficiency well before chlorophyll degradation was initiated. The use of longwave red-edge vegetation indices such as red edge NDVI (NDRE740) and red edge chlorophyll index (CI740) had significantly strong relationship with photosynthetic efficiency ($R^2 = 0.88$ and $0.72$ for stressed and non-stressed leaves, respectively) (Peng et al., 2017) (Table 1). The photochemical reflectance index (PRI) has similar strong relationship with photosynthetic efficiency in flowering plant species under control, drought, and warming scenarios ($R^2 = 0.78 - 0.85$) (Zhang et al., 2017) (Table 1).
The chlorophyll fluorescence, which is shown to quantify photosynthetic efficiency, has been used to measure the effective quantum yield (QY) of photosystem II in order to determine the exact change point at which senescence begins in leaves and floral tissue (Šebela et al., 2015, 2020). Chlorophyll fluorescence measured through QY provides information on the overall efficiency of photochemical reactions in PSII under light-adapted state (Genty et al., 1989), and has been effectively utilized to phenotype a rice diversity panel exposed to water-deficit stress (Šebela et al., 2019). Therefore, using QY as a case study trait, the transition from leaf (handheld) to the plot level using UAVs and the desired phenotype for stress prone environments with source-sink related stay green and senescence pattern is pictorially presented (Fig. 2). The UAV platforms provides the opportunity to move beyond point based leaf or inflorescence-based photosynthetic parameter measurements (Šebela et al., 2015, 2020; Fig. 2A) to whole plant (Fig. 2B) or canopy-based estimations (Fig. 2C), to capture genetic diversity for extending source-sink photosynthetic efficiency. Developing varieties that can trigger senescence in the lower half of the plant or plot while retaining active photosynthetic machinery in the top half or third is a desirable phenotype for heat and drought stress prone environments (Jagadish et al., 2015). This ideotype concept proposed can be realized using advances in the sensor-based technology to help capture the differential onset and rate of senescence at different positions along the plant or plot in large diversity panels or mapping populations (Fig. 2C). Photosynthetic efficiency is an integrated measure of many physiological processes which are difficult to be experimented individually, hence requiring a modelling framework to design a phenotype that can optimize both resource capture and use efficiency to increase yield. Determining opportunities to further enhance photosynthetic efficiency is an ideal target for designing an ideotype through model-based approaches (Hammer et al., 2010; Lobell et al., 2013, 2014; Wu et al., 2019). These approaches can help breed for varieties optimized with functional stay green versus
senescence, enhance assimilate production and transport efficiency to sustain productivity under heat and drought prone environments.

**Translocation of water-soluble carbohydrates (WSC)**

The end result of photosynthesis is the production of monosaccharides such as glucose and fructose, which form the foundation blocks for storage carbohydrates (polysaccharides) such as starch. Sugars including glucose and fructans, synthesized in leaves are transported to the stem and leaf sheaths and stored as water-soluble carbohydrates (WSC) (also known as non-structural carbohydrates) (Schnyder, 1993; Gebbing, 2003; Ehdai et al., 2006; Fernandez et al., 2020). Subsequently after storage, the accrued WSC in the stem and leaf sheaths are remobilized to the sink tissue during grain-filling (Scofield et al., 2009), with the efficiency of translocation influenced by the genetic diversity in sink strength depending on the crop or species (Cock and Cock and Yoshida 1971; Yoshida, 1981; Kiniry et al., 1992; Kiniry, 1993; Schnyder, 1993; Li et al., 2017).

After removing maintenance costs which can accounts for up to 68% of total WSC allocation, in wheat as much as 0.68 to 0.78 g of yield can be produced for each 1 g of WSC stored through apparent reserve use (Kiniry, 1993). Increased rate of reallocation due to terminal drought has been stated to contribute up to 50% of yield in traditional- and as much as 70% in elite-cultivars (van Herwaarden et al., 1998). Similar responses have been reported with heat (Schittenhelm et al., 2020) and other biotic stresses (Sadras et al., 2020). To minimize damage from stresses, newer phenotyping methods for high WSC storage and translocation are recommended in crops (Blum, 1998, Asseng and van Herwaarden, 2003; Wang et al., 2016; Schittenhelm et al., 2020). Studies exploring genotypic variation for WSC levels have been mainly focused on barley (Gay et al., 1999), wheat (van Herwaarden et al., 2003; Ruuska et al., 2006; Dreccher et al., 2009; Ovenden et al., 2017), rice (Xiong et al.,
2014; Wang et al., 2016; 2017; Moura et al., 2017), and maize (Jones and Simmons, 1983; Uhart and Andrade, 1995; Edreira et al., 2014; Wu et al., 2019; Fernandez et al., 2020).

Traditional methodology for quantifying WSC levels is destructive, time-consuming, expensive, and restricts the number of genotypes or samples that can be realistically processed. Due to the time-consuming nature of sample gathering and processing for WSC, temporal changes can occur within plant samples in response to the changes in the prevailing microclimate. This indicates the need for a high-throughput methodology which can quickly and accurately measure WSC levels in large number of samples. Currently, lab based methods for the extraction of WSC utilizes different approaches in wet chemistry. The original method was developed in 1954 by using anthrone and is still used to this day for ground-truthing or for generating benchmarks or references (Yemm and Willis, 1954; Giri, 2019). To increase throughput, near-infrared reflectance spectroscopy (NIRS) is being utilized alongside traditional wet chemistry methods. This medium-throughput methodology begins by determining the WSC levels in a subset of samples via wet chemistry and then the data generated was correlated with NIRS reflectance spectra. This methodology has been utilized on different crops including wheat (Rebetzke et al., 2008; Wang et al., 2011; Giri, 2019) rice (Wang et al., 2016), and maize (Campo et al., 2013).

The first step towards a true high-throughput phenotyping method for stem WSC levels was attempted on four recombinant inbred wheat lines utilizing a hyperspectral radiometer (Dreccer et al., 2014). The radiometer, with a sampling range from 350-2500 nm, was mounted onto a 4-wheel drive motorbike at 1.35 m above the soil. The remotely-sensed WSC levels were then confirmed in the laboratory utilizing the anthrone method, presenting a significantly strong relationship ($R^2 = 0.90$) averaged across two years (Dreccer et al., 2014) (Table 1). It was not until 2017 when hyperspectral imaging was used again to evaluate the concentration of WSC. A study involving estimation of sucrose content in maize leaves had
success in utilizing hyperspectral imaging of the adaxial surface of a leaf with an illuminated leaf clip contact probe and partial least squares regression (PLSR) models (Yendrek et al., 2017) (Table 1). While not as successful as Dreccer et al. (2014), the PLSR model was still able to predict sucrose content within the leaf with an $R^2$ value of 0.62. Garriga et al. (2017) utilized the same hyperspectral radiometer model as Dreccer et al. (2014) to predict WSC in a large variety trial, including 384 cultivars and advanced lines of spring wheat in both well-watered and watered-stressed environments. The radiometer was placed at a 45 degree angle and swept over the plot three times and, utilizing multivariate regression models, the study was able to predict stem WSC with $R^2$ of 0.56 (Garriga et al., 2017) (Table 1). It is unclear whether the difference in coefficients of determinations between Dreccer et al. (2014) and Garriga et al. (2017) was due to the angle at which the reflectance was obtained or other confounding factors, but these procedures need to be further standardized to accurately reflect the ground-truth observational data.

The next step forward in quantifying WSC levels via a high-throughput methodology is by implementing machine learning. This methodology has not been implemented with a row crop, however it was recently tested with perennial ryegrass. The authors used a hyperspectral radiometer as well as a light shield in order to capture the spectra under stable light conditions from 960 different plants, comprised of 50 experimental perennial ryegrass varieties (Smith et al., 2020). The light shield was manually placed on each plant and artificial light within the shield was used as the light source. Comparatively, the cubist model resulted in an $R^2$ value of 0.49 while the PLSR model was only able to obtain an $R^2$ of 0.19 (Smith et al., 2020). Although promising, the methodology may not be practical and too laborious to implement on multi-location trials that involve diversity panels or mapping populations in order to make it applicable to breeding programs. With limited research into the feasibility of utilizing hyperspectral imaging and machine learning for rapid, accurate
measurements, the methodology cannot be discredited nor confirmed as the path forward for accurate high-throughput evaluation.

**Estimating yield and key yield related parameters**

The economic yield of a crop is defined as the biological yield multiplied by the harvest index (HI) of dry matter or the product of grain number and grain weight (Osaki et al., 1994). The ability to accurately predict yield in both stressed and non-stressed environments is an endeavor that is being continued for decades. Yield prediction is a complicated undertaking due to the dynamic environmental changes that fluctuate on a large temporal scale, from daily to yearly, and on a large geographical area, from local to regional scales, resulting in large variations in attainable crop yields. This is particularly true for heat and drought-prone environments, which lead to lower seed numbers when stress occurs immediately before or coincides with flowering (Fischer, 1985; Jagadish et al., 2010; Prasad et al., 2015; Prasad et al., 2017; Bheemanahalli et al., 2019) or loss in seed weight with stress during grain-filling (Asana et al., 1958; Wardlaw, 1970; 1971; Lawas et al., 2018; Hein et al., 2020).

Yield forecasts for regional, national and international cropping systems involve highly intricate and complicated systems utilizing an enormous amount of data and multiple regression models or machine learning (Jeong et al., 2016; Iizumi et al., 2018; Han et al., 2020; Schwalbert et al., 2020). Advances are being made in order to estimate yield within the season in order to aid in making important management decisions in nominal, heat stress, or drought stress environments. Hence, to predict yield more reliably and accurately, particularly under abiotic stress prone environments, approaches to remotely determine the number of heads in a plot and the number of seeds on the head is required.

The first step to gaining the ability to predict yield is acquiring the capacity to accurately identify heads or panicles in crops. This area of remote sensing has garnered
increased interest and utilizes different strategies employing machine and deep learning tools to ascertain accurate counts. One such experiment in 2017 attempted to identify rice panicles by applying a Convolutional Neural Network (CNN) classification and entropy rate super-pixel optimization to 684 images of pot-grown rice (Xiong et al., 2017). This method outperformed three previously identified methods with an F-measure indicator, which accounts for precision and recall of 0.77 while the previous methodologies could only reach an F-measure indicator of 0.44 (Xiong et al., 2017) (Table 1).

The CNNs have also been utilized to detect and count the number of wheat spikes within a plot. This was achieved by employing a ground based steel cart, with a central overhead rail equipped with high resolution cameras capable of being mounted at differing angles in relation to the crop of interest (Hasan et al., 2018). The Faster R-CNN model using 305 training images at different growth stages was able to attain on average a 93% accuracy on the 30 test images after training (Ren et al., 2017; Hasan et al., 2018) (Table 1). Similarly, another study using the same approach was equally accurate during early stages after heading, but was more robust during later stages when the leaves senesced and contrasted with greener wheat spikes (Madec et al., 2019). The model achieved high relationship ($R^2 = 0.91$) when the resolution of the image was 0.26 mm but reduced ($R^2 = 0.33$) when the image resolution was decreased to 0.78 mm, indicating the need for high resolution imagery for accurate spike detection (Madec et al., 2019) (Table 1).

These advances in agricultural object identification are impressive, given how small wheat spikes are compared to other crops. Sorghum has had considerably more research into developing accurate models for extracting and counting heads (Ghosal et al., 2009; Malambo et al., 2019; Oh et al., 2019; Lin and Guo, 2020). Even though sorghum has much larger sized head than wheat spikes, research faces the same challenges while utilizing UAVs to obtain imagery: changing light conditions over the duration of a flight, complex and intricate
backgrounds, and genotypic variations in head color, size, or shape and overlapping heads (Guo et al., 2018) (Table 1). The same authors employed a pixel-based segmentation approach to train a digital terrain surface model (DTSM) which is a supervised machine learning based on the decision tree, resulting in a F-measure of 0.92 for 52 images and 0.89 for 40 images per plot. The research group was then able to establish a deep learning framework with minimum supervision using CNN for sorghum head detection, and achieved an $R^2$ of 0.88 with the training set comprising of only 40 randomly selected images (Ghosal et al., 2019) (Table 1). In a more recent study, CNN models with image segmentation accurately estimated the number of sorghum heads ($R^2 = 0.90$) and characterized the shape and size of individual heads (Lin and Guo, 2020) (Table 1). This advancement could be key to estimating yield in sorghum, but seed number and weight are additional traits to be determined for effective yield prediction.

Research into using remote sensing to quantify seed number and grain weight of a plant in a field environment is limited. There has been success in controlled environments in which a 3D reconstruction of rice showed that seed number for the panicle had a significant ($p < 0.05$) positive correlation with the voxel count of the reconstruction throughout the grain-filling period ($r = 0.61$ to 0.70) (Sandhu et al., 2019). This same experiment also found significant ($p < 0.05$) positive correlation ($r = 0.48$ to 0.74) between voxel count and seed weight which increased approaching maturity. This method of obtaining the estimated seed number and weight works moderately well in the laboratory setting but will be challenging to adopt under field conditions.

This challenge has been approached using a simpler method in order to allow for the methodology and the tool developed to be utilized by both researchers and farmers. This method follows an allometric determination method by taking RGB images with a digital camera of over 1000 sorghum heads (closed panicle type). The head volume is determined by...
using the head length and diameter (measured using a ruler) and assuming the head is cylindrical and comparing this volume to grain number per head resulted in a strong relationship ($R^2$ of 0.68 and 0.58) for commercial hybrids and inbreds, respectively (Ciampitti et al., 2014) (Fig. 3A). At last, this approach has been extended to estimate final yield using variables such as row spacing and estimated seed number per kilogram of grain harvested (Ciampitti et al., 2015) (Fig. 3B). The progress achieved using this method integrated with machine learning tools is currently under development (Fig. 3C). Currently, the method is under substantial refinement to consider a new machine learning approach via utilization of edge-detection technology for clearly defining head volume accounting for different sizes and types of panicles, i.e., open versus closed heads. Alternatively, current high-throughput estimations of yield are derived through the analysis of vegetation indices. While this method can provide relatively accurate prediction of yield, it is a secondary measure of yield and the reliability of the prediction only increases near maturity and could vary based on environmental changes (Galli et al., 2020). In the near future, the primary measurement based on remote sensing that is being developed (Fig. 3C), can be scalable to identify grain number on large populations in sorghum under field conditions.

**Limitations and future research directions**

Keeping in line with the scope of the review, we have indicated limitations and provided recommendations of utilizing advances in sensor technology to develop high-throughput phenotyping approaches to capture physiological aspects that will help enhance heat and drought stress resilience in crops.

*Time-of-day of flowering* - Achieving multiple flights at short temporal frequency to record TOF can be a limiting factor for many research programs. Hence, it is recommended to optimize flights that capture a large proportion of the variation on a flowering day to make
the approach of using UAVs for capturing TOF feasible. In addition, the distance between the aerial sensor platform and the flowering field (after accounting for differences in plant height) needs to be optimized for different crops to ensure high quality images for detecting genotypic differences. Algorithms will need to be developed and standardized to capture differences in color and area of foliage and anthers accounting for soil surface in crops such as wheat where the canopy does not close completely.

*Photosynthetic efficiency* – Designing ideotypes to maintain improved productivity under heat and drought stress and moving beyond stay-green versus senescence concepts implemented at the plant level and small plots to phenotype diversity panels on large area has been the major bottleneck. Progress achieved in sensor technology provides the vehicle to capture temporal (flowering till maturity) changes in stay green versus senescence patterns that will allow for capturing the diversity required to incorporate into breeding programs. Experiments involving large diversity panels will need to be designed innovatively to be able to capture the gradient of changes in stay green and senescence both within and between genotypes.

*Tracking water soluble carbohydrates translocation to grains* – Limited progress has been achieved in employing sensor-based technology to capture the storage and translocation of WSC in plants because of the dynamic changes, both spatially (leaf, stem and grain) and temporally (within and between days during grain-filling). This is further complicated by the stage, duration and intensity of stress which warrant the need to capture the dynamics but still establish a practically feasible approach. Taking sensor-based carbon balance in different plant parts in the morning and evening throughout the grain-filling period could help establish solid benchmarks. Using these established benchmarks, environment specific temporal intervals (in days) can be defined at which images needs to be taken that are both practical and capture >90% of changes between flowering and physiological maturity.
Further, the community would still need to improve the accuracy of capturing the changes in WSC in plant parts, building on the progress achieved by Dreccer et al. (2014) and Garriga et al. (2017).

*Estimating grain number and weight under stress* – Heat and drought stress during flowering and post-flowering stages induce non-uniform seed-set (gaps) within panicles and heads, which deviates from the normal fully filled panicles that the system (Fig 3A, B) has been optimized to estimate. Having a mosaic of loss in seeds within panicles due to stress will challenge the approach developed. This would require extensive training before it can be employed or used effectively to estimate the seed loss under stress. Currently, the integration of machine learning tools into the approach could help but would still require a large sample size with different proportion of loss in seed numbers in panicles or heads, before the technology can be standardized. Unlike loss in seed numbers, reduction in seed weight within panicles and different genotypes due to heat and drought stress presents a lesser challenge and can be captured using the current model.

**Conclusions**

The review provides an overview of current advances and future directions related to key physiological processes related to heat and drought stress resilience during reproductive and grain-filling periods. In order to take advantage of naturally occurring trait variation to increase heat and drought stress resilience in crop varieties, collaborative science is imperative and inevitable. Tools in machine and deep learning in relation to agriculture are becoming fundamentally critical for evaluation of these hard to quantify and time-sensitive
traits. In order to make progress at the rate which is required by global demand in a changing climate, traditional and hand-measurements must be evolved in order to accurately, quickly, and reliably obtain more scalable measurements with high-resolution. The limitations and future research directions highlighted for the four key areas provide the next steps to establish high-throughput phenotyping platforms for field-based estimations and for incorporating these traits into global abiotic stress breeding programs.
Acknowledgements

We thank the financial support by National Science Foundation, USA Award No. 1736192 to Krishna Jagadish, Kansas State University. Contribution 21-090-J from the Kansas Agricultural Experiment Station. We also thank Anuj Chiluwal and Paula Demarco for supplying the sorghum images in Figures 1 and 3, respectively.

Conflict of interest

Authors declare no conflict of interest
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Table 1. Overview of research advances for phenotyping target traits focused in the review.

| Trait                          | Crop                        | Throughput | Location | Platform   | Sensor                     | Sensor Measured Trait | Observed Agronomic Trait | Reference                  |
|-------------------------------|-----------------------------|------------|----------|------------|----------------------------|------------------------|--------------------------|---------------------------|
| Time-of-day of flowering      | Wheat                       | High       | Field    | Field Scanalyzer | RGB Digital Camera         | TOF                    | TOF                      | Sadeghi-Tehran et al., 2017 |
|                               | *Setaria viridis*           | Medium     | Lab      | Fixed Mount | RGB Digital Camera (Daytime) | TOF                    | TOF                      | Desai et al., 2018         |
|                               | Wheat                       | High       | Field    | Tractor Mount | RGB Digital Camera         | Percent Heading        | Percent Heading          | Wang et al., 2019          |
| Photosynthetic efficiency     | Barley and Sugar Beet       | Medium     | Field    | Fixed Mount | LIFT System                | Chl a                  | Daily Average Fluorescence Values | Raesch et al., 2014       |
|                               | Aspen and Cherry Tree       | Medium     | Field/Lab | Hand-Held   | Hyperspectral Radiometer   | NDRE<sub>740</sub>     | Photosynthetic Efficiency | Peng et al., 2016          |
|                               |                             |            |          |             | SPAD Meter                 | Chlorophyll Index       | Photosynthetic Efficiency |                           |
| Translocation of WSC | Evergreen Shrub Medium Field Hand-Held Field Spectroradiometer PRI Photosynthetic Efficiency Zhang et al., 2017 |
|---------------------|---------------------------------------------------------------|
| Wheat High Field Tractor Mount Hyperspectral Radiometer Spectral Region (350 - 1290 nm) WSC Amount Drecker et al., 2014 |
| Maize Medium Field Hand-Held Hyperspectral Radiometer Reflectance Spectra Sucrose Content Yendrek et al., 2017 |
| Wheat Medium Field Fixed Mount Hyperspectral Radiometer Spectral Region (350 - 2500 nm) WSC Concentration Garrig a et al., 2014 |
| Estimating yield and yield parameters | Rice Medium Field Fixed Mount RGB Digital Camera Panicle Count Panicle Count Xiong et al., 2017 |
| Wheat Medium Field Tractor Mount RGB Digital Camera Spike Count Spike Count Hasan et al., 2018 |
| Wheat Medium Field Hand-RGB Digital Ear Count Ear Density Madec et al., 2018 |
| Species     | Environment | Method                | Imaging System              | Head Count | Reference                      |
|-------------|-------------|-----------------------|----------------------------|------------|--------------------------------|
| Sorghum     | High        | UAV-Based             | RGB Digital Camera         | Head Count | Guo et al., 2018               |
|             | Field       |                       |                            |            | Ghosa et al., 2019             |
|             |             |                       |                            |            | Lin and Guo, 2020              |
Figure Legends

Figure 1: Quantifying time-of-day of flowering (TOF) in crops. Figure shows potential transition of methodologies in recording TOF in crops and provides cases studies related to TOF in sorghum and rice. Traditional low-throughput measurement via manual counts (A) which is labor intensive, induces temporal variability, and is subject to human error to use of low-altitude UAVs and high resolution imagery to easily acquire high-temporal and accurate data to record TOF (B). Natural alteration of flowering time in sorghum (C; Chiluwal et al., 2020) and the change in flower opening time in rice by genetic incorporation of early morning flowering trait (see far right pie charts) from wild rice into popular variety (D; Ishimaru et al., 2010).

Figure 2: Optimizing stay-green and senescence dynamics. Handheld, indoor high-throughput, and field-based high-throughput techniques for quantifying photosynthetic efficiency is presented using effective quantum yield of photosystem II (QY) as a case study. Handheld devices (A), though sensitive enough to detect subtle changes such as initiation of senescence, are highly laborious, provide data either at a leaf or spike level, and challenging to be deployed on large scale phenotyping. Indoor high-throughput platforms (B) having similar or higher sensing capability can easily acquire trait information on the whole plant automatically without human intervention. Field-based high-throughput platforms (C) have the capability of gathering reflectance data on a large number of genotypes with extreme sensitivity and low-temporal variation.
Figure 3: Estimation of yield and yield related parameters. Figure illustrates the progression from destructive field-based primary measurements in order to obtain an estimation of yield to new high-throughput measurements to estimate yield through both primary and secondary measurements. The methods of gathering information for yield estimation are ordered from least applicable but highly accurate to most applicable but less accurate or from low-throughput to high-throughput and include destructive sampling and lab-based primary measurements (A), field-based primary measurements (B), and current investigation on developing high-throughput non-destructive primary and secondary measurements (C).
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