Physiology of Growth, Development and Yield

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Abstract

Crop growth is a dynamic process whereby the sorghum plant germinates, emerges and begins to capture solar radiation and, via photosynthesis, accumulate biomass. Interacting with its surrounding environment, the sorghum plant adapts to the various biotic and abiotic challenges on its journey towards flowering and, ultimately, seed production. We will explain the physiology of growth and yield in sorghum using a framework based on crop growth and development. The process of evolution has enabled plants to utilise a variety of timing mechanisms that regulate development, improving the chance that germination and reproduction are aligned with favourable periods of growth. Crop development is predominantly affected by photoperiod and temperature. In contrast, crop growth, which represents the biomass produced, is predominantly affected by incoming radiation. Grain yield can be defined as the product of resource capture (light, water and nitrogen), resource use efficiency and partitioning of that resource into grain. Since water limitation is the key constraint to sorghum yield globally, crop growth will be considered in the context of water-limiting and non-limiting scenarios. In the absence of water limitation, the sorghum crop is largely limited by radiation, and in this scenario, biomass accumulation is the product of intercepted radiation and its conversion efficiency, the radiation use efficiency (RUE, biomass produced per unit of radiation intercepted). When water is a limitation, biomass accumulation under drought stress becomes a function of the total amount of water used by a crop (transpiration, T) and the transpiration efficiency (TE, biomass produced per unit of water transpired). For the first time in history, we now have the tools to measure physiological traits, such as dynamic biomass growth or canopy radiation use efficiency at a high-throughput scale that can match the genomic data. These new tools will allow us to phenotype thousands of lines that breeders have previously genotyped in multi-location field trials, a pre-requisite for the unravelling of the molecular basis of complex traits via association mapping approaches. This is particularly pertinent in sorghum due to its importance as a cereal for food, feed and fuel, especially in dry-land cropping systems.

Keywords

Crop physiology · Biomass accumulation · Light interception · Nitrogen dynamics · Panicle initiation · Radiation use efficiency · Transpiration efficiency · Water use

1 Introduction

Crop growth is a dynamic process whereby the sorghum plant germinates, emerges and begins to capture solar radiation and, via photosynthesis, accumulate biomass. Along the way, the sorghum plant interacts with the surrounding environment, adapting to the various biotic and abiotic challenges on its journey towards flowering and, ultimately, seed production.

Grain yield can be defined as the product of resource capture, resource use efficiency and partitioning of that resource into grain. We will explain the physiology of growth and yield in sorghum using a framework based on crop growth and development, drawing on learnings from the APSIM crop simulation model (Hammer et al. 2010; Holzworth et al. 2014). This approach quantifies the capture and use of radiation, water and nitrogen within a framework that predicts the growth of major organs based on their potential and then considers whether the supply of key resources (light, water and nitrogen) can, in fact, satisfy that potential demand (Hammer et al. 2010). The efficiency with which these resources are captured and utilised to produce carbohydrate (biomass), and the extent to which the biomass is ultimately partitioned into grain yield, will also be examined. Since water limitation is the key constraint to sorghum yield globally (Jordan et al. 2012; Borrell et al. 2014b), crop growth will be considered in the context of water-limiting and non-limiting scenarios. In the absence of water limitation, the sorghum crop is largely limited by radiation.

Progress in crop improvement is constrained by the capacity to identify favourable combinations of genotypes (G) and management practices (M) in the relevant target environments (E) given the limited resources available for searching all possible combinations (Hammer et al. 2010). Phenotypic performance of possible combinations can be viewed as an adaptation or fitness landscape (Cooper and Hammer 1996) and crop improvement can be viewed as a search strategy on that complex G × M × E landscape. Understanding the physiological basis of crop growth and yield will help to navigate this complex landscape by better integrating gene effects across scales of biological organisation (Hammer et al. 2016). As demonstrated in Australia's sorghum growing belt, the interactions between genetics and environment are confounded by differences, both spatially and seasonally, in crop water supply such that any given set of hybrids in a random set of locations would be ranked differently from season to season (Chapman et al. 2000).

2 Crop Phenology

Successful sorghum genotypes must match their phenology to prevalent environmental conditions in order to minimise adverse effects of abiotic stresses on crop growth and grain yield. However, to achieve such success, particular attention must be paid to the timing and extent of reproductive development. Shoot and root apical meristems have the capacity for unlimited growth along the axis of the elongating plant (Connor et al. 2011). Meristems transition from production of leaves to flowers, responding directly to environmental signals of temperature and daylength, and indirectly to environment through assimilate supply.

The process of evolution has enabled plants to utilise a variety of timing mechanisms that regulate development, improving the chance that germination and reproduction are aligned with favourable periods of growth. Distinct developmental events such as “emergence”, “floral initiation” and “flowering” are termed *phenostages*. *Developmental rate* ($1/t$) is the rate of advance within *phenophases*, and *phenology* is the study of progress of crop development in relation to environmental conditions (Connor et al. 2011). The switch from initiation of leaves to flowers in shoot meristems at a certain developmental stage can occur as a specific response to temperature and/or daylength (photoperiodism) in sorghum. Not surprisingly, plants have evolved adaptive responses to daylength, since it is precisely and invariably related to latitude and day of year (Connor et al. 2011).

Crop phenology is determined by the rate of development, which represents the ‘age’ of a plant and is predominantly affected by photoperiod and temperature (Caddel and Weibel 1971; Quinby et al. 1973; Gerik and Miller 1984; Hammer et al. 1989; Craufurd et al. 1999; Clerget et al. 2008; Ravi Kumar et al. 2009). In contrast, crop growth, which represents the biomass produced, is predominantly affected by incoming radiation (Hammer et al. 2010).

Cereal crop phenology is described by a number of well-defined development stages, which include (1) germination, (2) emergence, (3) panicle initiation (PI), (4) full flag leaf appearance, (5) anthesis, (6) start grain filling and (7) physiological maturity. Most phases between these stages have their own thermal time target (Muchow and Carberry 1990), with thermal time calculated from daily maximum and minimum temperature via a broken linear function that defines the response to temperature in terms of a base (T_b), optimum (T_{opt}) and maximum (T_m) temperature (Hammer and Muchow 1994). The T_b represents the temperature below which the rate of development is zero, T_{opt} the temperature at which the rate of development is maximum, and T_m the temperature above which the rate of development is zero again. These critical temperatures are called cardinal temperatures.

2.1 Emergence to Panicle Initiation

Panicle initiation marks the moment the apical meristem changes from initiating leaves to initiating florets. The duration of the phase from emergence to PI depends on both temperature and photoperiod and is important to phenology, as it determines the total leaf number (TLN) initiated on the main shoot and hence the timing of anthesis.

For the response to temperature of the rate of development of sorghum prior to anthesis, cardinal temperatures of 11, 30 and 42 °C for T_b, T_{opt} and T_m, respectively, have been reported (Alagarswamy et al. 1986; Hammer et al. 1993; Ravi Kumar et al. 2009). However, significant genotypic differences in T_b for this period have been observed (Craufurd et al. 1999; Tirfessa Woldetensaye 2019), with some indications that *caudatum* and Ethiopian highland *durra* genotypes have significantly lower T_b (range 0–7 °C) than *caudatum/guinea* and *kafir* genotypes (range 7–10 °C) (Tirfessa Woldetensaye 2019).

The thermal time target for the phase between emergence and PI is also a function of daylength (Hammer et al. 1989; Ravi Kumar et al. 2009), with photoperiod-sensitive genotypes flowering progressively later once daylength exceeds a threshold duration (Craufurd et al. 1999; Ravi Kumar et al. 2009). The flowering response of plants to daylength is called *photoperiodism*. Day-neutral plants (DNP) are insensitive to daylength, with time to flowering controlled by temperature only. However, plants generally respond to various combinations of changing photoperiod (Roberts and Summerfield 1987; Connor et al. 2011). Sorghum is a short-day plant (SDP), i.e. flowers in response to shortening days (lengthening nights). Variation in the response of sorghum to photoperiod and temperature determines its adaptation to the large range of different environments in which it is grown (Craufurd et al. 1999). A crop's adaptation to latitude is primarily determined by photoperiod responses.

For sorghum adapted to temperate conditions, photoperiod sensitivity has largely been removed through selection (Stephens et al. 1967). For tropically adapted sorghum, however, presence of photoperiod sensitivity is associated with both racial background and eco-geographical conditions. The highly photoperiod-sensitive germplasm used in West Africa is predominantly *guinea* type (Rattunde et al. 2013), and is adapted to a rainy season with a variable onset but a much more distinct end (Kouressy et al. 2008; Frappart et al. 2009). In addition, an association between latitude and photoperiod sensitivity exists within sorghum races, and for latitudes up to 20°N, the *guinea* race has a greater proportion of germplasm with medium to high photoperiod sensitivity than the *caudatum*, *durra*, and particularly *kafir* races (Grenier et al. 2001).

The number of leaves initiated during the phase between emergence and PI depends on the duration of the phase (°Cd) and the leaf initiation rate (LIR, °Cd/leaf). Assuming a T_b of 11 °C, the LIR of sorghum is ~21.6 °Cd/leaf, although genotypic variation for this parameter does exist (Hammer et al. 2010). As sorghum seeds already have four leaves initiated in the embryo (Paulson 1969), the TLN produced is four plus the number of leaves initiated between emergence and PI.

2.2 Emergence to Flag Leaf Appearance

The time from emergence to full flag leaf appearance depends on the TLN and the leaf appearance rate (LAR). Hence, the period from PI to flag leaf does not have a specific thermal time target, and its duration is rather an emergent property of TLN and LAR. In sorghum, a leaf is fully expanded when its ligule is visible above the ligule of the previous leaf. In general, leaves appear at a constant rate, which is approximately half the LIR (Hammer et al. 2010; Ravi Kumar et al. 2009). There is some evidence of genotypic differences in LAR. Tx642 (B35), a *durra* landrace from Ethiopia, has consistently been shown to have a high LAR (Borrell et al. 2000a; van Oosterom et al. 2011). This high LAR is likely associated with a low T_b for LAR, as there is some evidence of genotypic differences for this trait, with *caudatum* and Ethiopian highland *durra* germplasm having lower T_b than *kafir* germplasm (Tirfessa Woldetensaye 2019). These genotypic and racial differences in T_b for LAR align with differences in T_b for rate of development, but importantly, some *caudatum* and Ethiopian highland *durra* genotypes with low T_b for both processes tend to have a significantly higher T_b for LAR than for rate of development (Tirfessa Woldetensaye 2019). Because LAR is highly coordinated with LIR (Padilla and Otegui 2005), these differences in T_b are likely to extend to LIR. If a genotype has a higher T_b for LAR (LIR) than for rate of development, an increase in temperature between emergence and PI will increase TLN (van Oosterom et al. 2011; Tirfessa Woldetensaye 2019). Such an increase in TLN under high temperatures will partly offset the increased LAR. In contrast, for genotypes that have similar T_b for LAR and rate of development, such as some *kafir* genotypes (Tirfessa Woldetensaye 2019), TLN will be independent of temperatures between emergence and PI. Such genotypic differences in response of TLN to temperature can affect the response of time to flowering to increasing temperatures under climate change.

Abiotic stresses like drought and nitrogen can delay flowering through a reduction in the rate of development and of LAR (Craufurd et al. 1993; van Oosterom et al. 2010a). These effects are temporary, and upon relief from stress, these rates revert to those for non-stressed conditions (Craufurd et al. 1993).

2.3 Flag Leaf to Physiological Maturity

The duration of the phases between the stages of flag leaf, anthesis, and start and end of grain filling are all considered to have thermal time targets (Muchow and Carberry 1990; Hammer and Muchow 1994; Ravi Kumar et al. 2009; Hammer et al. 2010). Time from flag leaf appearance to anthesis is generally quite conserved across genotypes (Ravi Kumar et al. 2009). If stress is sufficiently severe that elongation of the peduncle is affected, flowering can happen within the boot.

Grain fill generally starts around 4 days after flowering and ends at physiological maturity (black layer). Post-anthesis cardinal temperatures for rate of development differ substantially from those before anthesis, and have been identified as 5.7 °C and 23.5 °C for T_b and T_{opt}, respectively (Hammer and Muchow 1994). There is no evidence of genotypic differences for these cardinal temperatures (Ravi Kumar et al. 2009; Tirfessa Woldetensaye 2019). However, significant genotypic differences in the duration of the grain filling period do exist (Ravi Kumar et al. 2009; Hammer et al. 2010) and these can be associated with differences in grain size (Yang et al. 2010).

2.4 Development of Tillers

The first basal tillers typically appear from the axil of Leaf 3 on the main shoot, when about four main shoot leaves have fully expanded (Lafarge and Hammer 2002a, b). Successive tillers appear at a rate similar to the main shoot LAR, and the LAR of tillers is similar to that of the main shoot (Carberry et al. 1993; Lafarge and Hammer 2002a, b; Kim et al. 2010a, b). Despite the late emergence of tillers compared to the main shoot, PI of tillers occurs only a few days after that of the main shoot (Craufurd and Bidinger 1988). Successive tillers progressively have fewer leaves (Carberry et al. 1993; Kim et al. 2010b), which offsets their later emergence, such that tillers typically reach flowering only a few days after the main shoot (Craufurd and Bidinger 1988). Phenology of tillers is thus highly synchronised with that of the main shoot.

3 Biomass Accumulation Under Well-Watered Conditions

Under well-watered conditions, biomass accumulation is limited by radiation and is the product of intercepted radiation and its conversion efficiency, the radiation use efficiency (RUE, biomass produced per unit of radiation intercepted). The amount of radiation intercepted by a crop is the product of incoming radiation and the fraction that is intercepted by the crop, which in turn depends on the leaf area index (LAI) and on the arrangement of foliage or canopy architecture (Connor et al. 2011). Despite its empirical nature, RUE is theoretically closely associated with leaf photosynthesis (Wu et al. 2016; Hammer and Wright 1994). When water or nutrients are non-limiting, productivity is thus reduced by either incomplete capture of radiation and/or less efficient utilisation (Connor et al. 2011).

3.1 Canopy Development

Canopy development, which represents the dynamics of LAI over time, depends on the number of leaves that has been produced on each shoot, the number of tillers, the individual leaf size and the plant density (Hammer et al. 2010). The green LAI is the balance between the total leaf area and the amount of leaf area that has senesced.

The number of fully expanded leaves is the product of thermal time elapsed since emergence, and the leaf appearance rate (LAR). The rate of tiller appearance is highly coordinated with the LAR (Kim et al. 2010b). Each tiller has a window of one phyllochron during which it can appear (Kim et al. 2010b), but actual emergence is contingent on the availability of sufficient excess assimilates during this window (Kim et al. 2010a; Alam et al. 2014). Because high radiation will increase assimilate supply, whereas low temperatures will increase the duration of a phyllochton, this supply/demand framework can explain reduced tillering under high plant density, when radiation interception per plant is low, and high tillering following sowing early in spring, when temperatures tend to be relatively low. The framework can also explain some of the genotypic differences in tillering, as high LAR shortens the window during which a tiller can appear, and thus reduces the capacity for sufficient assimilate accumulation. Moreover, high LAR, like large leaves, increases assimilate demand by the main shoot, potentially reducing excess assimilate availability for tillering (van Oosterom et al. 2011; Borrell et al. 2014a). In addition, genotypic differences in the propensity to tiller have been reported that are independent of the supply/demand balance and these are likely under hormonal regulation (Kim et al. 2010a; Alam et al. 2014). Auxin, cytokinin and strigolactones can each affect tillering, partly through an effect on apical dominance (Beveridge 2006; Gomez-Roldan et al. 2008; Ongaro and Leyser 2008; Umehara et al. 2008; McSteen 2009).

The size of individual leaves in sorghum is closely related to the rank of that leaf and can be described by a bell-shaped function, the parameters of which are a function of TLN (Carberry et al. 1993). Both the leaf length and leaf width increase linearly with leaf rank, resulting in an exponential increase in the size of successive leaves, until a maximum leaf size is reached (Lafarge and Hammer 2002a, b; Kim et al. 2010b). The position of the largest is a function of TLN and is generally located just below the flag leaf (Carberry et al. 1993). Genotypic differences in individual leaf size have been reported for sorghum and these are predominantly associated with differences in leaf width (Kim et al. 2010a; Alam et al. 2014). Leaf area profile of tillers can be derived from main shoot (Lafarge and Hammer 2002b). Canopy development is therefore the emergent consequence of a complex interaction between genotypic (G), environmental (E), and management (M) conditions and their G × E × M interactions.

3.2 Light Interception

Intercepted radiation is generally defined as the difference between that received at the canopy surface and that transmitted through the canopy, as measured by arrays of solarimeters (Squire 1990). The magnitude of total incoming solar radiation varies greatly throughout the tropics and sub-tropics where sorghum is often grown, with seasonal means ranging from 12 MJ m^{-2} day^{-1} in cloudy regions to more than 24 MJ m^{-2} day^{-1} in semi-arid regions.

When water is not limiting, fractional radiation interception (f) may be related to the leaf area index (LAI) of a canopy by the expression $f = 1 - \exp(-k\,\mathrm{LAI})$, where k is an extinction coefficient (Squire 1990; Fig. 1). Therefore, the fraction of the solar radiation intercepted by a given leaf area increases with k. In practice, k can be calculated from the slope of a linear regression of $\ln(1 - f)$ on LAI. Overall, k is reasonably stable for a given genotype over a wide range of conditions, and may differ consistently among canopies with contrasting architecture (Squire 1990). This can be in response to leaf angle (Hammer et al. 2009), although plant stature appears

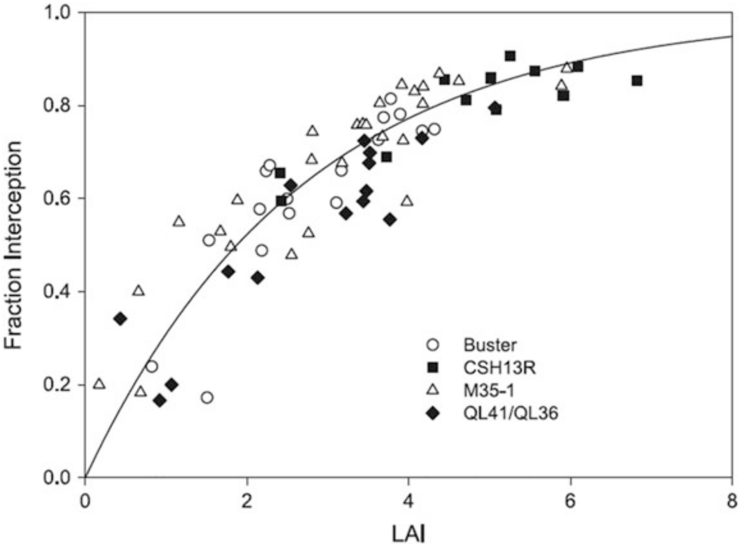


Fig. 1 The fraction of radiation intercepted (RI) versus leaf area index (LAI) for the set of non-limiting water and N experiments that included both Buster and M35–1. The fitted curve ($RI = 1 - e^{-k\ LAI}$, $R^2 = 0.91$) indicates a common extinction coefficient (k) of 0.37. (Source: Hammer et al. 2010)

to have limited effect on the extinction coefficient (Hammer et al. 2010). For sorghum, k values in the range of 0.33–0.39 have been reported (Hammer et al. 2010; George-Jaeggli et al. 2013), although Lafarge and Hammer (2002a) reported a higher value of 0.56. These values indicate that at $LAI = 4$, light interception is over 80% of that at $LAI = 7$, indicating that early canopy cover provides a useful means to maximise cumulative radiation interception.

3.3 Radiation Use Efficiency (RUE) and Leaf Photosynthetic Activity

Radiation use efficiency is generally presented as the biomass produced per unit of intercepted total solar radiation, about 50% of which is photosynthetically active radiation. Under optimum conditions, the RUE of triple dwarf short sorghum is about 1.25 g MJ^{-1} (Sinclair and Muchow 1998; Hammer et al. 2010). However, significantly greater RUE of 1.65 g MJ^{-1} has been observed for taller single dwarf sorghum (Hammer et al. 2010). Although there is a trend for mutations of the *dw3* height gene to increase RUE, this effect is context-dependent (George-Jaeggli et al. 2013). RUE is a function of the N-status of the leaves and for sorghum, RUE tends to decline once the specific leaf nitrogen (SLN) of the canopy drops below 1 g m^{-2} (Muchow and Sinclair 1994).

Causes for the genotypic differences in RUE in sorghum are still poorly understood. Although RUE is conceptually linked to leaf photosynthesis (Wu et al. 2016; Hammer and Wright 1994), differences in RUE do not necessarily translate to differences in photosynthetic rates. This was illustrated by Muchow and Sinclair (1994), who showed that triple dwarf sorghum had similar maximum assimilation rates as maize (~52 μmol m^{-2} s^{-1}), despite having a lower RUE (1.20 vs 1.70 g MJ^{-1}). Reduced internal CO_2 (c_i) concentration in the leaf, associated with reduced stomatal conductance, can reduce assimilation rates to values below the maximum photosynthetic capacity (Condon et al. 2004). Significant genotypic differences in c_i have been reported for sorghum, which were generally positively associated with stomatal conductance (g_s) (Xin et al. 2009). In addition, Geetika et al. (2019) reported genotypic differences in g_s, with above-average g_s generally associated with above-average photosynthetic capacity. Hence, scope exists to improve the photosynthetic capacity of sorghum and simulation studies have indicated that an increase in photosynthetic efficiency of 20% can increase grain yield of sorghum by ~9% under well-watered conditions, although yields are expected to be slightly less under drought stress (Wu et al. unpublished).

4 Biomass Accumulation Under Drought Stress

Drought stress is defined as the situation where supply (S) of water cannot meet demand (D) of the crop, such that water availability is the limiting factor for biomass accumulation. Under such circumstances, plants will need to reduce D in order to meet the limited S. Under mild stress, plants can achieve this by restricting the rate of leaf area expansion, resulting in smaller leaves or a reduced leaf appearance rate. If that does not sufficiently reduce demand, plants may senesce leaves to further reduce leaf area, and therefore D (Borrell et al. 2000a; Hammer et al. 2001; George-Jaeggli et al. 2017). As a consequence, biomass accumulation under drought stress becomes a function of the total amount of water used by a crop (transpiration, T) and the transpiration efficiency (TE, biomass produced per unit of water transpired) (Hammer et al. 2010). The fraction of biomass that is allocated to grain yield, however, depends on the amount of water available from anthesis onwards (Turner 2004). Hence, grain yield under drought can be increased by increasing (1) the total amount of water accessible to a plant throughout the cropping period, (2) the amount of water available during grain filling by restricting pre-anthesis water use, or (3) TE. This section will address the physiological processes and environmental conditions that determine these three factors. It will show that delayed leaf senescence (stay-green) in sorghum during grain filling can be a consequence of processes occurring earlier in crop growth (Fig. 2), resulting from an improved balance between the supply and demand of water, as well as the efficiency with which the crop converts water to biomass and grain yield (Borrell et al. 2009; Jordan et al. 2012). Stay-green has been shown to increase grain yield (Borrell et al. 2000b, 2014a, b), grain size (Borrell et al. 1999) and lodging resistance (Rosenow 1977) under post-anthesis drought.

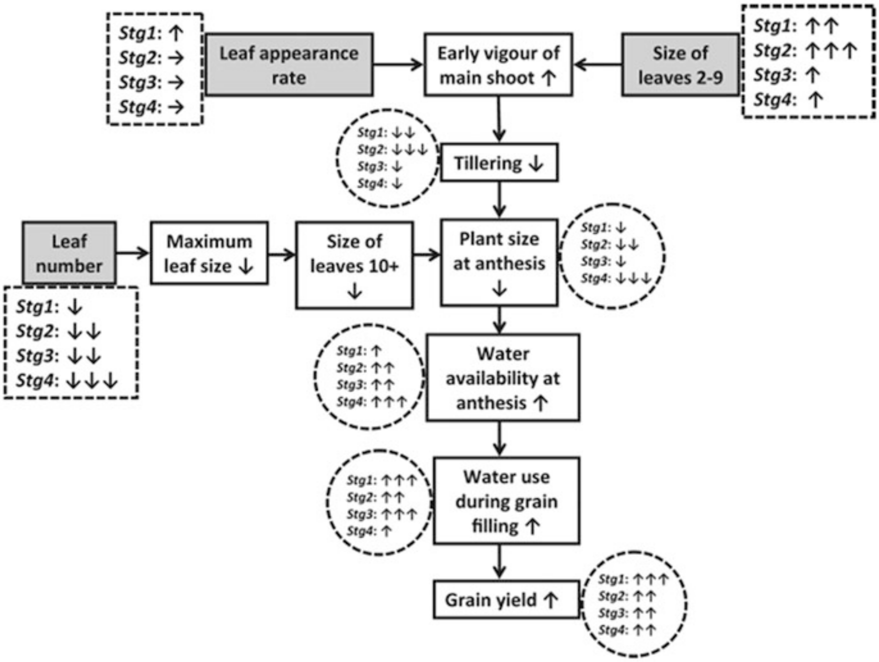


Fig. 2 Flow chart of crop physiological processes that determine plant size and crop water use of sorghum at anthesis, with flow-on consequences for water uptake during grain filling and grain yield. The effect of individual stay-green (*Stg*) quantitative trait loci (QTLs) on each process is indicated by arrows contained in either dotted squares (input traits; shaded grey) or dotted circles (derived traits). Upward arrow indicates increased size or number, downward arrow reduced size or number, and sideways arrow indicates no or little effect. The number of arrows represents the magnitude of the effect. The direction and number of arrows associated with each *Stg* QTL summarise the trait data from up to seven experiments and 14 environments relating to canopy development, grain yield and crop water use. (Source: Borrell et al. 2014a)

4.1 Increasing Total Transpiration

The total amount of water available to the crop can be increased by modifying the root system architecture of a plant (Manschadi et al. 2006). In sorghum, evidence exists that the spatial distribution of roots of mature plants is associated with the angle of the first flush of nodal roots, which appears when about five leaves have fully expanded (Singh et al. 2012). Plants with narrow root angle and more vertical nodal roots tend to have a larger proportion of their roots at depth during later developmental stages (Singh et al. 2012), which could increase access to water in deep soils. Conversely, genotypes with wider root angle and more horizontal nodal roots are better able to explore the soil in the inter-row space (Singh et al. 2012), which could increase access to water in skip-row systems (Whish et al. 2005). There is evidence that root angle is associated with stay-green, as root angle QTL co-locate with stay-green (*Stg*) QTL (Mace et al. 2012). Moreover, *Stg* QTL have been reported to increase total water use in field-grown crops (Borrell et al. 2014b). It is unlikely that increasing the root length density (RLD) in soil that is occupied by the root system will increase accessibility of water, as the RLD required to access all extractable water from the soil is relatively low at about 0.2 cm per cm^3 of soil volume (Robertson et al. 1993).

4.2 Restricting Pre-anthesis Water Use Through Reduced Canopy Size

Increasing post-anthesis water availability without increasing the total amount of water accessible to the plant can be achieved by restricting pre-anthesis water use, either through agronomic or genetic means. The skip-row planting configuration (Whish et al. 2005) provides an agronomic means to restrict pre-anthesis water use, as it generally takes time for roots to explore the soil under the skip row compared to a solid planting. Genetic means to minimise pre-anthesis water use include the selection for early flowering, which generally increases grain yield under end-of-season drought stress (Hammer et al. 2014). More recent strategies have emphasised the restriction of canopy size, either through smaller leaves or reduced tillering. Tillering can be restricted through a low propensity to tiller, likely regulated by hormones, or through vigorous main shoots (large leaf size or high leaf appearance rate), which alters the internal carbon S/D balance of the plant (Alam et al. 2014; Borrell et al. 2014a). The results of studies on near isogenic lines (NILs) involving sorghum *Stg* QTL found that *Stg* loci reduce canopy size at flowering by modifying tillering, leaf number and leaf size (Borrell et al. 2014a, b), although Vadez et al. (2011) found that this effect was dependent on the context of the genetic background in which they operated.

Early flowering also tends to reduce canopy size, through a reduction in the number of leaves produced (Hammer et al. 2010). However, this tends to have a yield penalty under well-watered conditions, where biomass accumulation is radiation limited and the shortened growth cycle limits cumulative intercepted radiation and thus biomass production and grain yield (Hammer et al. 2014). Restriction of canopy size through reduced tillering or leaf size is less likely to result in a yield penalty under well-watered conditions, provided the LAI reaches a value of at least 3, at which level most incoming radiation is intercepted by the crop (Hammer et al. 2010; Borrell et al. 2014a).

4.3 Restricting Pre-anthesis Water Use and Increasing Transpiration Efficiency

A more recent avenue that has been explored to restrict pre-anthesis water use is the restriction of transpiration rate per unit green leaf area (TGLA). TGLA depends on stomatal conductance (g_s) and the vapour pressure deficit (VPD) of the air, which determines the rate at which water is lost through the stomata to the atmosphere.

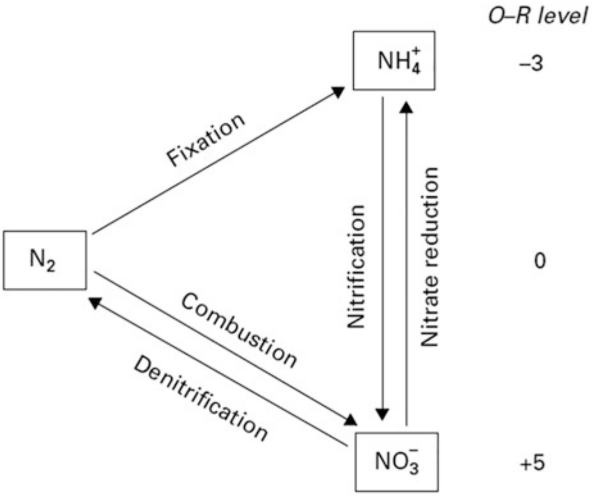
Stomata can close under high VPD (often associated with high temperatures), low radiation, or drought, resulting in reduced g_s (Geetika et al. 2019). Genotypic differences in TGLA have been reported for sorghum and these differences can be constitutive (independent of VPD), or adaptive, and only happen at high VPD (Gholipoor et al. 2013; Kholová et al. 2016; Geetika et al. 2019). Differences in whole-plant TGLA, in response to both environmental and genotypic effects, are closely related to differences in leaf-level stomatal conductance (g_s) (Geetika et al. 2019). Studies of stay-green NILs have found differences in leaf anatomy associated with variation in abaxial stomatal index and transpiration per leaf area among the lines (Borrell et al. 2014b). If low TGLA is associated with low g_s, then the slower diffusion rate of CO_2 through stomata compared to water vapour (von Caemmerer and Farquhar 1981) means that reduced g_s is likely to increase TE as an emergent consequence. This has been observed experimentally in wheat (Li et al. 2017) and through simulation studies in sorghum (Sinclair et al. 2005), and may explain the generally higher TE of sorghum under drought stress, compared with well-watered conditions (Donatelli et al. 1992; Mortlock and Hammer 1999; Kholová et al. 2010). Low TGLA will restrict pre-anthesis water use, particularly under high VPD, and simulation studies in both sorghum (Sinclair et al. 2005) and maize (Messina et al. 2015) have shown that this can increase post-anthesis water availability and hence grain yield under drought stress, although the restriction in gas exchange will lead to a yield penalty under well-watered conditions (Sinclair et al. 2005; Messina et al. 2015).

5 Nitrogen Uptake and Dynamics

Sorghum requires large quantities of nitrogen (N) to achieve maximum yields (Gelli et al. 2014), yet soil fertility is low in many regions where sorghum is grown. Nitrogen, an essential macronutrient affecting crop growth and development, is an important component of chlorophyll, amino acids, nucleic acids and secondary metabolites (O'Brien et al. 2016). Plants take up N from two sources: (1) N supply from the mineralisation of soil organic matter, biological N fixation and atmospheric deposition, and (2) applied N in manure, compost and mineral fertilisers (Connor et al. 2011). Nitrogen in soil organic matter and other organic forms is largely unavailable to higher plants. Therefore, mineral forms such as ammonium (NH_4^+) and nitrate (NO_3^-) are the primary N sources for uptake by crops (Connor et al. 2011; O'Brien et al. 2016; Fig. 3). Plants have developed sophisticated mechanisms to ensure adequate supply of nutrients in a variable environment because nitrate and other N nutrients are often limiting (O'Brien et al. 2016).

Unlike other elements, N must come from outside the plant–soil system since it cannot be released from rocks into the soil solution (O'Brien et al. 2016). High-yielding crop production systems remove N from the soil and rely heavily on application of large quantities of nitrogenous fertilisers for sustained productivity. Unfortunately, a large proportion of the N applied to crops is not directly absorbed by plants and is lost by leaching (Hirel et al. 2011) and other mechanisms. N-use

Fig. 3 Oxidation–reduction levels of nitrogen in nitrate (NO_3^-) and ammonium (NH_4^+) ions and dinitrogen gas (N_2) and the transformations between these important levels. Nitrite (NO_2^-) lies at +3 in most pathways to and from nitrate but has been omitted for simplicity. (Source: Connor et al. 2011)



efficiency for crops has not substantially improved over the last 50 years, despite considerable efforts by the scientific community (Cassman et al. 2002). Beyond the economic costs caused by applying large quantities of fertiliser, the high levels of N used in agriculture result in an array of environmental problems (Hirel et al. 2007; Galloway et al. 2008), including eutrophication of terrestrial and aquatic systems, global acidification and stratospheric ozone loss (Gruber and Galloway 2008). Therefore, understanding how plants sense, uptake, use and respond to N nutrients and metabolites is critical (O'Brien et al. 2016) for sorghum cropping systems.

5.1 N Dynamics Pre-anthesis

N uptake in cereals is closely related to canopy development (Borrell et al. 1998; van Oosterom et al. 2010a) and sorghum N dynamics are thus driven by physiological processes that account for the observation that most of the reduced N present in leaves is associated with photosynthetic structures and enzymes (Grindlay 1997). The rate of light-saturated net photosynthesis increases with the amount of leaf N per unit leaf area (specific leaf nitrogen, SLN), up to a critical SLN above which the maximum rate of photosynthesis is reached (Sinclair and Horie 1989; Anten et al. 1995; Grindlay 1997) and the rate of CO_2 fixation under radiation-saturated conditions becomes limited by Rubisco activity, chloroplast electron transport rate, or substrate regeneration (von Caemmerer and Furbank 2016). The N profile within a canopy is a function of the light penetration into the canopy, resulting in lower optimum SLN for photosynthesis at increasing depth in the canopy (Hirose and Werger 1987; van Oosterom et al. 2010a; Tominaga et al. 2015). Because the response of SLN to light is independent of the phenological stage (van Oosterom et al. 2010a), crop-level SLN tends to decline gradually as the canopy expands.

Similarly, the maximum, critical and minimum SLN values are independent of development stage (van Oosterom et al. 2010a). Therefore, expressing crop N demand relative to canopy expansion provides a physiological link between crop N status, light interception and dry matter accumulation (Grindlay 1997). Based on these concepts and experimental observations (van Oosterom et al. 2010a, b), a predictive model for N-dynamics in sorghum has been developed (Hammer et al. 2010). Its veracity has been validated in maize (Soufizadeh et al. 2018), which like sorghum is a C_4 monocot. Extrapolation of the framework to C_3 crops must be done with care though, as C_4 species respond to N-stress by maintaining leaf size (resource capture) and reducing SLN (resource use efficiency), whereas C_3 species reduce leaf size and maintain SLN (Vos and van der Putten 1998; Vos et al. 2005; Lemaire et al. 2008).

During the pre-anthesis period, the N demand of leaves and stems is met in a hierarchical manner (Hammer et al. 2010; van Oosterom et al. 2010a). First, structural N demand of the stem (and rachis) is met, which is required to support leaf growth and is represented by the minimum stem N%. If insufficient N has been taken up to meet structural stem N requirement, N can be translocated from leaves by dilution, or even leaf senescence if the minimum SLN is reached. Second, the N demand of expanding new leaves is met, which is represented by critical SLN. Any additional N uptake will first be allocated to leaves to meet their target (maximum) SLN and then to stems. For leaves, this luxury N uptake occurs after full expansion of a leaf and does not affect growth and development (van Oosterom et al. 2010a), although it can delay leaf senescence during grain filling (van Oosterom et al. 2010b). This hierarchical allocation of N can capture the observed larger proportion of N allocation to leaves under N-stress compared to high-N conditions (van Oosterom et al. 2010a) as an emergent consequence of N-stress.

The daily rate of crop N uptake is the minimum of demand for N by the crop and potential supply of N from the soil and senescing leaves, capped at a maximum N uptake rate (van Oosterom et al. 2010b). Two separate classes of NO_3^- influx transporters exist: high-affinity (HATS) and low-affinity transport systems (LATS) (Crawford and Glass 1998). Root NO_3^- influx is strongly upregulated by N limitation, and conversely, downregulated by high N supply (Lee 1993), suggesting a feedback regulation of root NO_3^- transporters by the plant's N status (Imsande and Touraine 1994). Root NO_3^- uptake is also dependent on photosynthesis, exhibiting significant diurnal rhythms attributed to a positive regulation by shoot-to-root transport of sugars (Delhon et al. 1995). In the absence of genotypic differences in the maximum rate of N uptake, genotypic differences in N allocation can be an emergent consequence of differences in organ size. Tall genotypes with larger stem size require more structural stem N than shorter genotypes, leaving less N available for luxury leaf N uptake, resulting in lower SLN (van Oosterom et al. 2010a). Similarly, genotypes with larger leaf area are likely to dilute leaf N, resulting in lower SLN (Hammer et al. 2010; van Oosterom et al. 2010a). Such lower SLN in response to differences in organ size can have profound effects on post-anthesis N dynamics and hence on the ability of a crop to retain green leaf area during grain filling (Borrell and Hammer 2000; Borrell et al. 2001; van Oosterom et al. 2010b).

5.2 N Dynamics Post-anthesis

After anthesis, the total N demand of grains, which are the major sink for N, is the product of grain number and N demand per grain. During the first part of grain filling, when endosperm cells are dividing and structural (metabolic) proteins accumulate in the grain (Martre et al. 2003), N demand per grain is independent of the rate of biomass accumulation per grain and of the N status of the crop (van Oosterom et al. 2010b). During the second half of grain filling, however, when grain growth is due to cell division (Martre et al. 2006) and storage proteins accumulate in the grains, the N uptake rate per grain is limited by the rate of biomass accumulation per grain (van Oosterom et al. 2010b). As a consequence, the reduced N content per grain under N stress will be predominantly associated with a decline in storage proteins (Martre et al. 2003). This framework provides a link to environmental effects on grain quality.

Grain N demand is initially met through stem (plus rachis) N translocation, and only if this is insufficient does leaf N translocation occur. Maximum N translocation rates from stem and leaves are a function of the N status of these organs and follows a first-order kinetic relationship, such that the translocation rate declines with declining N content and the amount of leaf area that is senescing at any one time will increase with declining SLN (van Oosterom et al. 2010b).

This framework can explain the observation that sorghum genotypes with high SLN at anthesis tend to have an ability to maintain green leaf area during grain filling (Borrell and Hammer 2000). At a leaf level, longevity of photosynthetic apparatus is intimately related to N status. For example, near-isogenic lines (NILs) containing particular stay-green chromosomal regions (*Stg2*, *Stg3* and *Stg4*) exhibited delayed onset and rate of senescence under post-anthesis water deficit compared to the senescent sorghum line RTx7000 (Harris et al. 2007). At a cell level, the retention of chloroplast proteins such as LHCP2, OEC33 and Rubisco until late in senescence has been reported in sorghum containing the KS19 source of stay-green (De Villiers et al. 1993), indicating that photosynthesis may be maintained for longer during senescence with this type of stay-green. Hence, extended foliar greenness during grain filling, known as stay-green, can be viewed as a consequence of the balance between N demand by the grain and N supply during grain filling (Borrell and Hammer 2000; Borrell et al. 2001; van Oosterom et al. 2010b).

5.3 Molecular Analysis of Soil Microbes Involved in the N Cycle

Nitrogen is a key nutrient determining the productivity of agroecosystems (Cabello et al. 2004; Dodds et al. 2000). Therefore, it is critical to optimise the balance of soil microbes involved in the N cycle such that losses of applied nitrogen are minimised and biological nitrogen fixation is increased, with the aim of decreasing leaching of nitrate, and production of nitrous oxide (N_2O) or dinitrogen (N_2). Using real-time PCR, Hai et al. (2009) investigated functional microbial communities involved in key processes of the nitrogen cycle (nitrogen fixation, ammonia oxidation and denitrification) in the rhizosphere of sorghum cultivars in tropical agroecosystems. Nitrogen-fixing populations were higher when organic fertilisers (manure and straw) were applied, and comparatively lower in urea-treated plots. In contrast, ammonia-oxidising bacteria increased in the urea-amended plots. Similarly, denitrifiers were also more abundant in the urea-treated plots. Importantly, these data imply that water availability may shape microbial communities in the rhizosphere, since low gene abundance data were obtained for all tested genes at the flowering stage when water stress was high.

6 Crop Stresses and Effects on Grain Yield Determination

Water stress is probably the most important abiotic stress faced by sorghum. For sorghum production in Australia and India (post-rainy), the crop is planted on residual moisture, usually in fairly deep and shallow soils in Australia and India, respectively, often resulting in terminal moisture stress (Jordan et al. 2012; Kholová et al. 2014). A similar situation occurs when sorghum is cultivated during the rainy season in sub-Saharan Africa, and faces terminal water stress at the end of the rains, for instance in the Sahel. This stress scenario principally affects the grain filling period, and ‘adapted’ genotypes have soil moisture available for that crop stage. Phenotypically, this can be observed by the expression of a stay-green phenotype (Borrell et al. 2014a). However, the expression of this stay-green phenotype is the consequence of water conserving mechanisms operating earlier during crop development (Vadez et al. 2011, 2013; Borrell et al. 2014a, b). Among these mechanisms, the capacity to restrict transpiration under high evaporative demand (Choudhary et al. 2013), a smaller crop canopy (Kholová et al. 2014; Borrell et al. 2014a, b), a lower number of tillers that decreases the canopy size (Kim et al. 2010a, b; van Oosterom et al. 2011; Borrell et al. 2014a, b), and a smaller size of the upper leaves (Borrell et al. 2014b). Deeper rooting is also known to influence sorghum performance under terminal water stress, due to growing roots with a steeper angle (Mace et al. 2012; Singh et al. 2012; Borrell et al. 2014b). In the sorghum cropping environment of West Africa, where sorghum is grown during the rainy season, adaptation comes also in the form of a sensitivity to photoperiod. This makes flowering coincide with a period just before the end of the rains, ensuring that grain filling takes place with, by and large, sufficient water and that dry conditions prevail during grain filling and maturity, also avoiding grain mould issues (Ellis et al. 1997), and synchronising the grain filling of the sorghum crop in a way that bird damage is spread across the entire crop.

The risks of surviving to complete a developmental phase are greatest during germination, emergence and the early phases of leaf and root initiation. Seeds of tropical species generally survive between 15 and 40 °C, though few survive below 10 °C or above 50 °C (Squire 1990). Flowering can also be a risky phase for tropical crops. Temperatures above 40 °C around flowering in sorghum growing areas in Australia have already caused widespread damage (GRDC 2014).

Lately, there has been increasing interest for tolerance to heat in sorghum. Earlier work reported that sorghum was sensitive to temperatures above 28 °C (Singh et al. 2015). However, in this work, the crop was maintained during the whole crop cycle under a higher temperature regime and the effect of temperature was confounded with an effect on the accumulation of thermal units, thereby reducing the duration of the crop. In addition, temperature treatment above 38 °C was necessary to screen genotypic variation (Nguyen et al. 2013). Under these conditions (38:21 °C day: night temperature), while crop growth was accelerated and height decreased, there was a significant decrease of pollen germination and seed setting. These thresholds are consistent with a study showing no effect of high temperature on seed set until about 38–40 °C (Vadez et al. unpublished). These thresholds are higher than earlier more conservative estimates fixing the high temperature regime at 36 °C (Prasad et al. 2006). Even lower thresholds have recently been reported in the sorghum US breeding program, i.e. 33 °C (Tack et al. 2017), reporting also a lack of genetic diversity for heat tolerance in the US sorghum breeding programs. However, in this latter study, heat stress was assessed by the yield reduction in a large meta-analysis of trials carried out across a wide range of temperature conditions. The analysis showed a temperature threshold of 33 °C beyond which yield decreased. However, this analysis did not allow the effects of heat stress on the reproductive biology to be separately assessed. In any case, the main effect of high temperature appears to be on the reproductive biology, especially pollen germination and seed set (Prasad et al. 2006), whereas the effects on plant growth and photosynthesis are considered to be minor (Jain et al. 2007; Prasad et al. 2008; van Oosterom et al. 2011).

A study on sorghum by Singh et al. (2016) found that pollen germination, seed set and grain yield were the most sensitive to high temperatures immediately around anthesis, with the greatest sensitivity of pollen germination and seed set to high temperatures occurring during a 10- to 15-day period commencing just before anthesis. Pollen germination and seed set were tightly associated in these studies (Singh et al. 2015, 2016). Furthermore, the potential effects of high temperature risks on sorghum have recently been quantified (Singh et al. 2017). The most common incidence of heat stress around anthesis in the Australia sorghum belt was the occurrence of individual days with maximum temperatures between 36 and 38 °C. These temperatures were near the threshold limiting seed set in tolerant genotypes, so increasing the temperature threshold within the APSIM-sorghum model generally minimised adverse yield effects. However, additional selection for increased heat tolerance above the threshold is justified based on the 1–5 °C predicted temperature increases in the coming decades through to 2070 (CSIRO BoM 2007). Since the adverse effects of climate change on grain yield in sorghum crops are more likely a consequence of increased incidence of heat rather than drought stress, more emphasis on heat tolerance is warranted in breeding programs (Lobell et al. 2015). At this stage, there are still only a limited number of studies on heat stress in sorghum, with only preliminary evidence of genetic variation for heat stress tolerance (Nguyen et al. 2013).

While frost tolerance is generally not an issue in sorghum (although frost can be a problem for late-planted crops in north-eastern Australia that mature into decreasing autumn temperatures), cold tolerance can be important in specific situations. Cold affects germination and early plant development in temperate settings when crops are planted around spring (Tiryaki and Andrews 2001) at temperatures below 15 °C. This is an issue because it affects plant stand, reduces the capacity to compete against weeds, and delays canopy development and hence full light interception. Genetic variation for cold tolerance has been found in landraces that evolved in temperate regions of China (Lu and Dahlberg 2001). Several QTLs for cold tolerance of germination have been identified (Knoll and Ejeta 2008; Burrow et al. 2011). The mechanisms for enhanced germination under cold conditions are still unknown in sorghum. In rice, a gene encoding for a peptide involved in endosperm rupture was hypothesised to be involved in differences in germination (Fujino et al. 2008). Cold temperatures also impact reproduction since temperatures below 8 °C affect pollen viability, eventually decreasing seed set percentage (Knoll et al. 2008; Osuna-Ortega et al. 2003).

7 New Horizons in Crop Physiology Phenotyping

The recent revolution in sequencing and whole-genome genotyping techniques, such as Next-Gen Sequencing and whole-genome marker arrays, has enabled the assembly of comprehensive genetic resources in sorghum (Mace et al. 2009, 2013; Morris et al. 2013; McCormick et al. 2018). However, to keep up with the pace of developments in genomics and fully exploit the potential of these resources to map genetic loci and potentially genes underlying traits of interest, high-throughput methods to phenotype breeding material are needed. As a consequence, phenotyping has become the new frontier in crop breeding (Araus and Cairns 2014). It is timely then that technologies, such as microcontrollers and most importantly, geolocation at high resolution, have become affordable. The invention of massive parallel sequencing, at first made available through the Sanger 454 and the concurrent development of alignment algorithms enabled by the increase in computing power, was at the core of the genomics revolution (Muir et al. 2016). Furthermore, the development of affordable micro-electronic machines (MEMS) and miniature sensors tapping into the global positioning system (GPS) has laid the foundation for a revolution in field phenotyping.

The chloroplasts in plants absorb specific parts of the full spectrum of sunlight (between 400 and 710 nm) and hence what they reflect, in a sense, is the inverse signature of what they have absorbed (mainly in the infrared region, 710–1000 nm). This signature can be captured via optical sensors and interpreted by plant physiologists. First applications of this go back as far as the 1970s when reflectance from vegetation on Earth acquired on the Landsat I satellite was used to monitor seasonal conditions of grasslands and crops as a management tool for farm enterprises in the Great Plains of the United States (Rouse Jr et al. 1974). Since then, various combinations of specific spectra, so-called vegetation indices (VI, e.g. Normalised Difference Vegetation Index = NDVI; Enhanced Vegetation Index = EVI; Normalised Difference Red Edge = NDRE) have been related to specific characteristics of crop canopies, such as greenness, leaf area and biomass (Huete et al. 2002; White et al. 2012; Hanes et al. 2014). More recently, light-weight multi-spectral cameras that measure reflectance in a small number of selected bands attached to Unmanned Aerial Vehicles (UAVs) have been deployed to construct VI of individual trial plots.

Traits such as biomass and leaf area, which previously involved destructive sampling and plant characteristics invisible to the human eye, are now becoming tractable for assessment in breeding programs. As they can be used to gather spectral information from hundreds of breeding plots relatively quickly, traits can now be assessed not only once, but at several stages during the growth of a trial, which enabled the development of models to derive dynamic traits such as leaf area duration (Potgieter et al. 2017), biomass, and crop growth (Potgieter et al. 2018a, b).

Artificial intelligence, also known as machine or deep learning, underpins the construction of image classification algorithms. In their simplest form, these algorithms classify pixels in an image based on the characteristic spectral responses of different objects, and in more sophisticated models they also take into account other information such as shape or position. The term ‘machine learning’ comes from the fact that the computer algorithm is developed via a series of semi-automated iterations using a set of training images involving continuous refinement of the classification criteria through correction by a human eye. Applications of such image analysis techniques in sorghum so far include number (Guo et al. 2018) and volume of panicles (Chang et al. 2017).

The greatest advances are usually made when several technologies come together and this is no different in plant phenotyping. From the use of single sensors to derive vegetation indices for entire crops, the field is now moving towards entire assemblies of suites of sensors on various platforms, from stationary platforms in glasshouses (Fahlgren et al. 2015) and fields (Kirchgessner et al. 2017; Virlet et al. 2017), to mobile platforms including both ground (Deery et al. 2014; Potgieter et al. 2018b) and aerial vehicles (Yang et al. 2017). The individual platforms have different advantages and disadvantages, for example overhead gantry systems and UAVs avoid soil compaction and allow access when the field is wet, however, gantries are usually not as easily moved from field to field as mobile systems, but UAVs, on the other hand, are further removed from the crop canopy. Combining platforms not only allows more flexibility, but it also enables the simultaneous data gathering from various sensor types, such as multi- and hyper-spectral and thermal sensors, digital cameras, LiDAR (Light Detection and Ranging) and ultrasonic sensors. This allows the user to derive not just spectral, but also two- and three-dimensional information of the sorghum canopy and traits such as plant height and stem diameter (Salas Fernandez et al. 2017), or even complex traits such as radiation use efficiency become tractable (George-Jaeggli and Potgieter, unpublished). With the amount of data that is quickly accumulated with such systems, a well-designed data and image-analysis pipeline that not only brings together the outputs from the various sensors on a per-plot basis and makes the data amenable for the development of algorithms for each target trait, but also provides for safe data storage for future re-analysis of raw data, becomes paramount. However, only a few examples of such pipelines have been published to date (Potgieter et al. 2018b).

For the first time in history, we now have the tools to measure physiological traits, such as dynamic biomass growth or canopy radiation use efficiency at a high-throughput scale that can match the genomic data. These new tools will allow us to phenotype thousands of lines breeders have previously genotyped in multi-location field trials—a pre-requisite for the unravelling of the molecular basis of complex traits via association mapping approaches. This is particularly pertinent in cereals generally, as biomass growth and photosynthetic capacity have been identified as the new frontier in increasing yields (Murchie et al. 2009; Zhu et al. 2010; Long Stephen et al. 2015; Ort et al. 2015), and sorghum in particular, as it is such an important cereal for food, feed and fuel, especially in dry-land cropping systems.

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