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# Field crop phenomics: enabling breeding for radiation use efficiency and biomass in cereal crops

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## Contents

## Summary

Plant phenotyping forms the core of crop breeding, allowing breeders to build on physiological traits and mechanistic science to inform their selection of material for crossing and genetic gain. Recent rapid progress in high throughput techniques based on machine vision, robotics and computing (Plant Phenomics) enables crop physiologists and breeders to quantitatively measure complex and previously intractable traits. By combining these techniques with affordable genomic sequencing and genotyping, machine learning and genome selection approaches, breeders have an opportunity to make rapid genetic progress. This review focusses on how field based plant phenomics can enable next generation physiological breeding in cereal crops for traits related to radiation use efficiency, photosynthesis and crop biomass. These traits have previously been regarded as difficult and laborious to measure but have recently become a focus as cereal breeders find genetic progress from “Green Revolution” traits such as harvest index become exhausted. Application of LiDAR, thermal imaging, leaf and canopy spectral reflectance, chlorophyll fluorescence and machine learning are discussed using wheat and sorghum phenotyping as case studies. A vision of how crop genomics and high-throughput phenotyping could enable the next generation of crop research and breeding is presented.



## Key words

Crop breeding
Sorghum
Wheat
Photosynthesis
Stomatal conductance
Canopy temperature
Big data
Crop physiology


# I. Introduction: phenotyping for trait-based crop breeding

Phenotyping has been at the heart of plant breeding since the domestication of crops thousands of years ago. The terms “phenotype” and “genotype” were coined more than a century ago (reviewd in Walter *et al.*, 2015) and highly heritable phenotypes are the basis for modern crop breeding. The skilled eye of the crop breeder has enabled early-generation selection of material for crossing based on both elimination of “defects” (such as disease susceptibility and inferior agronomic qualities) and maximisation of yield across multiple environments and seasons (Donald, 1968). Subsequent crossing of the “best with the best” has been a successful strategy in the past, however, understanding of the component processes or genes underpinning the yield advantage was often lacking. A more mechanistic approach, which is now commonly used in cereal breeding is “ideotype” breeding. This breeding philosophy has more recently referred to as “physiological breeding” since it has become more technologically tractable to phenotype genetically complex quantitative physiological traits rather than simple visible phenotypes such as grain number and weight

(Reynolds & Langridge, 2016). This approach requires construction of a "model" or ideal plant with attributes combined to maximise yield and has been used extensively in cereal breeding; first in wheat (Donald, 1968) and rice (Yoshida & Parao, 1972; Peng *et al.*, 2008). The advantage of a trait-based approach is that the heritability of a yield component may be much higher than that of yield itself, thus maximising genetic gain over that achievable with selection for yield alone. The limitation of this approach is, of course, whether our model we are breeding toward is the appropriate one. For example, Donald (1968) proposed an ideotype for wheat, which has become a paradigm for wheat breeding in Australia, containing a number of attributes based on the relationship between these traits and yield in relevant environments and our knowledge of the physiology of the crop. A cartoon representing the elements of such a wheat ideotype is shown in Fig.1.

With the addition of responsiveness to inputs such as water and fertiliser and resistance to common foliar diseases, Borlaug's semi-dwarfed wheats and the short-statured rice varieties that led to the Green Revolution and saved millions of human lives, were the first examples of these ideotypes (Borlaug, 1968). Donald also introduced the term "harvest index"; the proportion of the plant biomass partitioned to harvestable grain, which has become a major morphological driver of cereal yields since the 1960s (Fischer *et al.*, 2014).

While still surprisingly relevant today, whether the component traits of this ideotype will deliver in future breeding scenarios is debatable. Firstly, at least in our major cereal crops, we appear to have reached an asymptote in harvest index achieved primarily through adoption of dwarfing genes and hence traits that target biomass itself, such as photosynthetic efficiency, have become major breeding targets (Foulkes *et al.*, 2011; Parry *et al.*, 2011). Secondly, due to elevated atmospheric $CO_2$ levels, increased frequencies of heat and drought events, desirable traits of an ideotype may change. For example, free-tillering, tall wheat tends to yield better under elevated $CO_2$ (Zhu *et al.*, 2012).

In many dry-land production areas, attributes that maximise the productive use of water are becoming more important (Ludlow & Muchow, 1990; Richards, 2006; Richards *et al.*, 2010). This increased focus on breeding for water-limited environments is already evident in sorghum, which is the world's fifth most important cereal and also a significant summer crop in north-eastern Australia. Sorghum is a $C_4$ crop and known for its drought adaptation. A recent study has shown that yield advances in sorghum are 2.5 times more in dry years than in wet years (Potgieter *et al.*, 2016).

Generally, annual genetic gain in our major cereal crops is currently in the range of 0.5 to 1%; clearly not sufficient to meet future global demands of a burgeoning population (Fischer *et al.*, 2014). If we assume that physiological breeding will play a key part in future efforts to remedy this stagnation in yield progress, what is required to fuel the engine of this selection process?

Two major technologies underpinning crop breeding have advanced exponentially in capability since the work of Donald: crop genomics and phenomics. A flowchart of how these two fields of research can contribute to crop breeding and accelerate genetic gain is shown in Figure 2. We have seen a revolution in our capacity to produce high-density genetic maps of breeding populations for marker-assisted selection (MAS; (Langridge & Reynolds, 2015)) now commonly used in cereal breeding programs, particularly for genes of

major effect such as flowering time, height and disease resistance. However, many other agronomically important traits typically have more complicated genetic architecture and are often governed by quantitative trait loci (QTL) that may be population specific, or made up of multiple QTL of minor effects, particularly in the case of QTL derived from genome-wide association studies (GWAS) of large diversity sets developed to introgress novel germplasm into breeding programs (see Langridge & Reynolds, 2015; Reynolds & Langridge, 2016).

More recently though, so-called next-gen sequencing (NGS), which has revolutionised the study of genomics has made high-throughput whole-genome sequencing possible and affordable for many breeding programs. Genome-wide selection is now becoming a widely adopted tool in crop breeding and is particularly successful when applied to trait-based breeding matched to target environments using agronomic models or physiological experiments (Cooper *et al.*, 2014). Genomic selection models attempt to produce a barcode of single nucleotide polymorphisms (SNPs) generated from high-density sequence-based marker information (GBS), SNP arrays (Gene chips) or genome re-sequence information matched to high-value traits for a target environment (or in its bluntest application, yield itself). A genome selection statistical model in its purest form, once developed and validated against yield data across many sites and seasons, can be used to increase genetic gain without subsequent phenotyping or high-throughput phenomics but in reality, combining both genomics and phenomics in the workflow is most valuable (Crossa *et al.*, 2017; Montesinos-López *et al.*, 2017). To develop a genome selection model to determine the predicted breeding value of an individual in a cross, a “training set” must be developed, which links patterns of SNPs to the traits of interest. High-throughput phenomics is crucial at this step to develop a robust model across target environments. The statistical model is then “tested” on an uncharacterised population and the allelic variation identified in the model validated. This approach is very similar to machine learning-based phenomics approaches, which will be described below (see Cooper *et al.*, 2014; Singh *et al.*, 2016; Crossa *et al.*, 2017; Montesinos-López *et al.*, 2017; Silva-Perez *et al.*, 2018).

While this combined genomics and phenomics approach can be used to accelerate genetic gain in a breeding system, it can also be used to identify valuable new trait / SNP relationships in germplasm diversity sets and the identified allelic variation can then be checked for in breeding populations or introgressed through crossing or by genome engineering (Bortesi & Fischer, 2015). With the rapid advancement of sequencing technologies, synthetic biology and genome engineering, high-throughput, non-destructive plant phenomics must match the pace of these developments to maximise our ability to meet the demands of global food consumption. While mass parallelisation of sequencing reactions - as first achieved by Life Sciences’ 454 next-gen sequencing machine - was at the heart of this paradigm shift in genomics (Koboldt *et al.*, 2013; Heather & Chain, 2016), miniaturisation and increased affordability of sensors, and importantly, of geo-positioning systems (GPS) with centimetre rather than metre accuracy, has opened the doors for the development of high-throughput phenotyping techniques that are necessary to rapidly assess thousands of breeders’ plots in field trials. In the sections below we discuss the recent application of field-based phenomics technologies to trait-based pre-breeding and breeding in grain crops, focusing on the globally important cereals wheat and sorghum. A vision for the future of in-silico breeding is outlined. Key cereal traits contributing to yield formation are summarised in Table 1, together with their primary effect contributing to yield and the respective sensor technology used for phenotyping.

# II. Biomass, radiation use efficiency and photosynthesis: new frontiers in crop breeding

As alluded to in the introduction, improvements to harvest index are becoming increasingly harder to achieve as we approach a biological limit in our major cereal crops (Fischer *et al.*, 2014). Yield improvements therefore will have to come from more efficient biomass accumulation in response to greater sink strength and in many cases, such as under water-limited conditions, increased biomass (and yield) per unit of water used. At the basis of biomass accumulation is crop photosynthetic capacity and the efficiency with which plants use light for growth for a given set of inputs. At the leaf level, screening for genetic variation in photosynthetic traits using traditional methods such as gas exchange are time-consuming (even single point measurements of assimilation can take up to 20 minutes for a stable value) and are highly sensitive to crop water status (see Silva-Pérez *et al.*, 2017). There are also several issues with scaling leaf-level data to the canopy as photosynthetic performance of leaves at different positions in the canopy can vary. However, assimilation chambers have been used to measure canopy apparent photosynthesis in wheat, demonstrating that the genotypes with greater canopy photosynthesis at single time points during the growth period had greater leaf chlorophyll (as measured by SPAD) and were also higher yielding (Tang *et al.*, 2015; Tang *et al.*, 2017). Nevertheless, it is likely that “whole-of-life-cycle” canopy photosynthesis may be more relevant to final yield (Murchie *et al.*, 2018), which would include photosynthate stored in stems pre-flowering and remobilized to the grain during grain filling (Blum, 1998), photosynthesis in organs such as spikes or other floral parts (Sanchez-Bragado *et al.*, 2016), and the persistence of green leaf photosynthetic area later in grain filling; a trait known as “functional stay-green”, which occurs in wheat (Christopher *et al.*, 2016; Rebetzke *et al.*, 2016). To screen for differences in photosynthetic capacity at the canopy level, such contributions to photosynthesis have to be integrated over time. Crop physiologists commonly do this by dividing the amount of biomass accumulated by a crop (in the absence of abiotic and biotic stresses) by the amount of radiation intercepted by the canopy over a certain period of time. This ratio is termed canopy radiation use efficiency (RUE) and is usually measured in g $MJ^{-1}$. As RUE represents the sum of a number of sub-traits related to photosynthetic performance, it is often quite grossly estimated at maturity with many assumptions by dividing final biomass by total light absorbed during the growing season. Given the challenges of measuring leaf or canopy photosynthetic capacity rapidly on many hundreds or thousands of germplasm entries, it is not surprising that these traits have failed to be a major focus of cereal breeding programs (Murchie *et al.*, 2018). However, there have recently been considerable advances in high-throughput estimation of photosynthetic and biomass-related traits at the leaf and canopy level, which make them more tractable.

## 1 Leaf estimation of photosynthesis-related traits

While measuring leaf photosynthetic properties across genotypes using traditional gas exchange is not practical, a number of optical techniques can provide surrogate measurements in high throughput. Prediction of a range of agronomic traits and crop chemical components through measurements of radiation reflected from crop leaves and canopies is well established and gaining in popularity for plant phenomics. Reflectance in the

visible to near-infrared part of the electromagnetic spectrum has been related to a range of photosynthesis-related traits such as pigment concentration (xanthophylls, chlorophylls, carotenoids) and also water content of plants, and the red-edge in the derivative of reflectance is commonly used to extract these parameters (Peñuelas & Filella, 1998). The SPAD chlorophyll meter is a widely used optical instrument, which measures the transmittance of red light (560 nm) through the leaf and normalised to infrared (940nm) light transmission to predict leaf chlorophyll content (Benedict & Swidler, 1961). Such "indices" based on wavelengths in the visible and infrared part of the electromagnetic spectrum have long been used in remote sensing to predict vegetation biomass, biochemical leaf components and some physiological traits. A widely used example of this approach is the normalised difference vegetation index (NDVI), which uses reflected red and near-infrared wavelengths to estimate relative greenness, canopy ground cover, senescence, biomass and chlorophyll content (Tucker, 1979; Gamon *et al.*, 1995; Pinto *et al.*, 2016). Also, the photochemical reflectance index at 531 and 570 nm (PRI) has often been used to estimate photosynthetic traits and photoprotective pigment pools in leaves (Gamon *et al.*, 1992).

The indices described above are derived from LED/filter/photodiode combinations restricted to the wavelengths of light determined by the filter sets. However, visible / near-infrared spectrometers and full-range visible, NIR, SWIR spectrometers are now available from a range of manufacturers and are often attached to a leaf clip with a light source incorporated. Such spectrometers permit rapid collection of not just two or 3 wavelengths of reflectance data but reflected light across many hundreds or even thousands of wavelengths. Recent advances in computational processor speeds and artificial intelligence/machine learning algorithms mean that the entire spectral data set can be analysed and used for statistical prediction of photosynthesis-related traits. By generating a "training set" of statistical correlations between every wavelength of reflected light from a leaf or canopy and the trait of interest, predictive models have been derived for photosynthesis related traits. Leaf nitrogen, leaf mass per area and photosynthetic traits in plants ranging from trees to both $C_3$ and $C_4$ annual crops can be derived in around 20 seconds per leaf measurement (Serbin *et al.*, 2012; Ainsworth *et al.*, 2014; Singh *et al.*, 2015; Yang *et al.*, 2016; Dechant *et al.*, 2017; Yendrek *et al.*, 2017; Silva-Perez *et al.*, 2018). Silva Perez *et al*. (Silva-Perez *et al.*, 2018) derived such algorithms using partial least squares regression analysis for wheat leaf nitrogen content, the modelled photosynthetic parameters $V_{cmax}$ (an indicator of Rubisco amount and photosynthetic capacity) and *J* (chloroplast electron transport capacity) (Von Caemmerer, 2000) in addition to leaf mass per area. These models allow photosynthetic variation to be examined in the field in many hundreds or even thousands of diverse crop genotypes, potentially making photosynthesis a tractable breeding target. In wheat, this is enabling large-scale screening of germplasm resources and combined with genotype by sequence data, mapping of alleles underpinning this diversity in photosynthetic performance (http://iwyp.org/funded-projects/ ).

There are several obstacles to the widespread use of a machine learning approach to extract trait-based information for breeding. First, generation of the initial "training set" to develop the model requires a large number of validation measurements using the older, slower traditional measurement systems (many hundreds or even thousands of measurements may be required, depending on the dimensionality of the trait surrogate; for example, in the case of leaf reflectance, the number of wavelengths measured). If sufficiently large training sets are not developed, spurious "over-fitting" occurs and the predictive power

of models is diminished (see Heckmann *et al* 2017). Another equally important issue is the applicability of predictive models across genotypes, tissue types and environments. In the case of Silva-Perez et al (2018), leaf reflectance models for photosynthetic parameters in wheat were robust across Australian and Mexican field conditions and across field versus glasshouse-grown plants, and other studies have shown that such models can even predict across species boundaries (Heckmann *et al.* 2017). As with most machine learning approaches, the larger and more diverse the training set, the more likely the model is to predict when applied to other unknown samples, which the model has not "seen" before.

A high-throughput alternative to gas exchange for photosynthetic screening, is to monitor chlorophyll fluorescence which is a direct measure of photosynthetic capacity, rather than a statistical model (reviewed in Maxwell & Johnson, 2000; Murchie & Lawson, 2013). Since the mid 1980's, commercial "leaf clip" pulse amplitude modulated chlorophyll fluorescence (PAM) systems have been commercially available to provide not only steady- state chlorophyll fluorescence measurements at a given actinic light intensity, but by applying a brief saturating flash of light, allow calculation of photosynthetic electron transport rate (ETR or J), intrinsic light harvesting efficiency (estimated from the fluorescence parameter dark adapted Fv/Fm) and NPQ (non-photochemical quenching such as dissipation of energy as heat) (Maxwell & Johnson, 2000). Small, affordable, handheld PAM and similar devices that are now available (Cessna *et al.*, 2010; Kuhlgert *et al.*, 2016) make high-throughput screening for electron transport related traits possible in the field. However, QTL mapping in field crops has so far mostly used genetic variation in dark-adapted Fv/Fm for abiotic stress tolerance mapping (Sharma *et al.*, 2017). It is difficult to scale chlorophyll fluorescence imaging to a remote sensing platform due to the difficulty of applying a uniform, high intensity saturating flash across a canopy. However, recent advances in using Laser Induced Fluorescence Transient (LIFT) techniques to de-convolute components of fluorescence quenching remotely offer the promise of canopy-level estimates of ETR and NPQ (Raesch *et al.* 2014). Furthermore, various retrieval techniques (theoretical and empirical) and sensing (index based) approaches exist to remotely detect solar-induced fluorescence (SIF) across large fields (Meroni *et al.*, 2009).

## 2 Estimation of photosynthetic traits, biomass and radiation use efficiency at the canopy level

While leaf-level measurements provide relative high-throughput methods for screening field crop germplasm, they are restricted to collecting data on one leaf at a time in isolation from the behaviour of the crop canopy as a whole. A given "leaf class" (e.g. flag leaf or penultimate leaf) is chosen for analysis and often at a particular developmental stage (e.g. tillering, booting, anthesis or grainfill), which is easily recognised and normalised across diverse material (e.g. the leaf hyperspectral work of Silva-Perez *et al.*, 2018). However, scaling these observations to the canopy level is not trivial. Even if total green leaf area could be estimated using high-throughput alternatives (Liu *et al.*, 2017; Potgieter *et al.*, 2017), leaf age affecting photosynthetic capacity or light interception in the different layers of the canopy profile will play a crucial role when integrating leaf-level photosynthetic traits at the canopy scale.

To understand the genetic architecture of a complex trait such as biomass accumulation or RUE, a more comprehensive analysis of the canopy as a whole, over a range of developmental stages is desirable. This can be achieved by ground-based proximal remote sensing using phenomobiles (Deery *et al.*, 2014; Liu *et al.*, 2017; Madec *et al.*, 2017; Salas Fernandez *et al.*, 2017; Jimenez-Berni *et al.*, 2018) or fixed platforms (Kirchgessner *et al.*, 2017; Virlet *et al.*, 2017), and aerial imaging, both manned and UAV (Aasen *et al.*, 2015; Gonzalez-Dugo *et al.*, 2015; Deery *et al.*, 2016; Yang *et al.*, 2017) using a range of devices similar in principle to those deployed at the leaf level but in most cases based on imaging sensors.

Several instruments are now commercially available for multispectral sensing whereby data are collected from discrete wavelengths. Such sensors work in either active mode (a light source is provided), such as Greenseeker and Crop Circle (Govaerts & Verhulst, 2010; Shaver *et al.*, 2011) or passive mode (relying on the ambient light), where options include single point sensors (Balzarolo *et al.*, 2011) and imaging sensors (see review by Yang *et al.*, 2017). In contrast, hyperspectral sensors collect hundreds or thousands of continuous bands across the whole spectrum. The ASD FieldSpec (Malvern Panalytical, The Netherlands) is a commonly used hyperspectral sensor for single point spectral measurements at the canopy level (Tilling *et al.*, 2007; Botha *et al.*, 2010; Gnyp *et al.*, 2014; Kaur *et al.*, 2015; Singh *et al.*, 2017a; Yendrek *et al.*, 2017). However, as hyperspectral cameras are becoming miniaturised and more affordable, they are becoming a viable alternative to the point spectrometers that can be mounted on ground- (Busemeyer *et al.*, 2013; Deery *et al.*, 2014; Virlet *et al.*, 2017) and aerial phenotyping platforms (Gonzalez-Dugo *et al.*, 2015; Habib *et al.*, 2016). Recent examples have demonstrated the potential of hyperspectral imaging for estimating nitrogen content in maize and wheat (Vigneau *et al.*, 2011; Gabriel *et al.*, 2017; Singh *et al.*, 2017a; Camino *et al.*, 2018). However, the workflow of imaging spectroscopy presents some challenges (Aasen *et al.*, 2018) such as the radiometric correction required to turn images into reflectance or the geometric corrections required to obtain georeferenced images. However, recent advances in ground-based imaging spectroscopy (Underwood *et al.*, 2017; Wendel & Underwood, 2017b; Wendel & Underwood, 2017a) present an opportunity for implementing novel algorithms for phenotyping photosynthesis-based traits using hyperspectral sensing at the canopy level.

Canopy reflectance has successfully been used to estimate leaf N concentration in two Sweet Sorghum cultivars (Singh *et al.*, 2017b) and leaf N is usually correlated with RUE in $C_3$ and $C_4$ crops, however, especially in $C_4$ this relationship reaches a plateau where growth is light limited (Sinclair & Horie, 1989). Therefore, to detect differences in canopy RUE of genotypes grown under high N conditions, such as in a breeding trial, estimates of biomass and accumulated canopy light interception are needed.

Recent attempts to estimate above-ground biomass in the phenomics context include the use of LiDAR (Eitel *et al.*, 2014; Jimenez-Berni *et al.*, 2018) or 3D canopy reconstruction from ground cameras (Salas Fernandez *et al.*, 2017), as well as aerial surveys combining crop height and multispectral imagery (Bendig *et al.*, 2015; Tilly *et al.*, 2015a; Yue *et al.*, 2017; Zhang *et al.*, 2017; Li *et al.*, 2018). By combining spectral reflectance with manually measured traits, such as stem diameter, biomass predictions could be improved in maize (Varela *et al.*, 2017). However, these methods, based on volumetric estimates of biomass still require crop-specific calibration or parameters that depend on the crop developmental

stage (Tilly *et al.*, 2015b; Jimenez-Berni *et al.*, 2018). The use of combined new technologies such as aerial radar in combination with Lidar (Kaasalainen *et al.*, 2015) and combining machine learning algorithms and crop growth models (Liu *et al.*, 2017) could improve these estimates in the future.

Another important attribute required for estimating RUE is light intercepted by the canopy, which traditionally is measured with methodologies based on light interception using ceptometers, canopy analysers or hemispheric photography. However, measuring light interception with these tools can be time-consuming and there are constraints regarding the time of the day or light conditions at which these measurements can be performed. Other methodologies based on indirect estimates of light interception such as canopy ground cover are becoming very popular and new tools available for measuring ground cover with mobile phones can speed up light interception measurements (Shepherd *et al.*, 2018)

Fractional ground cover - as a surrogate for canopy light interception - has successfully been estimated for a maize crop planted at two different populations using Red Green Blue (RGB) cameras fitted with filters that rendered them sensitive to wavelengths in the photosynthetically active radiation (PAR) range mounted on UAVs (Tewes & Schellberg, 2018). The authors then combined the interception estimates with incident radiation from a weather station to calculate accumulated radiation and by plotting that against biomass from manual cuts at different intervals, they derived RUE at different stages of crop growth.

Similarly, multispectral cameras, such as the RedEdge (MicaSense, Seattle, USA) are specifically designed to augment the red green blue bands with rededge and near-infrared, and are light enough to be carried on UAVs. They can be used to estimate canopy NDVI, which has been significantly correlated with traits relating to seasonal leaf area dynamics in sorghum (Potgieter *et al.*, 2017).

However, these methodologies cannot account for the canopy structure or estimate how much light is intercepted at different times of the day. New methodologies based on a combination of LiDAR and 3D modelling of the canopy (Perez *et al.*, 2018) have been used to accurately estimate light interception accumulated over time in different genotypes of palm trees (Perez *et al.*, 2018). A similar approach can be applied in annual crops and the combination of LiDAR and 3D modelling has also been used in wheat for estimating green area index (Liu *et al.*, 2017). LiDAR can provide very valuable information about the vertical distribution of light interception within the canopy, which combined with the photosynthetic capacity (Rebetzke *et al.*, 2016) and 3D models for simulating light penetration and light interception at different heights throughout the canopy and at different times of the day (Figure 3). Repeated measurement of LiDAR throughout crop development can potentially provide a much more accurate estimation of RUE and reveal subtle genotypic differences. The different shapes of the profiles can also be used as features in machine learning algorithms (Zhao *et al.*, 2011; Jin *et al.*, 2018) to predict complex physiological traits related to RUE and eventually map genetic regions related to these traits.

Combining ground-based platforms and aerial platforms for phenotyping offers flexibility, for example if the ground is too wet to be accessible via a phenomobile measurements can still be taken by UAVs and if UAVs cannot be used measurements can be taken with the ground vehicle. Integrating outputs from various platforms and many different sensor types further

offers the opportunity to design analysis pipelines around specific target traits. Such a platform (Figure 4) in combination with a UAV-based platform is currently being used to target complex traits such as growth (Potgieter, AB *et al.*, 2018) and RUE in sorghum (B. George-Jaeggli and A. Potgieter, unpublished).

Outputs from all of the sensors from the ground-based and aerial platform are streamlined in a custom-designed analysis pipeline and algorithms are developed by constructing multivariate statistical models for each target trait much in the same way as for leaf-level traits. Each model is initially fit on a training data set with parameters measured manually on a subset of the field plots. Both the raw data and results of processing are stored on a cloud-based storage infrastructure, which provides data redundancy across sites, and fast access to both the raw data and a custom web server. This also enables future re-analysis of previously gathered field data as new algorithms and research questions arise and leverages the initial costs of expensive field trials.

If RUE shows useful heritability, meaning the variation due to genetic factors (characterised via SNPs) is greater than the variation due to environmental factors or measurement error, the genetic loci and potentially candidate genes contributing to canopy photosynthetic capacity may be identified via Genome Wide Association Studies (GWAS) and the trait can be selected for in the sorghum breeding program (see Fig 2). Learnings from sorghum may then transfer to other cereals via sequence homology. A better understanding of the variability and genetic basis of RUE can also be used to parameterise sophisticated crop models such as APSIM (Holzworth *et al.*, 2014), which predict genotype performance in various environments and under different agronomic management (GxExM simulations) (Chapman, 2008; Hammer *et al.*, 2010; Chenu *et al.*, 2017; Messina *et al.*, 2018). Together, genomics and phenomics and crop modelling are potentially powerful tools for the breeding program to select lines with increased growth capacity adapted to various production environments. Nevertheless, there is evidence that conventional breeding has increased RUE along with grain yield (Shearman *et al.*, 2005; Sadras & Lawson, 2011; Sadras *et al.*, 2012). However, progress is not universal and, in some examples, improvement in RUE and grain yield has in fact slowed (Aisawi *et al.*, 2015; Flohr *et al.*, 2018). Thus, genomics and phenomics enabling tools can potentially augment current efforts in conventional plant breeding to improve cereal yield potential even in the face of climate change.

# III. Photosynthesis, stomatal conductance and canopy temperature

Stomatal conductance ($g_s$) is defined as the rate of carbon dioxide entering or water vapor exiting through the leaf stomata. The particular importance of $g_s$ for crop improvement, more so in $C_3$ crop species, is evidenced through the many studies showing a concomitant increase in $g_s$ with higher yields (Roche, 2015): achieved through conventional plant breeding. Herein, particular attention is granted to $g_s$ in $C_3$ species because of their dependence of photosynthetic gas exchange on $g_s$, whereby the two are often highly correlated (Farquhar & Sharkey, 1982; Fischer *et al.*, 1998; Gago *et al.*, 2016). Due to their carbon dioxide concentrating mechanism, $C_4$ species are not limited by $g_s$ in the same way as $C_3$ species (von Caemmerer & Furbank, 2003; Osborne & Sack, 2012). However, similar

studies reporting on the link between $g_s$ and yield also exist for some $C_4$ crops (Basnayake *et al.*, 2016). In the context of improving photosynthetic performance of $C_3$ crops under both high-yield and water- limited conditions, $g_s$ and canopy conductance to water and $CO_2$ is of great importance Thus, surrogate measures of $g_s$ that enable sampling of many lines in a short time potentially have high utility for plant breeding.

Canopy temperature (CT) is a well-established surrogate measure of $g_s$ (Blum *et al.*, 1982; Smith *et al.*, 1988; Amani *et al.*, 1996; Fischer *et al.*, 1998; Jones & Vaughan, 2010; Rebetzke *et al.*, 2013) and its application in field phenotyping of crops dates back to the 1960s (Fuchs & Tanner, 1966). The principle underlying the effectiveness of CT is akin to evaporative cooling: surfaces within the plant canopy are cooled by evaporation, so that their temperature decreases in proportion to the evaporation rate. Therefore, stomatal opening and higher transpiration rates manifest with cooler CT, while warmer CT is symptomatic of stomatal closure and lower transpiration rates (Jones, 2004). This relationship has been exploited to great effect at the International Maize and Wheat Improvement Center (CIMMYT), where studies reporting the association between cooler CT and grain yield are ubiquitous (Reynolds *et al.*, 1994; Amani *et al.*, 1996; Fischer *et al.*, 1998; Ayeneh *et al.*, 2002; Aisawi *et al.*, 2015; Rutkoski *et al.*, 2016). Although these studies typically relate CT directly to yield via greater stomatal conductance under yield potential studies, an alternative scenario arises under water limitation: whereby cooler CT during grain-filling has been linked to greater rooting depth, water use and yield (Lopes & Reynolds, 2010). Other studies on wheat (Blum *et al.*, 1989; Rashid *et al.*, 1999; Olivares-Villegas *et al.*, 2007) and sugarcane grown under water limitation (Basnayake *et al.*, 2015) have also shown an association between cooler CT and yield, further highlighting the utility of CT phenotyping. In summary, the use of CT as an effective phenotype for $g_s$ is underscored by the multiple studies relating historical yield progress with increased $g_s$ (Roche, 2015): where plant breeders have unintentionally increased $g_s$ in the quest for greater yields. While these studies highlight the commendable progress of conventional plant breeding, they also illustrate the opportunity for indirect selection for yield in early generations using CT as a surrogate measure of $g_s$ (Fischer & Rebetzke, 2018).

Recent technology advances in thermal imaging and data processing have greatly increased the efficacy of CT field phenotyping. For example, thermal cameras fitted to manned aircraft (Figure 5(a) and (b)) together with data processing systems are now used to measure CT on hundreds of experimental plots in a few seconds at a spatial resolution of 100 to 200 pixels per square metre (Deery *et al.*, 2016; Rutkoski *et al.*, 2016). As these airborne CT systems acquire a near-simultaneous measurement on all the plots in a given experiment, the confounding effects of changes in local weather conditions are mitigated. By measuring CT on all plots within an experiment at essentially the same time, the statistical analyses need only account for the spatial variation in CT through the experimental design (Gilmour *et al.*, 1997) and the need to account for time-of-measurement effects is avoided. Thus, the use of airborne thermography has greatly increased the repeatability of CT, with reported broad-sense heritability estimates typically ranging from 0.5 to 0.9 (Deery *et al.*, 2016; Rutkoski *et al.*, 2016). In these studies, the sensor payload comprising a high-precision thermal camera carried on a manned aircraft, with less than 0.05$^{o}$C pixel-to-pixel sensitivity, is typically too heavy for a conventional UAV. Therefore, although there are many examples of thermal image acquisition with UAVs (Sullivan *et al.*, 2007; Berni, J. A. J. *et al.*, 2009; Berni, Jose A. J. *et al.*, 2009; Zarco-Tejada *et al.*, 2012; Chapman *et al.*, 2014; Basnayake *et al.*, 2016;

Gómez-Candón *et al.*, 2016), their effectiveness for quantifying repeatable CT differences between genotypes remains unclear and to the best of our knowledge, no study has reported high estimates of CT repeatability or heritability from a UAV.

Although many studies have shown that CT measurements alone are a useful enabling tool for discriminating amongst genotypes, additional measurements, including local micrometeorological data and in particular net radiation, are required to estimate absolute evaporation rates and hence the pattern of crop water use (Jones, 2004; Leinonen *et al.*, 2006; Berni, J. A. J. *et al.*, 2009; Jones & Vaughan, 2010). The possibility also exists for the use of reference surfaces that mimic the aerodynamic and radiative properties of the canopy and thereby reduce the need for net radiation measurements (Jones *et al.*, 2018). Such an application is possibly more suited to continuous CT measurements. Wireless sensor networks where sensors record CT values continuously and every few minutes report these to a base station via a radio-frequency transmitter have commonly been used for irrigation management in field crops (http://www.smartfield.com/smartfield-products/equipment/smartcrop-system/). The ArduCrop wireless sensor network CT measurement system (Rebetzke *et al.*, 2016; Jones *et al.*, 2018) developed at CSIRO, is shown in Figure 5(c) and an example time-course across two days for three elite wheat varieties is shown in Figure 5(d). These technologies present the opportunity to remotely assess the pattern of crop water use across multiple environments, perhaps more effectively than using buried soil moisture sensors. Thus, the potential to non-destructively estimate crop water use together with the capacity to remotely sense biomass and leaf area development presents the opportunity to better understand the physiological basis of high-performing elite lines grown under water limitation and thereby inform research and breeding efforts.

# IV. Turning data into knowledge

Crop breeding in the ‘omic era is a multidisciplinary and “big data” challenge involving high-density genomics data combined with phenotyping data from replicated experiments in multiple environments. The activities of data processing, statistical inference and making reliable predictions to inform selection must scale to many thousands, if not millions, of individuals if they are to be useful. This will likely require a multidisciplinary effort blending non-traditional crop science capabilities, including remote sensing, software engineering, statistical inference, machine learning and artificial intelligence, with traditional capabilities like crop physiology, quantitative genetics and plant breeding. Published examples of the successful deployment of field phenotyping within experiments have relied on a multidisciplinary approach to develop dedicated data processing and statistical analysis pipelines (Salehi *et al.*, 2015; Deery *et al.*, 2016; Rutkoski *et al.*, 2016; Hu *et al.*, 2018; Jimenez-Berni *et al.*, 2018; Potgieter, A *et al.*, 2018) to segment large volumes of raw data into individual phenotypes for analysis. The ever-increasing availability of scripting software (e.g. Python (www.python.org) and R (www.r-project.org)) for data processing and analysis should to some extent alleviate this challenge.

Interoperability of data sets and uniform, publicly accessible data processing pipelines are essential to ensure utility of Phenomics data for researchers and breeders. Solutions developed for individual Phenomics Centres or research groups can tend to be monolithic, slowing uptake of technology and methodologies. While much of the work done in the

commercial sector in the data analytics domain will remain inaccessible, publicly funded activities are making analysis pipelines open and accessible via web portals. Examples of this are the collaborative activities funded by the International Plant Phenotyping Network (IPPN; https://www.plant-phenotyping.org/ ) and the PhenoSmart analytical platform of the Australian Plant Phenomics Facility (https://www.phenosmart.org.au/ ).

# V. The "Big Data" problem

Whole genome sequencing has recently become very affordable with the advent of high-throughput Illumina and now Nanopore sequencing technologies (https://nanoporetech.com/how-it-works). Informatics solutions for storing, assembling, annotating and searching sequence data have now become limiting. This problem is multiplied many fold with plant phenomics data. The information "unit" of gene sequence is limited to any combination of 4 base pairs for translation of gene sequence to protein, hence putative functional identification by BLAST searching is tractable while in Plant Phenomics it is not. One solution to this problem is "data reduction" or the distillation of phenotyping data to known traits of interest and applying established statistical methods to map these traits to the genotypic information, as described above. This may make data sets more tractable but data reduction without retention of primary data sets may remove many of the complexities in the data, which could potentially be very valuable, including for traits yet to be identified in crop breeding. We then have a dilemma where on one hand we retain a vast body of raw digital data and the traits or parameters derived from it, which could become just an intractable, chaotic collection of data. On the other hand, we retain only processed information, which is limited by our current capacity to "turn data into knowledge", wherein the capacity to use large-scale machine learning and statistics retrospectively is lost.

The technologies described above are essentially a modernisation and acceleration of techniques breeders have used for centuries to establish the relationship between phenotype and genotype and more recently incorporate into whole genome selection. The challenge then is to provide a data storage and retrieval system, which makes sense to crop breeders, physiologists, molecular geneticists and biochemists alike. Trait ontologies (e.g. http://aims.fao.org/activity/blog/crop-ontology-harmonizing-semantics-phenotyping-and-agronomy-data ) are necessary to enable cross referencing of the diversity of descriptions used for a single trait or process. A cereal breeder interested in starch quality and dough extensibility is unlikely to use the same terms for grain storage protein properties as a researcher working on Arabidopsis functional genomics of seed development. Ontologies must be dynamic, curated and agreed upon by the community.

Insufficient metadata descriptors have severely limited the utility of other classes of 'omics data sets and a variety of software solutions have been developed. For example, for gene expression data, Hannemann *et al*. (2009) used an ontology driven approach where metadata labels are attached to data using XML tags. In the case of large image-based plant phenomics data sets, such solutions are only now becoming available. One such ontology based approach to managing phenomics metadata and linked image data is PODD, (Phenomics Ontology Driven Database; Ansell *et al*. 2013). European and international programs have been recently launched to develop data standards and agreed metadata and data formats for phenotyping information (eg. https://emphasis.plant-phenotyping.eu ) and

the MIAPPE and ISA-TAB standards for Plant Phenotyping (Ćwiek-Kupczyńska *et al*. 2016). It is evident, however, that a database linking phenotype and genotype across crops and gene discovery in model plant species, which is accessible to crop breeders is still a way off.

# VI. Conclusion: crop breeding for the future

The adoption of Plant Phenomics has been a global phenomenon over the last decade with a burgeoning number of "Phenomics Centres" promising next-generation solutions to high-throughput phenotyping for gene discovery and breeding. It is gratifying that discussions at Plant Phenomics conferences have evolved from "how many plants can you pass through your imaging system?" or "what is the payload of your drone?" to "what is the genetic discrimination of that phenotyping pipeline for drought tolerance" or "how heritable is that trait surrogate?". Fit-for-purpose, affordable solutions for plant phenotyping will no doubt have the greatest impact on crop breeding over the next decade. It is also worthy of note that, while controlled environment, image-based phenotyping platforms have been gaining popularity in almost every corner of the globe, the majority of crop breeding occurs in the field with little if any selection in controlled environments.

What will breeding of our major cereal crops look like in the year 2050; the date when the human population is predicted to reach 10 billion? Given the rapid pace with which sequencing, phenotyping technologies, robotics and artificial intelligence are progressing, it is hard to escape the conclusion that an "in-silico" breeding platform will result from these advances. Agriculture has been oddly resistant to digital disruption until relatively recently but adoption of "digital agriculture" in all its forms is now rapid and widespread (Walter *et al.*, 2017). Already, mining allelic diversity through genome sequence and high-resolution, high-throughput phenotyping in combination with the use of crop models to predict trait value (Keating *et al.*, 2003) is not only "doable" but commercially proven in maize (Cooper *et al.*, 2014). We are currently amassing large sequenced or at least well genotyped collections of diverse rice (Wang *et al.*, 2018), wheat, sorghum (Mace *et al.*, 2013) and maize accessions (http://seedsofdiscovery.org/). Matching this wealth of allelic diversity to phenotypic data could result in a massive atlas of material to be used in cereal pre-breeding and breeding. The data fabric to enable crop breeders to utilise this wealth of information, however, is still a work in progress.

One can envisage a very near future where a breeder may not only walk his trial plots assessing germplasm using his "human spectrometer" but utilise the phenome / genome atlas to refine genome selection models, guide selection of parents in crosses, or target a new set of CRISPR-Cas constructs for genome engineering (Feng *et al.*, 2017; Ricroch *et al.*, 2017).

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# Tables

Table 1: Summary of traits amenable to field phenotyping and the primary effect contributing to yield.

| Trait | Primary Effect | Sensor Technology |
|---|---|---|
| *Canopy structure* | | |
| Height | HI/WUE/RUE | LiDAR, 2D and 3D RGB photogrammetry |
| Fraction of canopy ground cover and instantaneous fAPAR | RI/WUE | LiDAR, 2D and 3D RGB photogrammetry, spectral vegetation indices, pyranometer |
| Biomass and crop growth rate | WUE/RUE | LiDAR, 2D and 3D RGB photogrammetry, spectral vegetation indices |
| Stem strength / lodging tolerance | HI | LiDAR, 2D and 3D RGB photogrammetry |
| Plant and head number | HI | LiDAR, 2D RGB photogrammetry, multi spectral camera & machine learning |
| *Function* | | |
| Canopy photosynthesis | RUE | Estimation from biomass and fAPAR accumulation (see above), instantaneous high-resolution hyperspectral sensor (in-filling of O2 band) to measure SIF |
| Stomatal conductance | WUE/RUE | Thermal camera, infrared temperature sensor |

RI = radiation interception; RUE = radiation use efficiency; WUE = water use efficiency; HI = harvest index; fAPAR = fraction of incident photosynthetically active radiation absorbed; SIF = sun induced chlorophyll fluorescence; RGB = red, green and blue.

# Figure captions

**Figure 1: Ideotype breeding**
Five key traits identified for a wheat breeding ideotype. Yield gains in harvest index (HI) have been obtained by the “green revolution” breeding strategies for grain number and dwarf stature, while future gains over and above these so-called “partitioning traits” are believed likely to come from improvements in productive biomass and associated radiation use efficiency. The value of each of these traits depends on the target environment.

**Figure 2: Linking genome and phenome**
Flowchart to show how genomics and phenomics can be used in combination to enhance both crop breeding and more mechanistic research targeted to translational outcomes in crops. Genotyped diversity sets or mapping populations can be utilised in two ways. Phenome to Genome (P2G) approaches use high- throughput phenotyping tools to associate **S**ingle **N**ucleotide **P**olymorphisms (SNPs) and genomic regions with traits of proposed agronomic advantage in breeding for yield (which can be targeted to an environment and agronomic system via modelling approaches; i.e. **G**enotypeX**E**nvironmentX**M**anagement). In the current context, radiation use efficiency (RUE) trait targets might be photosynthetic capacity / efficiency, cooler canopies, digital biomass or growth rate, spectroscopic trait “surrogates” or raw digital data. QTLs, “perfect markers” or patterns of SNPs can be used directly in breeding programs for genetic gain or candidate genes identified for transgenic or gene-editing deployment. Genome to Phenome (G2P) utilises pre-existing mechanistic knowledge to identify candidate genes likely to be linked to traits of agronomic importance. In photosynthesis research, allelic variation in Rubisco, other enzymes of the Benson-Calvin cycle, chloroplast electron transport components or transcription factors known to control levels of photosynthetic proteins can be examined *in silico* across diverse sequenced populations. Diversity in these alleles is then compared with existing agronomic data and known QTLs to validate the importance of the SNPs identified. In both cases, proposed causative SNPs can be validated by making and comparing isogenic lines or “allele mimics” using gene editing. Material identified can be used directly in crossing, alleles used as gene-editing targets or SNP patterns included to enrich genome selection models. MAS, marker-assisted selection.

**Figure 3: LiDAR profiles of wheat canopies**
Evolution of the vertical profiles of LiDAR point density for five different wheat genotypes (identified as 1001, 1003, 1005, 1007, 1009) at 10 different dates (from 2017-06-05 to 2017-08-21). The dimension of the X-axis represents the fraction of LiDAR points intercepted by the canopy at a particular height (Y-axis).

**Figure 4: Tractor based proximal crop sensing platform**
Tractor-based platform used in Queensland Australia to screen diverse sorghum mapping populations for radiation use efficiency (RUE). 1) infrared thermal camera 2) hyperspectral line scanner (3) LiDAR 4) downward pointing spectrometers (two pointing to planted rows and one to interrow) 5) infrared radiometers and ultrasonic sensors 6) spectrometer hub 7) thermal radiometer hub 8) power hub 9) Global Positioning System (GPS) and computer 10)

upward pointing spectrometer (to detect direct solar radiance) 11) GPS antenna 12) tractor 13) weather station (on site)

**Figure 5: Canopy temperature sensing**
Manned helicopter for airborne canopy temperature (CT) comprising white cargo pod mounted on skid of helicopter with high-resolution thermal camera inside (a). Visualisation of airborne CT obtained using (a) travelling in a single pass above an experiment comprising advanced wheat breeding lines grown in 2x6m plots (b). The rectangles denote the area sampled from a given plot with darker hues associated with cooler canopies. The red hues denote the warmer soil between the plots. (c) ArduCrop wireless infrared sensors for continuous CT measurement. (d) Visualisation of CT time-course across two days for three elite wheat varieties.

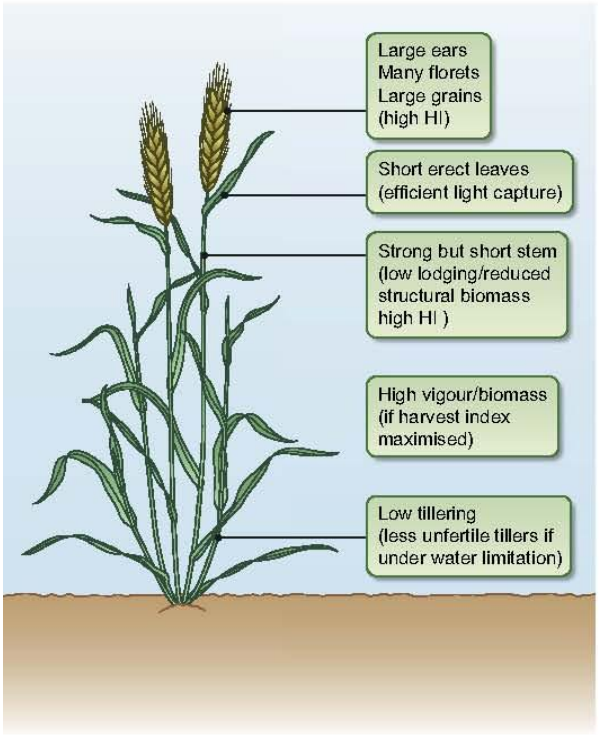


Figure 1

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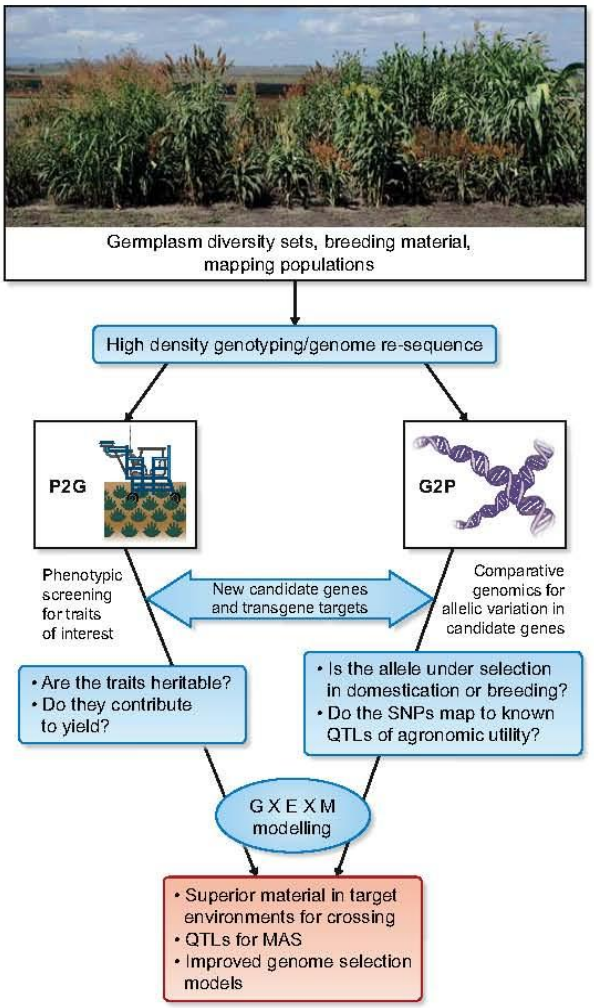


Figure 2

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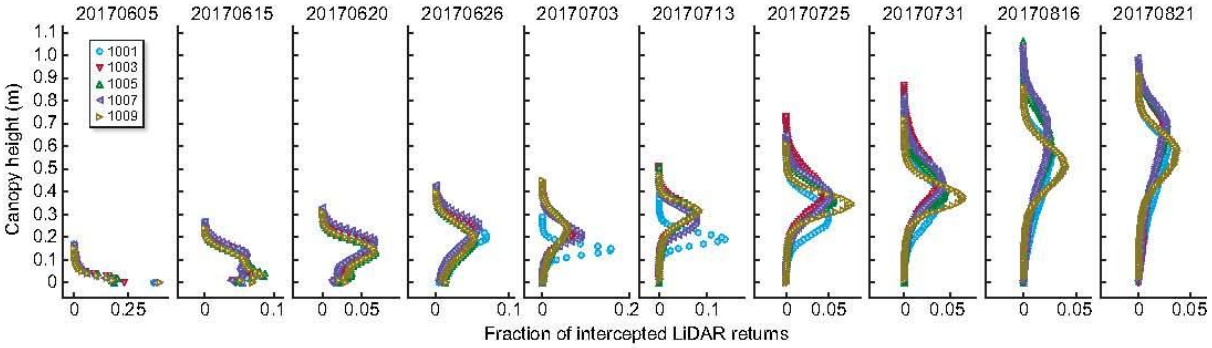


Figure 3

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Figure 4

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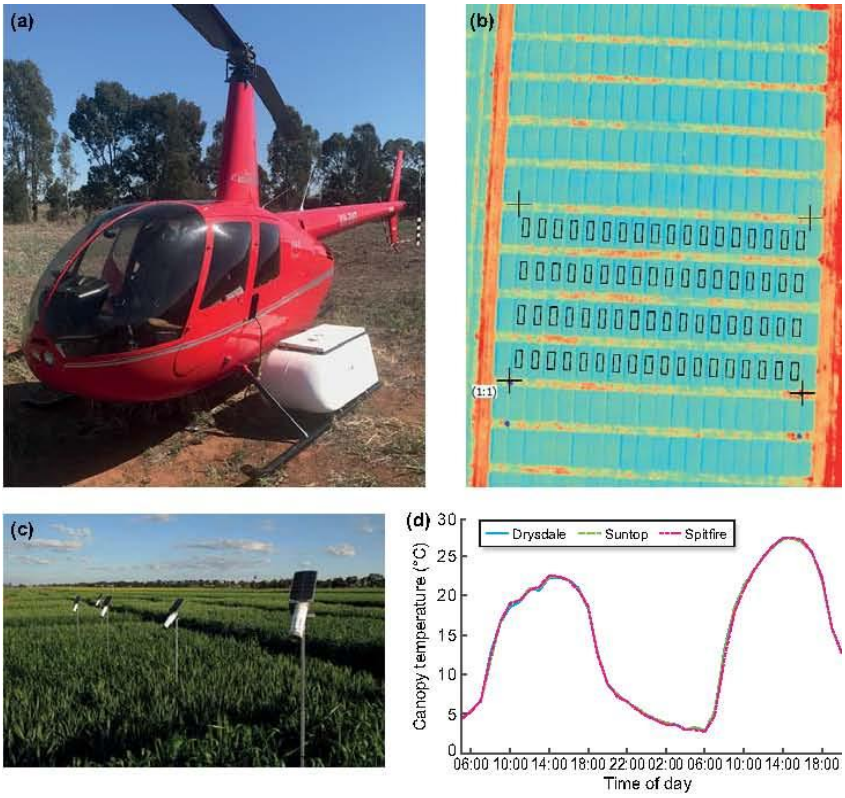


Figure 5

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