

Advances in Multi-Scale Remote Sensing and Machine Learning for Canopy-to-Root Phenotyping of Drought Adaptation in Sorghum: A Systematic Review

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Highlights

What are the main findings?

- Drought adaptation in sorghum is governed by coordinated trait networks integrating canopy development, water-use dynamics, photosynthesis, and root-mediated water capture, rather than single traits.
- Combining remote sensing with radiative transfer modelling and machine learning enables retrieval of physiologically meaningful canopy traits and provides scalable proxies for below-ground root function.

What are the implications of the main findings?

- Integrating multi-modal remote sensing data with physics-based models strengthens remote sensing as a mechanistically informed phenotyping framework for breeding.
- Hybrid radiative transfer modelling (RTM) and machine learning (ML) approaches enable high-throughput, physiology-informed trait retrieval, supporting genetic analysis and breeding for drought-resilient sorghum and other cereals.

Abstract

Sorghum (*Sorghum bicolor* L. Moench) is a major cereal in water-limited environments. Its C₄ carbon-concentrating pathway suppresses photorespiration and supports comparatively high photosynthetic and water-use efficiency at high temperature, although yield remains sensitive to the timing and intensity of drought. This systematic review critically evaluates how coordinated variation in phenology, canopy development, transpiration regulation, photosynthetic resilience and root-mediated water capture can be phenotyped for sorghum improvement. The review was conducted and reported in accordance with the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) 2020 statement. Eligible primary studies examined sorghum drought physiology, sensing-based phenotyping, trait retrieval, root-associated water capture, or breeding applications. Following duplicate removal and title, abstract and full-text screening, 45 sorghum-specific studies were included. Owing to substantial heterogeneity in experimental design, drought treatment, sensing platform, target trait, and validation metric, evidence was synthesised narratively rather than by meta-analysis. We compare sorghum studies across Light Detection and Ranging (LiDAR), multi-spectral, hyperspectral, thermal, structural, and fluorescence sensing, with emphasis on reported accuracy, transferability

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and physiological interpretation. We then examine how PROSAIL (PROSPECT coupled with Scattering by Arbitrarily Inclined Leaves) and SCOPE (Soil Canopy Observation, Photochemistry and Energy Fluxes) can be constrained for sorghum canopies and combined with machine learning. The central contribution is a sorghum-specific framework that distinguishes directly observed or model-retrieved canopy traits from indirect root-function predictions requiring ground validation. The synthesis identifies practical routes for measuring functional stay-green, high-vapour-pressure-deficit responses and post-anthesis water capture, while defining priorities for cross-environment validation and breeding deployment.

Keywords: drought adaptation; high-throughput phenotyping; machine learning; radiative transfer modelling; remote sensing; sorghum

1. Introduction

Climate variability and the increasing frequency of drought events pose a major challenge to global crop production, particularly in rainfed agricultural systems where yield depends strongly on seasonal water availability. Rising temperatures and shifts in rainfall patterns are expected to increase the intensity and unpredictability of drought stress, making the development of drought-resilient cropping systems a key priority for ensuring food security. Drought adaptation in crops is not controlled by a single trait but is an emergent from the interaction of multiple physiological and developmental processes. These include phenological timing, canopy development, transpiration regulation, photosynthetic performance, and root-mediated water uptake (Figure 1). Their effectiveness depends not only on individual expression but also on how they are coordinated across growth stages and in response to water limitation. For example, in sorghum, the well-studied stay-green phenotype reflects an integrated drought-adaptive strategy linking canopy development, water capture, and water use, leading to sustained photosynthetic function during grain filling and consequently reducing carbon stress-induced senescence [1,2].

Despite advances in plant physiology and genetics, the deployment of drought-adaptive traits in breeding programs remains constrained by phenotyping limitations. Many key traits, particularly those related to root function, water-use dynamics, and temporal stress responses, are difficult to measure non-destructively and at scale under field conditions. Traditional phenotyping approaches are often labour-intensive and limited to single time points, restricting their ability to capture the dynamic nature of crop responses to drought across environments [3,4].

Advances in remote and proximal sensing technologies provide new opportunities to address these challenges. Multi-spectral and hyperspectral imaging, thermal sensing, LiDAR, and solar-induced chlorophyll fluorescence enable high-throughput monitoring of canopy structure, biochemical properties, and physiological status across spatial and temporal scales. These technologies enable repeated, non-destructive measurement of crop traits under field conditions, supporting large-scale phenotyping. However, sensor-derived observations alone provide limited biological interpretation and often lack transferability across environments without retraining. Integrating these data within a mechanistic framework is therefore essential for generating biologically meaningful insights [5].

As such, radiative transfer models (RTMs) link spectral observations to plant traits by simulating radiation interactions within leaves and canopies. Models such as PROSAIL and SCOPE are widely used to retrieve key variables including leaf area index, chlorophyll content, canopy temperature, and photosynthetic activity from remote sensing data

[6,7]. When combined with machine learning approaches, these models enable scalable retrieval of physiologically meaningful traits, while maintaining a connection to underlying biological processes. These hybrid frameworks enable process-based phenotyping rather than purely empirical prediction. However, a major frontier is the integration of above-ground sensing with below-ground trait inference. Root systems play a central role in drought adaptation through their capacity to acquire water from the soil profile. However, root growth and function are inherently influenced by the surrounding soil environment, including factors such as soil nutrients, texture, structure, compaction, bulk density, and water-holding capacity, which collectively determine water availability to plants [8,9]. This interaction between roots and soil presents a challenge for large-scale phenotyping, as both below-ground traits and soil heterogeneity contribute to drought responses. Emerging studies suggest that canopy spectral and thermal dynamics can reflect root-mediated water use, providing a potential pathway to infer below-ground function indirectly using above-ground observations [10,11].

Network of Drought Adaptation Traits in Sorghum

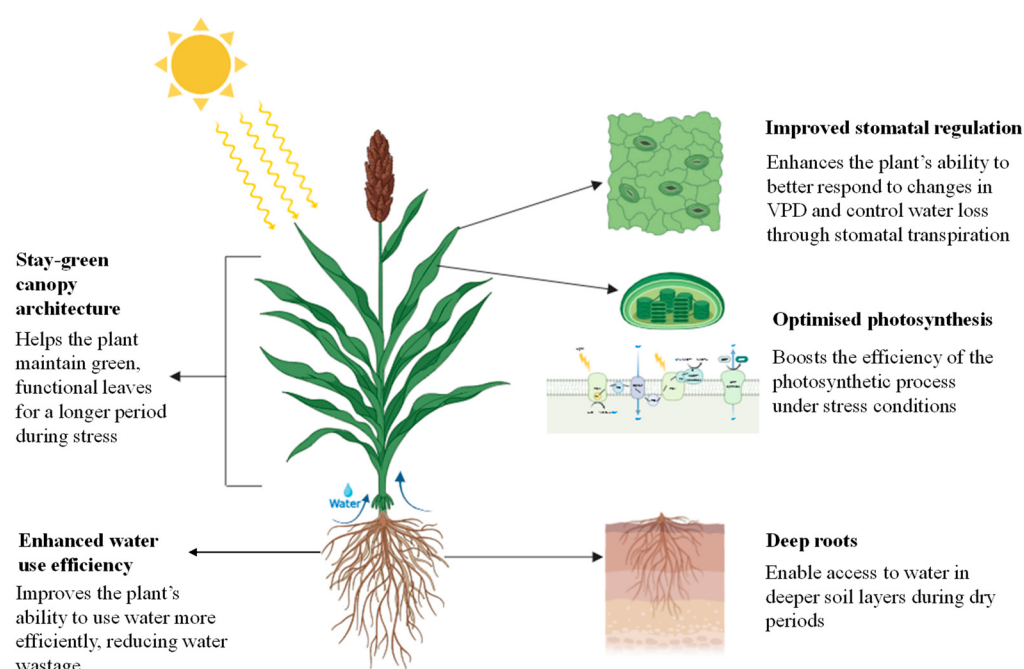


Figure 1. Conceptual framework illustrating coordinated drought-adaptive trait networks in sorghum, linking canopy architecture, photosynthetic regulation, transpiration control and root-mediated water capture.

In this context, sorghum (*Sorghum bicolor* L. Moench) provides a valuable system for studying drought adaptation. As a C_4 cereal widely grown in arid and semi-arid environments, sorghum exhibits substantial genetic variation in traits related to water use, canopy function, and root architecture. While previous studies primarily focused on above-ground traits or individual sensing approaches, this review synthesises the available literature to highlight the mechanistic links between canopy responses and below-ground function. This framework highlights opportunities to infer root-mediated water acquisition and drought resilience from above-ground observations, thereby bridging the gap between sensor-derived signals and adaptive traits relevant to breeding. By framing phenotyping within a process-based, physiology-driven context, this review aims to bridge the gap between sensing, modelling, and genomics, and outlines a pathway toward predictive, data-driven breeding for drought-prone environments.

2. Materials and Methods

2.1. Review Design and Reporting

This systematic review was conducted and reported in accordance with the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) 2020 statement [12]. Because the eligible literature differed substantially in experimental environment, drought timing, sensing platform, target trait, and validation metric, the evidence was synthesised using a structured narrative approach rather than statistical meta-analysis. The review was not registered, and no protocol was prepared before the review commenced.

2.2. Review Question and Eligibility Criteria

The review addressed the following question: How have remote and proximal sensing, radiative transfer modelling, and machine-learning approaches been used to phenotype canopy and root-associated mechanisms of drought adaptation in sorghum? Primary peer-reviewed studies were eligible when they: (i) included sorghum or reported sorghum results separately from other crops (ii) examined drought adaptation, water-use regulation, stay-green, photosynthetic resilience, root traits, or related breeding outcomes and (iii) evaluated a sensing, modelling, phenotyping, or genetic-analysis approach relevant to these traits. Reviews, editorials, conference abstracts, webpages, and studies without separable sorghum evidence were excluded from the systematic evidence set but could be cited as contextual or methodological sources. Foundational studies published before the main search period were retained only as background references and were not counted as included studies.

2.3. Literature Search, Study Selection, and Thematic Synthesis

The literature search was conducted using major scientific databases and publisher platforms, including Web of Science, Scopus, Google Scholar, PubMed, ScienceDirect, SpringerLink, Elsevier, MDPI, Frontiers, and CAB Abstracts. Additional sources were identified through reference lists of relevant review articles and key papers. The search combined terms related to sorghum, drought adaptation, phenotyping, remote sensing technologies, radiative transfer modelling, machine learning, and root function. Representative search terms included “sorghum”, “drought adaptation”, “stay-green”, “water-use efficiency”, “root architecture”, “root phenotyping”, “high-throughput phenotyping”, “multispectral”, “hyperspectral”, “thermal imaging”, “LiDAR”, “solar-induced fluorescence”, “PROSAIL”, “SCOPE”, “radiative transfer modelling”, “Random Forest”, “XGBoost”, “machine learning”, “trait retrieval”, and “canopy-to-root relationships”.

2.4. Data Extraction and Data Sources

Data were extracted using a standardised form containing the citation, country, study environment, number and type of sorghum genotypes, drought treatment and timing, sensing platform, sensor characteristics, measurement scale, target trait, reference measurement, modelling or machine-learning method, validation design, reported accuracy, physiological interpretation, breeding relevance, and study limitations. Extraction was performed by SN and checked by AP. Missing or unclear information was recorded as not reported rather than inferred.

To contextualise sorghum production dynamics in Australia, publicly available datasets were obtained from the Australian Bureau of Agricultural and Resource Economics and Sciences (ABARES), the Australian Bureau of Statistics (ABS), and the FAOSTAT database. Annual records of harvested area, grain production, and yield were compiled for Australia for the most recent ten-year period.

Spatial patterns of sorghum production were visualised using aggregated regional production statistics linked to Statistical Area Level 2 (SA2) boundary shapefiles. Official digital boundary files were obtained from the Australian Statistical Geography Standard (ASGS), published by the ABS. The national locator map was generated by dissolving the boundaries of the eight principal Australian states and territories into a single national geometry. Offshore external territories were excluded because they were outside the geographical scope of the production analysis.

Spatial analyses were conducted using a reproducible R-based workflow in which tabular production data were joined to spatial polygons to generate regional production maps. These analyses were intended to provide descriptive and contextual insights into sorghum distribution rather than formal spatial modelling or causal inference.

All statistical calculations and visualisations were performed using R (version, 2024.12.1 +563; R Core Team, Vienna, Austria).

2.5. Synthesis Methods

Included studies were grouped by a drought-adaptive mechanism and phenotyping approach: phenology and canopy development, stay-green and senescence, transpiration and thermal response, photosynthetic and fluorescence traits, root architecture and water capture, RTM-based retrieval, machine learning, and integration with genetic analysis. Study characteristics and reported performance statistics were tabulated. R^2 , RMSE, correlation, and heritability estimates were compared only when their target traits and validation settings were sufficiently similar. Statistical pooling was not attempted because of methodological and biological heterogeneity. The synthesis emphasised consistency of findings, external validation, transferability, and limitations.

2.6. Systematic Review Results

The searches identified 263 records through bibliographic databases and 5 reports. After removal of 43 duplicates and other pre-screening exclusions, 225 titles and abstracts were screened. Full texts were assessed for 141 studies and reports, of which 96 were excluded for the reasons reported in Figure 2. The final synthesis included 45 unique studies including three reports.

Studies were prioritised when they addressed one or more of the following themes: (i) physiological mechanisms underlying drought adaptation in sorghum; (ii) remote and proximal sensing approaches for quantifying drought-related traits; (iii) applications of radiative transfer models for retrieving physiologically meaningful canopy traits; (iv) machine-learning approaches for trait prediction and phenotyping; (v) root phenotyping and root–soil interactions relevant to drought adaptation; and (vi) integration of sensing, modelling, and breeding frameworks. Preference was given to peer-reviewed articles published between 2000 and 2025, although seminal studies predating this period were included where they provided foundational concepts or methodologies.

Studies were excluded when they lacked relevance to drought adaptation, sorghum physiology, phenotyping applications, or biological interpretation of sensing data. Conference abstracts, non-peer-reviewed sources, and purely technical sensor studies without agronomic or physiological context were generally excluded. The final body of literature was synthesised into thematic sections 4–11 covering drought-adaptive trait networks, remote sensing phenotyping, radiative transfer modelling, machine-learning integration, canopy-to-root phenotyping, and implications for genomics-assisted breeding.

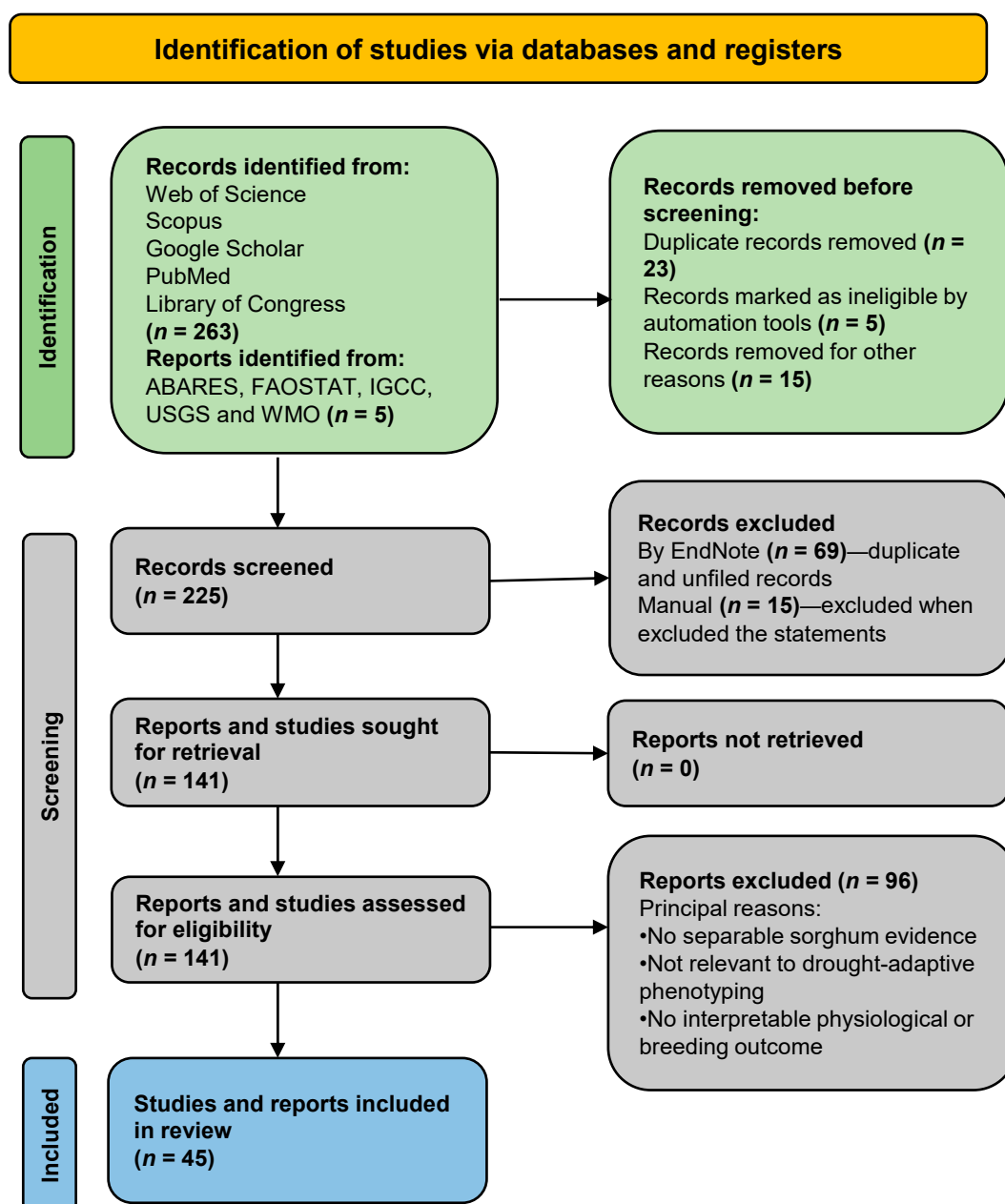


Figure 2. PRISMA-based workflow describing the literature search, screening, and study selection process.

3. Sorghum: Production, Distribution, and Agronomic Importance

Sorghum is one of the world's most important cereal crops, ranking fifth in global importance after wheat, rice, maize, and barley [13]. It plays a crucial role in arid and semi-arid regions, where it is not only a staple food for millions but is also widely used as animal feed. More recently, it has gained traction as a promising bioenergy crop [14,15]. Often referred to as the “king of millets”, it is cultivated across a wide range of agro-ecological regions, including Africa, China, the United States, Mexico, and India [16]. Increasing attention has been directed towards sorghum as a food crop, driven by its favourable nutritional profile and functional health attributes [17,18]. While sorghum serves as a food for human consumption in many parts of Asia and Africa, its production in countries such as Australia, Brazil, and the United States is largely oriented towards livestock feed systems [19,20]. In Australia, sorghum is mainly grown in the north-eastern grain belt (Queensland and northern New South Wales) under rainfed conditions, as shown in Figure 3. Based on recent ABARES statistics [21], sorghum ranks as Australia's dominant summer grain crop

by production volume, accounting for approximately 65–70% of total summer grain output. Cultivation typically covers 0.5–0.7 million hectares annually depending on seasonal rainfall, national sorghum production in recent seasons has ranged between ~1.8 and 2.5 million tonnes, depending on seasonal conditions, placing it well below major winter cereals such as wheat (~25–30 Mt) but comparable to or exceeding other summer crops such as rice and grain maize.

The importance of sorghum in Australian farming systems extends beyond production volume. The crop is particularly well suited to the highly variable climatic conditions of northern Australia, where grain production is frequently constrained by erratic rainfall, recurrent drought events, and a strong reliance on soil water stored during fallow periods [22]. Across Queensland and northern New South Wales, water availability is often the primary determinant of crop productivity [23]. The ability of sorghum to efficiently utilise stored soil moisture and maintain productivity under intermittent heat and water stress makes it a relatively low-risk summer cropping option in these environments.

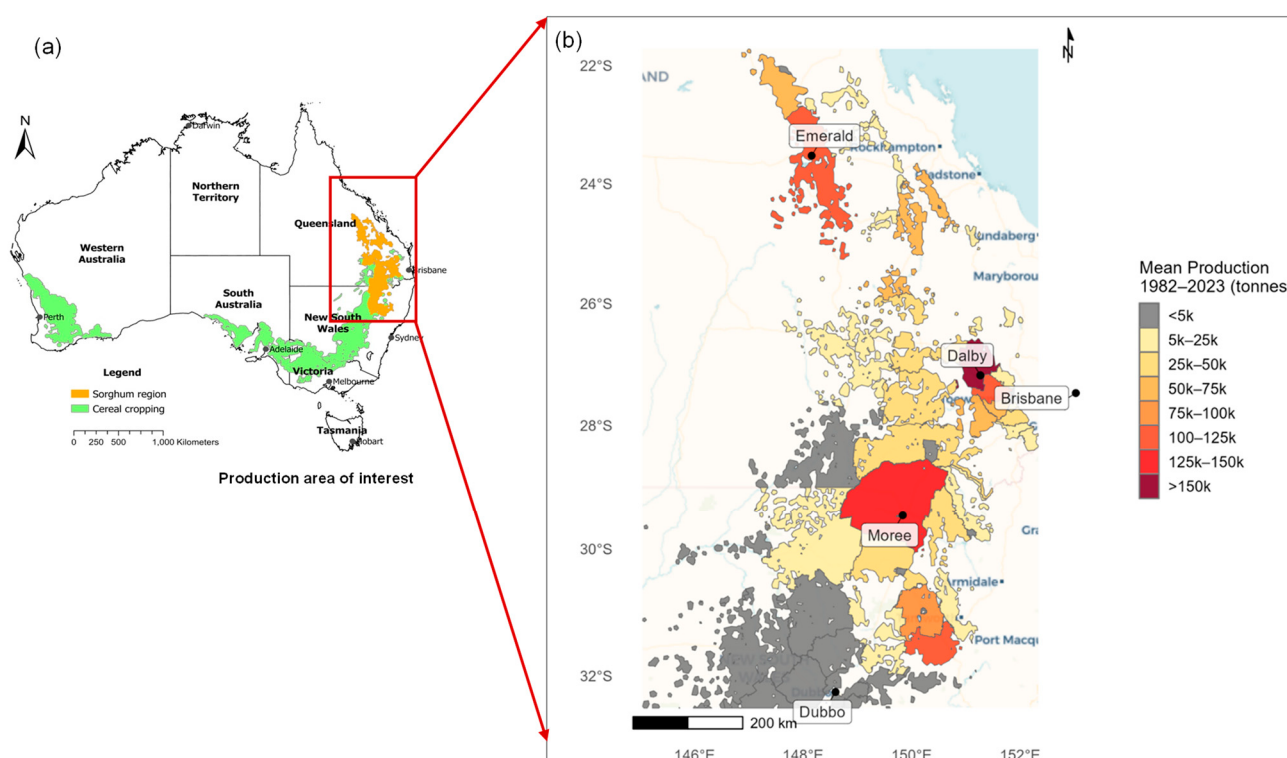


Figure 3. Spatial distribution of sorghum production in Australia. (a) National distribution of cereal-cropping areas and major sorghum-producing regions in Australia. Green indicates the broader cereal-cropping zone, whereas orange identifies the principal sorghum producing region, the red rectangle marks the area enlarged in panel b (adapted from Potgieter et al. 2026 [24]). (b) Mean annual sorghum production across the principal north-eastern production zone during 1982–2023, derived from Australian Bureau of Statistics (ABS) regional production data. Grey represents regions producing <5000 tonnes annually, while the yellow-to-dark-red gradient indicates progressively greater mean production, ranging from 5000–25,000 to >150,000 tonnes annually. Major sorghum-growing locations are labelled for geographical reference.

The FAOSTAT data indicate substantial variability in sorghum metrics in Australia [13]. The mean area harvested (~550,970 ha), production (~1,686,332 t), and yield (~2952 kg ha⁻¹) in the last ten years exhibited moderate to high dispersion, with coefficients of variation (CV) of 31.7%, 43.3%, and 22.5%, respectively. The comparatively higher CV for production suggests stronger year-to-year fluctuations compared to yield and harvested area. Overall, the decadal trend implies that variability in production is strongly

influenced by interannual environmental variability, particularly rainfall patterns and timing of drought occurrence, rather than changes in cultivated area alone [25]. This highlights the importance of understanding how crops respond dynamically to water limitation across seasons. In this context, scalable phenotyping approaches that capture temporal canopy responses and water-use dynamics become essential for linking environmental variability to crop performance and drought adaptation.

4. Drought Adaptation in Sorghum

Sorghum's adaptability across diverse tropical and sub-tropical regions is largely attributed to its C₄ photosynthetic pathway, which confers high photosynthetic efficiency, superior water use efficiency and enhanced heat tolerance, traits that are especially advantageous under conditions of climate variability and limited resources, especially on marginal lands where other cereals frequently underperform [26–28]. On soils with good water-holding capacity, as in the majority of the sorghum production areas in Australia, drought adaptation emerges from coordinated trait networks that regulate when water (i.e., sub-soil moisture) is used, how rapidly it is depleted, and how effectively canopy function is maintained during grain filling. Genotypes vary in phenology, canopy architecture, water-use regulation, and root water capture and these differences shape stress exposure and yield stability in these particular environments [1].

4.1. Growth Stages and Phenological Development of Sorghum

Sorghum phenology is typically described as a sequence of clearly identifiable growth stages spanning vegetative development, the transition to reproduction, grain filling, and physiological maturity. A widely used staging framework numbers development from emergence through key leaf-collar stages, flag leaf, booting, flowering (anthesis), and then soft dough, hard dough, and physiological maturity (Figure 4), which helps standardise field observations and management timing across environments [29]. Progress through these stages is strongly regulated by temperature (via thermal time) and, in many genotypes, by photoperiod sensitivity: longer daylengths above a cultivar-specific threshold can delay floral initiation and extend the vegetative phase, shifting the timing of panicle initiation and anthesis [30]. Within the vegetative phase, leaf appearance rate (often summarised as the phyllochron, °C d per leaf) provides a practical link between canopy development and phenological timing, with sowing date and temperature regimes altering the thermal time to key transitions such as panicle initiation [31]. Because these phenological controls also shape leaf area dynamics and radiation capture, many process-based crop models represent sorghum development using thermal-time driven stages to simulate both phenology and canopy expansion across genotypes and environments [32,33].

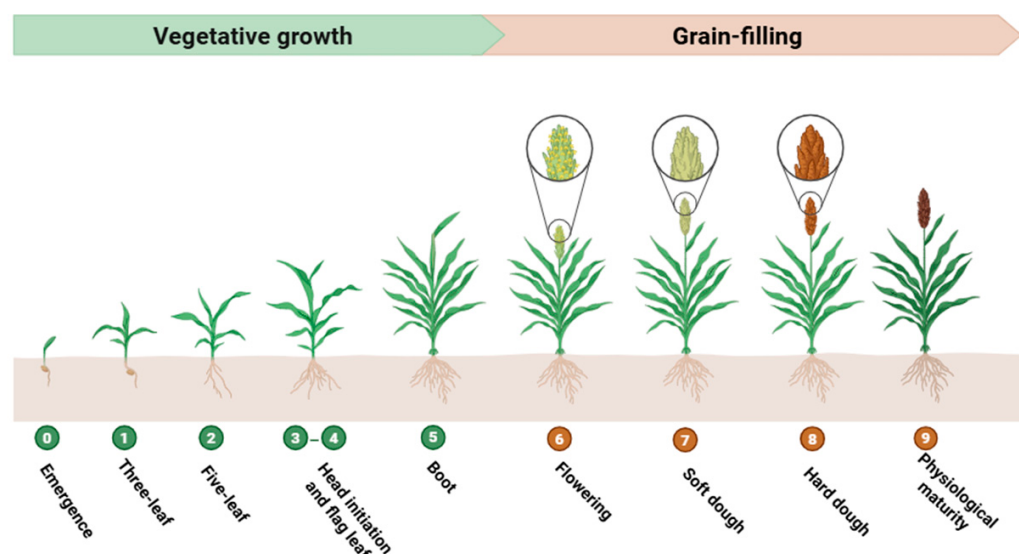


Figure 4. Schematic representation of sorghum growth stages from emergence through vegetative development, flowering, and grain filling to physiological maturity.

4.2. Drought Timing Matters: Pre-Flowering vs. Post-Flowering Stress

In rainfed systems, drought may occur early (restricting canopy expansion and biomass accumulation), around flowering (high risk for seed set), or after flowering (limiting grain filling and increasing lodging risk). Genome-wide association studies (GWAS) have shown that post-anthesis drought is particularly damaging for grain yield and lodging because it pushes the crop to remobilise stem carbohydrates, while simultaneously losing green leaf area (LA) and hence photo-assimilate supply [34]. Remobilisation cannot be measured directly from a single vegetation index; it requires sequential biomass or carbon measurements, or calibrated time-series proxies for stem reserves, senescence, and grain filling. This “timing” lens is crucial because the same trait can be beneficial or harmful depending on when water becomes limiting. A recent study showed that canopy size before flowering was only weakly and, in some cases, negatively associated with visual leaf-senescence scores. In contrast, canopy traits related to green leaf area measured after flowering were strongly and positively correlated with stay-green breeding values ($r \approx 0.7$ – 0.8). This indicates that maintenance of green LA during the post-anthesis period, rather than differences in early canopy expansion, underpinned the functional stay-green phenotype in sorghum—at least in the populations examined in the study [35].

4.3. Phenology and Developmental Plasticity: Escaping the Worst of It

Phenotypic plasticity refers to the capacity of a single genotype to express different phenotypes across environments, through changes in development, morphology, or physiology [36]. In drought-prone rainfed systems, this matters because the environment is not just “dry versus wet” but highly variable in when water becomes limiting, how evaporative demand evolves, and how rapidly soil water is depleted. Plasticity therefore shapes whether stress coincides with the most drought-sensitive physiological stages, particularly flowering and early grain set, versus the later grain filling stages. In sorghum, plasticity is commonly expressed through shifts in flowering time and plant stature across environments. Recent multi-environment field analyses have demonstrated substantial plastic responses for these traits across diverse germplasm, indicating that environmental responsiveness is under partial genetic control [37]. At the mechanistic level, sorghum phenology is strongly regulated by photoperiod and temperature, and variation in photoperiod sensitivity functions as an adaptive switch, allowing genotypes to delay floral

initiation under long days, or accelerate under short days, thereby aligning flowering with more favourable rainfall and radiation regimes in the tropical environments in which sorghum evolved [38]. Sorghum grown at higher latitudes is usually made photo-period-insensitive by the introgression of maturity genes to allow flowering during long days [39]. These responses extend beyond simple developmental regulation, as changes in flowering influence canopy longevity, seasonal radiation capture, and the timing of maximum water demand. A recent simulation study using Agricultural Production Systems Simulator (APSIM) showed that maturity class interacts with seasonal rainfall patterns, and that sowing date $\times$ maturity combinations can operate as drought escape or risk management strategies depending on whether stress occurs pre-flowering, at flowering, or during grain filling [40]. Viewed in this context, these responses highlight phenological plasticity as a timing mechanism that determines whether drought-adaptive traits act synergistically or fail under stress. Its importance lies less in escaping drought entirely, and more in shaping how and when drought is experienced by the crop.

4.4. Stay-Green: The Flagship Trait, but Not Just About “Greener Leaves”

The most influential drought-adaptation phenotype in Australian sorghum breeding has been functional stay-green, defined by delayed leaf and stem senescence during grain filling under water limitation. The key insight from physiological dissection is that stay-green is not simply a “leaf colour” trait. It is an emergent outcome of seasonal water-use dynamics and canopy development that preserves green leaf area when it matters most, sustaining grain filling and reducing lodging risk [1,2]. Research conducted on near-isogenic lines carrying a major stay-green QTL (Stg1–Stg4) showed that these loci influence (a) canopy size and architecture, (b) leaf anatomy, and (c) root growth and water uptake. These stg loci collectively shift water use away from the pre-flowering to the post-flowering period, i.e., conserving water to maintain green leaf area and hence photosynthesis during grain filling [1]. Complementary work demonstrated that individual stay-green alleles can enhance yield under drought by modifying canopy development and water uptake patterns, reinforcing the idea that the mechanism is partly “water budgeting” across the season rather than a single leaf-level tolerance switch [2]. One consistent finding is that stay-green genotypes often achieve a smaller canopy at flowering (via reduced tillering and/or smaller upper leaves), which reduces early-season water use and increases the likelihood that water remains available during grain filling [41]. In sorghum, therefore, the physiology associated with the stay-green trait points to a whole-crop resource allocation strategy: conservative water use early, sustained function later.

4.5. Root Systems: Water Capture, Geometry, and “Where” Uptake Happens

Avoidance of drought stress also depends heavily on the root system’s ability to access water at depth and later in the season. For sorghum, deep and effective rooting is frequently invoked, but the breeding-relevant question is more specific: which root architectures reliably translate into higher grain yield under late-season drought? Recent works link stay-green phenotypes to root traits such as greater root length in deeper layers and favourable nodal root angles. Experiments comparing stay-green with senescent genotypes showed that stay-green lines have greater root length in deeper soil profiles and a more conservative transpiration response under stress, supporting improved performance under reproductive-stage drought [42,43]. Therefore, in practical terms, roots contribute in two coupled ways. Firstly, access: depth and distribution determine whether water remains available after flowering. Secondly, timing: interaction with canopy demand determines whether deep water is “saved” or “spent” too early. Therefore, root traits and canopy traits are best treated as a coordinated phenotype rather than independently optimised modules.

4.6. Water-Saving Traits: Transpiration Control Under High Evaporative Demand

In hot, dry air (high vapour pressure deficit, VPD), crops can lose water rapidly even when soil moisture is not yet limiting. A potentially valuable adaptation is limited transpiration (LT) at high VPD: stomata restrict water loss once atmospheric demand crosses a threshold, conserving soil water for later stages. An APSIM modelling study showed that breeding for LT could increase sorghum yield in drought-prone regions [44] with similar benefits reported in wheat [45]. Empirical studies in sorghum also point to meaningful genetic variation in transpiration response and its link to drought adaptation, although expression can be environment-dependent and may interact with soil hydraulic properties and canopy conductance [46]. The transpiration ratio represents the mass of water transpired per unit of dry matter produced, whereas its reciprocal, transpiration efficiency represents the dry matter produced per unit of water transpired and therefore links canopy water loss with biomass accumulation [47].

Thermal sensing does not measure either quantity directly. Under comparable radiation, wind, and canopy structure, warmer canopies at high VPD can indicate reduced stomatal conductance and transpiration, but the same temperature difference may arise from architecture, stand density, or soil–water variation. Consequently, remote phenotyping of LT requires repeated canopy temperature across a VPD gradient, paired with stomatal conductance or sap-flow measurements, canopy structural covariates and soil–water depletion [33,46]. Recent sorghum work confirms large genotypic variation in canopy transpiration under high evaporative demand but also shows that the relationship between water saving and water-use efficiency is environment dependent [48].

The breeding challenge is that “water saving” can reduce carbon gain if stomata close too early or too strongly. The sweet spot is water saving that reallocates water use toward grain filling without collapsing assimilation.

4.7. Photosynthesis, Stomata, Hydraulics, and Intrinsic Water Use Efficiency

At the leaf level, drought adaptation involves stomatal regulation, maintenance of photosynthetic capacity, photoprotection, and hydraulic function. A recent physiology study examined intrinsic water use efficiency (iWUE) and found that some sorghum genotypes maintain iWUE under water stress by maintaining photosynthetic capacity, with links to aquaporin-associated haplotypes [49]. Aquaporins facilitate hydraulic water transport. This finding also reinforces that drought adaptation is not purely stomatal but biochemical capacity and hydraulic pathways influence whether plants can keep assimilating when conditions tighten. Genetic studies also support substantial natural variation in photosynthetic traits under water limitation, offering targets for mapping and selection [50]. Functional stay-green emerges from the integration of reduced early-season water use, improved regulation of transpiration under high evaporative demand, maintenance of photosynthetic capacity during grain filling and access to deep soil water through root system architecture. Together, these traits determine when water is used, how rapidly it is depleted, and whether water availability is sustained to support post-anthesis canopy function and grain filling under drought.

4.8. Compound Heat–Drought Stress and Environmentally Targeted Management

Heat and drought often co-occur, but their canopy signatures are not interchangeable. High air temperature increases VPD and can warm a well-watered canopy, whereas drought restricts evaporative cooling; reproductive heat can additionally reduce pollen viability and grain set even when vegetation indices remain high [51]. A useful phenotyping design therefore combines canopy temperature depression, spectral senescence trajectories, phenology, and weather rather than classifying stress from temperature alone. Remote sensing can support synergistic environmental management by identifying

genotype $\times$ sowing date $\times$ density combinations that avoid flowering during extreme heat, conserve pre-flowering water and sustain post-anthesis cooling. These responses should be evaluated within target-population-of-environments analyses, because a smaller or more conservative canopy can be advantageous under terminal drought but penalise yield where water remains available [33,40,44].

4.9. Operationalising Drought-Adaptive Trait Networks

Collectively, drought adaptation in sorghum arises from coordinated regulation of canopy architecture, seasonal water use, photosynthetic function, senescence dynamics, and root-mediated water capture. These processes determine when water is expended, how efficiently carbon is assimilated per unit water lost and whether functional leaf area is maintained to support grain filling under late season drought. Reviews on genomics-assisted sorghum improvement outline how phenology, stay-green, transpiration efficiency, and root traits can be integrated through marker-assisted and genomic selection pipelines, providing a pathway to intentionally select for adaptive response patterns rather than single time-point traits [52]. However, stay-green can arise through multiple mechanisms. While enhanced water capture and conservative water use may contribute to improved drought adaptation, similar phenotypes can also result from reduced carbon demand associated with smaller canopies or lower yield potential. Consequently, breeding efforts should focus on identifying the physiological processes underpinning functional stay-green rather than selecting solely for the phenotype itself. Many key processes are inherently temporal and environment-dependent, making them challenging to capture using conventional phenotyping approaches. This creates a critical need for scalable tools that can quantify these dynamic responses in real time. Remote and proximal sensing technologies provide a pathway to address this gap by enabling continuous, high-throughput monitoring of canopy-level responses that are functionally linked to underlying physiological processes, thereby supporting their integration into breeding pipelines.

5. Remote Sensing of Sorghum Drought-Adaptive Traits

Remote sensing records spatial and temporal variation in reflected or emitted electromagnetic energy. In crop canopies, the signal combines leaf optical properties, canopy geometry, soil background, illumination and viewing direction [53,54].

5.1. Evolution of Remote Sensing as a Tool for Enhancing Functional Phenotyping

Optical remote sensing exploits the fact that canopy reflectance is shaped by leaf biochemistry and canopy structure. The earliest use of satellite remote sensing in crop studies relied on coarse-resolution multi-spectral imagery from Landsat and NOAA platforms [53,54]. Remote sensing has evolved from coarse-resolution satellite observations to high-temporal, spatial and spectral resolutions. Multi-sensor phenotyping platforms onboard UAVs now enables the accurate capturing of crop dynamics across spatial and temporal scales. Early work relied on aerial photography (initially balloon-based), with the first successful aerial photograph commonly traced to 1858 by Gaspard-Félix Tournachon—known by his pseudonym Nadar [55]. Space-based Earth observation accelerated in the 1960s with meteorological satellites, including TIROS-1 (launched 1 April 1960), which enabled synoptic monitoring of weather systems relevant to crop risk and drought surveillance [56]. NASA reports that the decisive step for agricultural applications came with Landsat 1 (ERTS-1) in 1972, which established systematic multi-spectral monitoring of Earth's land surface and underpinned decades of land and crop observation [57].

While these early satellite systems provided proof of concept for quantitative crop monitoring, their spatial resolution (tens of metres), revisit frequency and vulnerability to cloud cover limited their direct utility for breeding-scale phenotyping [4]. To address

these constraints, proximal and ground-based sensing platforms were developed in the late 1990s and early 2000s, including tractor-mounted sensors and field phenotyping carts that enabled high-resolution, plot-scale measurement of canopy spectral and thermal properties [58]. These systems provided precise physiological data but remained constrained by logistical challenges, limited throughput and reduced operational feasibility under tall canopies or wet soil conditions.

The advent of lightweight unmanned aerial vehicles (UAVs) in the last decade has transformed crop phenotyping by combining high spatial resolution, flexible deployment, and multi-sensor integration. UAV platforms can acquire centimetre-scale multi-spectral, thermal and hyperspectral imagery, allowing on-demand, repeatable observation of breeding trials and production fields [59,60]. UAV-based phenotyping has been demonstrated across cereals, including sorghum, enabling quantification of canopy development, senescence progression, canopy temperature, and biomass proxies under water-limited environments [61–64].

Modern platforms can carry multiple sensor types, such as multi-spectral, thermal, and LiDAR sensors (Table 1). Providing a rich range of datasets, e.g., spectral indices reflect leaf chlorophyll and water content, while thermal imagery reveals whether the canopy is undergoing evaporative cooling or experiencing stress, and LiDAR or photogrammetry gives plant height and structural traits. Integrating these can provide a holistic picture of plant performance under drought [5]. Moreover, image analysis and machine learning can automatically extract features (like counting heads or measuring leaf angles) with consistency and high precision [65,66].

Table 1. Summary of remote sensing technologies applied across major crops over the past two decades, highlighting sensor type, observation scale, spatial resolution, target traits, and reported model accuracies for physiological or yield-related phenotyping.

Sensor Type (Platform)	Scale	Typical Spatial /Spectral Resolution	Crop	Trait Focused	Reported Accuracy (As Published)	Study
Thermal IR camera (ground proximal imaging)	Plot/field micro-scale	~meter-scale footprint (camera scenes of ~1 m ² canopy)	Wheat	Canopy stress and nitrogen (N) status via canopy temperature patterns	The canopy stress index (CSI) showed a strong relationship with yield ($R^2 = 0.8$)	[67]
Multi-spectral camera (UAV)	Plot/field	cm-level (typically 2–10 cm GSD)	Maize	Leaf Area Index (LAI)/chlorophyll (SPAD)/yield proxies	Best-performing index/model reported $R^2 = 0.86$, RMSE = 0.14 from WDRVI index	[68]
LiDAR (UAV)	Plot/field	cm-dm (point cloud dependent)	Maize	Canopy/plant height (lodging-related structural trait)	Plant height estimation: $R^2 = 0.964$, RMSE = 0.127, nRMSE = 7.449%	[69]
RGB + multi-spectral (UAV) + 3D point cloud features	Plot/field	cm-level	Rice	Above-ground biomass (AGB) using spectral + 3D/temporal features	Plant height: $R^2 = 0.89$, RMSE = 5.08 cm Best accuracy for above-ground Biomass: $R^2 = 0.88$, RMSE = 1111 kg/ha, nRMSE = 9.76%	[70]
Multi-spectral (Sentinel-2 satellite)	Field/region	10–20 m	Wheat	Within-field grain yield using multi-date S2 + RTM/ML	Best performing model: Random Forest (RF) $R^2 = 0.89$, RMSE = 0.74 t/ha when used LAI retrieved from RTM	[71]

Multi-spectral indices (satellite) + panel regression (simulated S2)	Farm/region	10 m class (Sentinel-2 family)	Cotton	Yield estimation from red-edge indices	Best-fit date/index: R ² up to 0.96, RMSE = 0.21 (t/ha)	[72]
Sentinel-2 VIs (satellite)	Commercial plots/region	10–20 m	Cotton	Yield mapping (multi-season)	Yield estimation using EVI at pixel-level showed the best accuracy with R ² = 0.78 and RMSE = 0.695 t/ha	[73]
Multi-satellite comparison (PlanetScope vs. Sentinel-2 vs. Landsat 8)	Field/region	~3 m (PlanetScope), 10 m (S2), 30 m (L8)	Soybean	Yield estimation with meteorological/topographic covariates	Yield estimation, model: RF: MAE: PlanetScope = 0.091 t/ha, Sentinel-2 = 0.120 t/ha, Landsat8 = 0.097 t/ha	[74]
UAV multi-spectral time series	Field/Region	cm-level (typically 2–10 cm GSD)	Sorghum	LAI, canopy cover (R ² = NDVI/EVI-LAI 0.58, RMSE = 0.03), senescence	Good within-trial relationships, NDRE best separated contrasting senescence trajectories	[61]
Proximal hyperspectral spectroscopy (ground, field experiments)	Leaf/canopy/plot	Very high spectral resolution (nm-scale bands)	Wheat	Plant N concentration (PNC)	The best PNC prediction was by combining proximal hyperspectral sensing with weather data R ² = 0.79–0.85, RMSE = 0.23–0.27%	[75]
Hyperspectral reflectance (FieldSpec HandHeld 2 (ASD Inc., Boulder, CO, USA))	Plot/breeding trials	<3 nm at 700 nm	Soybean	Genetic variation in N accumulation/fixation-related traits	The best prediction of seed protein content was by PLSR model, R ² = 0.805	[76]
UAV RGB + multi-spectral + thermal	Plot/breeding trial	RGB Camera = 4608 × 3456 pixels Multispectral = 1280 × 960 pixels Thermal = 640 × 512 pixels	Sorghum	Above-ground biomass and drought indices	R ² = 0.40–0.53 under stress; R ² = 0.11–0.35 when well-watered	[51,77]
Thermal aircraft + UAV multi-spectral + interpretable ML	Field/plot	Thermal aircraft = five Megapixels (per band)	Sorghum	Partial root biomass (0–40 cm)	Best sorghum model R ² = 0.659	[78]

An emerging approach is the integration of these sensors into tractor-mounted high-throughput (HTTP) platforms, such as GECKO (Genotype and Environment Characterisation through Kinetic Observation), which allows comprehensive evaluation of important plant traits. The platform incorporates a Headwall NANO-Hyperspec pushbroom hyperspectral sensor (Headwall Photonics Inc., Bolton, MA, USA) and an Ocean Optics USB2000+ spectrometer (Ocean Optics Inc., Dunedin, FL, USA). The NANO sensor acquires 640 spatial pixels and 270 spectral bands per scan across the 400–1000 nm spectral range with a bandwidth of approximately 6 nm, enabling detailed

characterization of canopy spectral properties. In contrast, the Ocean Optics USB2000+ measures irradiance (downwelling) across a broader spectral range (200–1100 nm) with configurable spectral resolution (~ 0.1 –10 nm), providing reference measurements for reflectance calculations. During field operation, the NANO and Ocean Optics sensors were positioned approximately 3 m and 0.5 m above the canopy, respectively, while the platform travelled at a constant speed of approximately 1.1 m s^{-1} [79,80].

Collectively, these studies demonstrate that multi-sensor integration consistently improves trait retrieval accuracy, reinforcing the importance of combining structural, spectral and thermal information for robust phenotyping under field conditions. Transforming data collected from these sensors into meaningful and actionable information remains a critical area of research.

5.2. Spectral Reflectance as a Proxy for Canopy Structure, Chlorophyll Dynamics, and Physiological Traits

Energy from the sun interacts with plant canopies across the electromagnetic spectrum, where incoming radiation can be absorbed, reflected, transmitted or re-emitted depending on leaf biochemical and structural properties.

- (i) Optical remote sensing: At the leaf level, pigments such as chlorophyll strongly absorb radiation in the blue (~ 400 –500 nm) and red (~ 600 –700 nm) regions for photosynthesis, while a substantial portion of near-infrared radiation (~ 700 –1300 nm) is reflected or transmitted due to internal leaf structure and air–cell interfaces [81]. At canopy scale, these absorption, reflection, and transmission processes are further influenced by leaf area, orientation, and canopy architecture, shaping the spectral signals observed by remote sensors [82,83]. Thus, reflectance in the visible and red-edge spectral regions is strongly controlled by chlorophyll concentration and green leaf area, while near-infrared reflectance is primarily governed by canopy architecture and internal leaf scattering [6]. Vegetation indices derived from these spectral domains therefore provide scalable proxies for biomass accumulation, canopy development and senescence dynamics. A seminal milestone was the development of the Normalised Difference Vegetation Index (NDVI) formulation for broad-area vegetation monitoring using ERTS-1 (Landsat-1) data. This demonstrated that spectral reflectance ratios could be quantitatively linked to vegetation greenness and green biomass at the continental scale [53,54]. Beyond greenness and structure, remote sensing has increasingly enabled early detection of physiological stress before visible senescence occurs.
- (ii) Solar-Induced chlorophyll Fluorescence (SIF): SIF is the faint red and far-red light emitted by chlorophyll molecules when absorbed solar energy is re-emitted during photosynthesis [84]. It directly reflects the efficiency of photosystem II and responds rapidly to down-regulation of photosynthesis under drought and heat stress. Space-borne and airborne studies have demonstrated that declines in SIF precede reductions in greenness and biomass, providing early warning of physiological stress in crops [85,86]. SIF has further been shown to track gross primary productivity and photosynthetic down-regulation under water limitation, establishing its value as a functional stress indicator rather than a structural proxy [87,88]. A substantial research gap remains, as few field-based sorghum breeding trials have validated plot-scale passive solar-induced fluorescence (SIF) measurements against genotypic variation in drought response. The strongest sorghum evidence currently comes from proximal hyperspectral prediction of photosynthetic capacity and hybrid PRO4SAIL-SCOPE analyses, not from operational UAV SIF selection [89,90]. For field trials, sub-nanometer spectrometers around the O_2 -A feature provide the most defensible passive retrieval; wider-band UAV hyperspectral sensors should be used

for relative plot contrasts only after spectral calibration and validation [91,92]. The photochemical reflectance index (PRI), derived near 531 and 570 nm, offers a lower-cost reflectance proxy for xanthophyll-cycle regulation and light-use efficiency; it complements rather than substitutes for SIF because it is also sensitive to canopy structure, pigment pools, and viewing geometry [93].

- (iii) Thermal remote sensing: Thermal infrared (TIR) sensing operates in the $\sim 3\text{--}14\ \mu\text{m}$ region of the electromagnetic spectrum and differs fundamentally from visible and near-infrared observations because it measures emitted radiance rather than reflected solar energy. At typical Earth-surface temperatures, vegetation and soil emit strongly within the long-wave infrared window ($\sim 8\text{--}14\ \mu\text{m}$), which allows retrieval of land surface or canopy temperature from airborne and satellite sensors [94,95]. This region is particularly important because it coincides with atmospheric transmission windows where absorption by gases such as water vapour is relatively low, enabling surface thermal emission to reach sensors with minimal attenuation [96]. Operational platforms therefore position thermal bands within this window; for example, Landsat 8/9 TIRS acquires data around $10.6\text{--}12.5\ \mu\text{m}$, while ASTER provides multiple thermal bands between approximately 8.1 and $11.6\ \mu\text{m}$ for detailed surface temperature retrieval [97–99].

From a physiological perspective, canopy temperature represents an integrative signal of plant water status because it is governed by the surface energy balance and the degree of transpiration-driven evaporative cooling. Under adequate soil moisture, open stomata support transpiration and maintain cooler canopy temperatures, whereas water limitation restricts transpiration and results in canopy warming relative to the surrounding environment [100,101]. Thermal observations therefore provide a functional indicator of stomatal conductance and crop water status. When combined with optical measures of canopy development, thermal data enable interpretable, process-relevant indicators of drought response across scales. For instance, thermal-greenness frameworks such as the Temperature-Vegetation Dryness Index (TVDI) integrate canopy temperature with spectral indices (e.g., NDVI) to quantify evaporative cooling capacity relative to canopy size and have been widely applied to assess soil and plant water stress across cropping systems [102–104].

Table 2 summarises some of the commonly applied spectral and fluorescence-based vegetation indices, their physiological interpretation, and their relevance for breeding drought-adaptive sorghum genotypes. The metrics capture complementary components of canopy structure, chlorophyll dynamics, photosynthetic regulation, transpiration cooling, and plant water status, providing scalable proxies for functional traits such as stay-green expression, radiation use efficiency, canopy dehydration, and stress tolerance. In drought-adaptive sorghum phenotypes, these remotely sensed derivatives align closely with key physiological processes such as (i) delayed senescence and sustained chlorophyll content underpinning stay-green expression, (ii) conservative transpiration behaviour influencing canopy temperature, and (iii) structural canopy traits determining radiation interception and soil water depletion trajectories [3,5,79,105].

Importantly, the temporal trajectories of these signals provide insight into the timing and progression of stress responses, which is central to understanding post-anthesis drought adaptation. Repeated measurements increase the precision and heritability of sensing metrics like NDVI or canopy temperature, since each plot's response can be tracked across developmental stages or stress progression [106].

Table 2. Summary of remote sensing indices used to capture canopy structure, water status, and photosynthetic responses relevant to drought adaptation and breeding in sorghum.

Metric	Full Form	Physiological Meaning	What It Captures	Breeding Relevance	Source
NDVI	Normalised Difference Vegetation Index	Fractional canopy cover and chlorophyll presence	Canopy size, senescence dynamics, stay-green expression	Moderate-high heritability ($H^2 = 40.7\text{--}92.5$), correlates with biomass and drought yield	[35,53]
NDRE	Normalised Difference Red Edge Index	Chlorophyll sensitivity under dense canopies	Delayed senescence, nitrogen status	Strong discriminator of stay-green genotypes post-flowering	[35]
EVI	Enhanced Vegetation Index	Reduces soil/background influence	Canopy vigour at high biomass	Biomass estimation under dense stands	[107]
NDVI-TVDI	NDVI-Temperature Vegetation Dryness Index	Thermal-greenness drought framework	Evaporative cooling vs. canopy size	Interpretable drought adaptation proxy (R^2 up to 0.815, between MTVDI and soil moisture)	[108]
SIF (O ₂ -A/O ₂ -B)	Solar-Induced Fluorescence	Photosynthetic regulation	Early stress signalling	Detects stress before greenness decline	[109]
PRI	Photochemical Reflectance Index	Photochemical efficiency	Light-use efficiency	RUE proxy	[110]
WI	Water Index	Leaf water content	Canopy dehydration	Rapid drought screening	[111]
MSI	Moisture Stress Dndex	Leaf/canopy water content	Tissue dehydration	Screening moisture stress tolerance	[112]
NDWI	Normalised Difference Water Index	Canopy water status	Relative water content and stress	Rapid drought screening	[111]
MSAVI	Modified Soil Adjusted Vegetation Index	Minimises soil noise	Early canopy development	Seedling vigour screening	[113]
OSAVI	Optimised Soil Adjusted Vegetation Index	Soil-adjusted greenness	Low-LAI canopy structure	Early drought vigour selection	[114]
CRledg	Carotenoid Reflectance Index (Red-edge)	Carotenoid stress pigments	Oxidative stress/photoprotection	Stress-tolerant genotype detection	[115]

5.3. Proximal Leaf- and Canopy-Level Sensors

At the proximal scale, leaf- and canopy-level sensors complement remote and aerial observations by directly quantifying the physiological processes that underlie spectral and thermal signals. These instruments provide mechanistic measurements of photosynthesis, water status, and canopy structure that are essential for calibrating and interpreting remote sensing metrics. Handheld fluorometers and gas-exchange systems such as LI-600 enable simultaneous measurement of leaf temperature, stomatal conductance, and chlorophyll fluorescence parameters. These variables are directly linked to canopy energy balance and SIF emission mechanisms (LI-COR Biosciences, Lincoln, NE, USA; [116]). Proximal chlorophyll fluorescence measurements (e.g., F_v/F_m , Φ_{PSII}) have been widely used to diagnose photoinhibition and drought-induced down-

regulation of photosynthesis and are mechanistically consistent with canopy-scale SIF responses [116,117]. In addition, proximal measurements of vapour pressure deficit (VPD) and leaf temperature provide direct context for interpreting thermal imagery and transpiration-based drought responses [101]. In addition to fluorescence and gas exchange, portable chlorophyll meters such as the SPAD-502 (Minolta Camera Co., Ltd., Osaka, Japan), provide rapid, non-destructive estimates of leaf chlorophyll concentration, which is closely associated with nitrogen status and photosynthetic capacity [118]. Structural traits can also be quantified using proximal instruments; for example, Ceptometers and optical canopy analysers are widely used to estimate LAI from measurements of radiation interception, providing key information on canopy development and light-use efficiency [119,120]. Handheld thermal sensors and infrared thermometers further extend proximal measurements by directly capturing canopy or leaf temperature, which reflects stomatal conductance and transpiration-driven evaporative cooling. These measurements provide ground-truthed indicators of plant water status and help interpret thermal imagery acquired from UAV or satellite platforms [100,101].

Together, these advances demonstrate that modern remote and proximal sensing no longer merely quantify canopy greenness, but capture integrative physiological responses including photosynthetic regulation, evaporative cooling capacity, and photochemical stress. These sensing-derived metrics therefore provide mechanistically interpretable proxies for drought adaptation processes, such as transpiration regulation, stay-green expression, and photosynthetic resilience. This forms a critical foundation for high-throughput physiological phenotyping.

5.4. Remote Sensing Limitations and Challenges

- (i) Radiometric, geometric, and directional effects: Reflectance and temperature vary with irradiance, atmosphere, wind, and sun-sensor geometry. Row-structured sorghum is especially anisotropic because the proportions of sunlit leaf, shaded leaf, and soil change with view azimuth. Best practice is to use calibrated reflectance panels and downwelling irradiance, stable acquisition windows, accurate surface models, and either near-nadir standardisation, multi-angle BRDF modelling or RTM simulations that reproduce row orientation and leaf-angle distribution [121]. Corrections should be evaluated on invariant targets and repeated flight lines rather than assumed effective [35].
- (ii) Spatial Resolution vs. Scale Trade-offs: High-resolution platforms like UAVs cover relatively small areas per flight (e.g., a few tens of hectares) and have limited flight endurance [122,123], whereas satellites cover vast areas but with coarser resolution—though this is improving with newer constellations [124]. For breeding trials, UAVs or ground systems are often preferred for resolution, but they are labour-intensive to deploy repeatedly. Scaling phenotyping to hundreds of field sites may still rely on a combination of satellite or aerial imaging for broad coverage and drones for finer sampling [61,122,123]. Synthetic aperture radar (SAR) adds all-weather sensitivity to surface roughness, vegetation water content, and soil moisture. Coupling Sentinel-1 SAR with optical vegetation information can improve soil-moisture retrieval under vegetation, but dense tall canopies attenuate and scatter the microwave signal [125]. SAR should therefore constrain surface or near-surface water status within a data-assimilation framework; it does not directly observe deep sorghum roots or root-zone water without a soil-water model and in-field profile validation.
- (iii) Data Management and Processing: Remote sensing generates huge data volumes (hundreds of gigabytes of images). Processing these into meaningful trait data requires computational infrastructure and expertise in image analysis. Specialised software is needed for stitching images (orthomosaics), extracting indices, or

building 3D models, and algorithms (sometimes machine learning) are needed to translate raw sensor data into trait values. Breeding programs often face a bottleneck in bioinformatics capacity to handle this “big data” [126,127]. A practical workflow is to harmonise reflectance and thermal units, align observations by phenology and thermal time, include weather and management covariates, pre-train on multi-environment data, then fine-tune with a small, stratified target-domain sample. Leave-one-site or leave-one-year-out validation should be reported alongside random cross-validation.

- (iv) Cost and Practicality: While the cost of drones and sensors has decreased [128], deploying them routinely still requires investment and training. Equipment maintenance, regulatory compliance (for UAV flight permissions), and field logistics (launching/landing drones, etc.) add complexity. In some cases, simpler tools (like ground handheld sensors or fixed cameras) might be easier to integrate even if throughput is lower. The optimal phenotyping tool thus depends on specific project needs and resource constraints [127,129].

Despite these challenges, the trend in plant phenotyping is clearly toward greater use of remote sensing. The consensus from all the above recent literature is that the advantages of remote sensing (speed, scale, novel trait insights) greatly outweigh the bottlenecks, especially as technology improves (Table 3). In summary, remote sensing has evolved from a niche research tool to a central component of modern crop phenotyping, enabling breeders to select for complex adaptive traits with unprecedented precision.

Table 3. Summary of key phenotyping bottlenecks limiting the assessment of drought-adaptive traits in sorghum, alongside emerging methodological solutions and representative studies published.

Bottleneck	Solutions Demonstrated	Representative Studies (2020–2025)
Scale and Throughput	UAV and tractor HTP platforms; automated plot extraction; time-series canopy metrics (growth curves, senescence, height).	[35,106,127]
Radiometric, geometric and directional effects	Multi-sensor fusion (RGB + MS + HS + thermal); radiometric and BRDF corrections; repeated flights; proximal sensors for calibration.	[59,90,127,130]
Complex and Dynamic Traits	Time-series VIs and AUC; hyperspectral + SIF-based photosynthesis estimation; ML linking canopy dynamics to stay-green and root traits.	[5,11,35,88–90]
Sensor and Technology Limitations	Miniaturised hyperspectral sensors; radiometric calibration workflows; 3D canopy reconstruction (SfM, LiDAR); RGB-HS-FLUO fusion.	[131–133]
Data Annotation Bottleneck	Deep learning segmentation; weak/self-supervised learning; automated head/stay-green detection; synthetic datasets for training.	[134–136]
Integration with Genomics and Modelling	Genomic prediction using UAV traits; multi-modal ML (phenomics + weather + genomics); physiology traits feeding crop models.	[5,137–139]
Root Traits (“Hidden Half”)	Predicting root traits from UAV canopy trajectories (ML); integrating soil sensing (EM, ERT); modelling root plasticity and water capture.	[11,140,141]

While remote sensing enables high-throughput quantification of canopy structural, biochemical, and thermal traits associated with drought adaptation, these observations remain largely descriptive unless interpreted within a process-based crop growth

framework [142]. Vegetation indices and thermal metrics capture canopy state and stress expression, but do not directly resolve how traits influence soil water use, radiation interception, carbon assimilation, and yield formation across environments. Process-based models like RTMs provide this mechanistic context by explicitly representing canopy development, transpiration, photosynthesis, and soil–plant–atmosphere water balance. Integrating remotely sensed trait dynamics into process-based models therefore allows translation of spectral and thermal signals into functional drought-adaptive parameters, forming the conceptual basis for hybrid phenotyping frameworks.

Hybrid frameworks (Figure 5) that integrate hyperspectral observations, RTM, and machine-learning inversion offer a promising pathway for bridging the gap between sensor-derived signals and biologically meaningful plant traits. By embedding physical and physiological constraints within the modelling process, these approaches enable the mechanistically informed retrieval of drought-adaptive traits while reducing the reliance on purely empirical relationships. Consequently, RTM-ML frameworks can improve model interpretability, enhance transferability across environments, and mitigate equifinality commonly associated with data-driven approaches. This transforms remote sensing from a high-throughput screening tool into a physiological phenotyping platform capable of supporting trait discovery, genetic analysis, and predictive breeding for drought resilience.

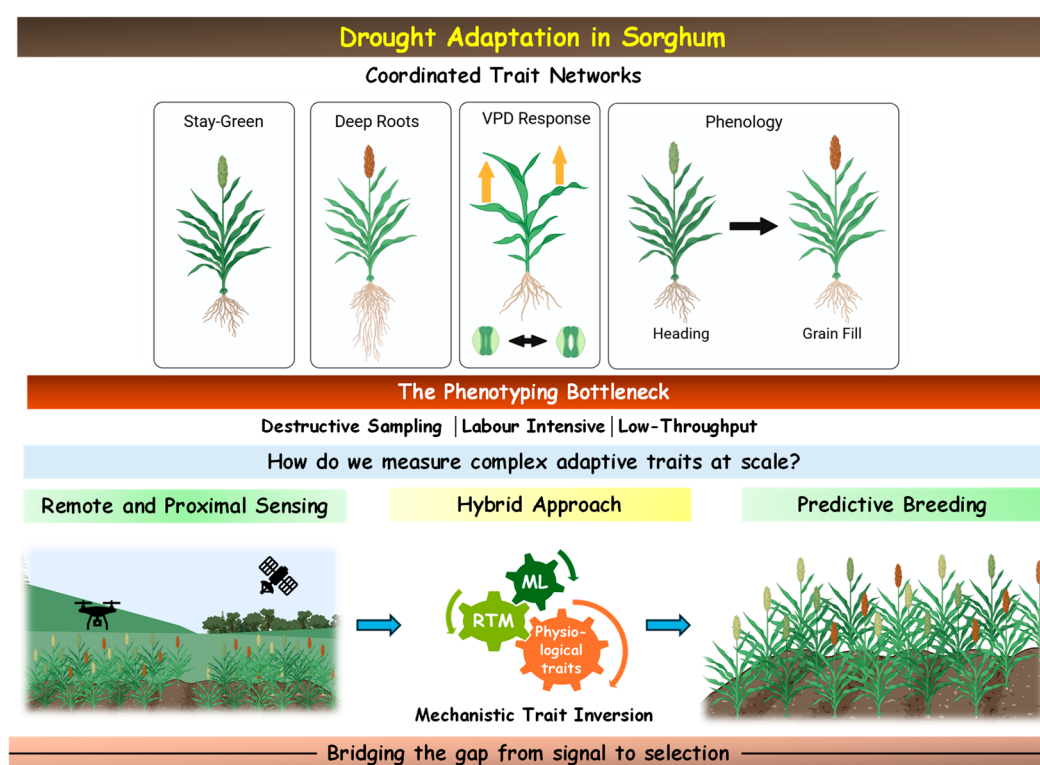


Figure 5. Generalised framework illustrating coordinated drought-adaptive trait networks in sorghum and their operationalisation through hybrid physiological phenotyping.

6. Physics-Derived Traits Using Leaf–Canopy Reflectance–Transmittance Models

6.1. Application of Radiative Transfer Models for Phenotyping

RTMs are physics-based representations of how solar radiation interacts with plant leaves and canopies, allowing the translation of remote sensing observables into interpretable biophysical and biochemical traits [6]. By simulating the absorption, transmission, and scattering of radiation across multiple wavelengths, RTMs provide a

principled framework to estimate canopy attributes such as LAI, chlorophyll content, and leaf water content from optical and thermal data, thereby addressing key limitations of empirical vegetation indices which often saturate at high canopy density or vary with background and illumination conditions [6,143]. Empirical red-NIR indices commonly saturate at LAI near 2–3 because red reflectance approaches an asymptote [144]. Figure 6 illustrates the concept of RTM: incoming solar radiation interacts with sorghum leaves and soil through absorption, scattering, and transmission, generating canopy and soil reflectance signals. These signals are captured by remote sensing platforms and used within RTMs to simulate robust reflectance realistic to the field data and generate look-up tables. Machine-learning or inversion approaches then retrieve plant traits such as LAI, chlorophyll content, and other physiological parameters for crop monitoring and improvement.

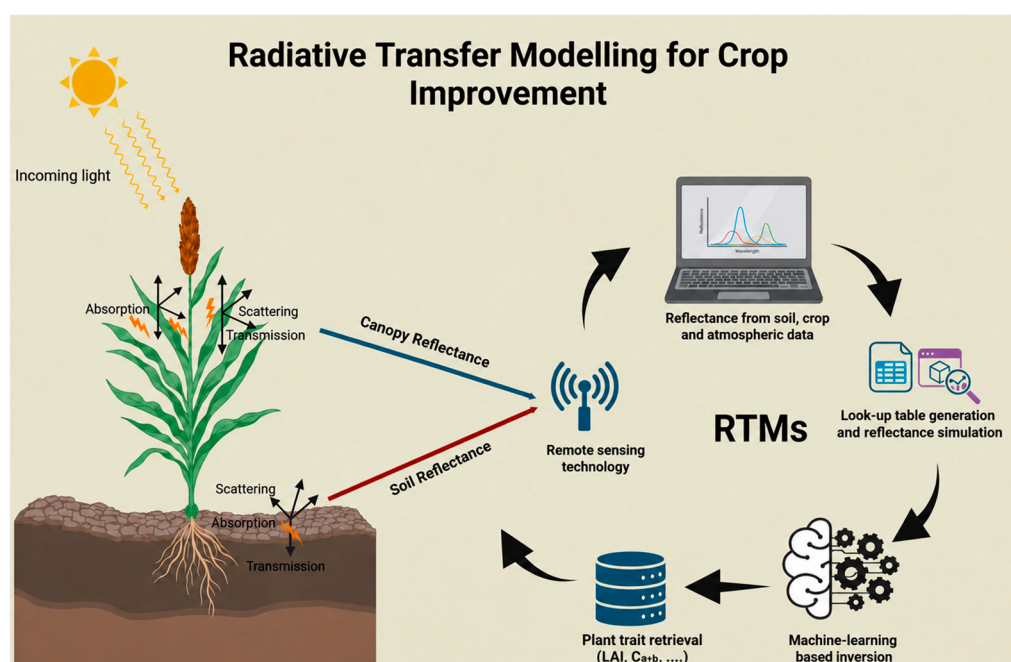


Figure 6. Simplified workflow of radiative transfer modelling (RTM) for sorghum trait retrieval.

(i) PROSPECT-SAIL model:

Among RTMs, PROSAIL, the coupled combination of the leaf optical model PROSPECT [145] and the canopy reflectance model SAIL [146,147], has become the most widely used model for crop trait retrieval in phenotyping studies. PROSPECT represents leaf reflectance and transmittance as a function of leaf structure and pigment concentrations, while SAIL describes directional reflectance from canopy architecture under varying sun-sensor geometries [143]. PROSAIL's capacity to simulate reflectance spectra across visible to shortwave infrared bands has made it a cornerstone of trait inversion studies in many crops. PROSAIL enables retrieval of LAI and chlorophyll content from remote and proximal sensing platforms with acceptable accuracy (e.g., R^2 values often above 0.7–0.8 for LAI and chlorophyll) when calibrated with field measurements [6,148].

In practical phenotyping applications, PROSAIL inversion has been implemented using look-up tables, optimisation algorithms, or machine learning emulators to link observed reflectance to trait combinations, providing estimates that would otherwise require laborious and destructive measurement [149].

For sorghum canopies, PROSAIL and SCOPE inversion require crop-specific parameterisation because canopy architecture, row spacing, soil background and growth

stage influence the simulated reflectance and fluorescence signals. Appropriate prior ranges should therefore be assigned to leaf area index (LAI), leaf angle distribution, chlorophyll content, leaf water and dry-matter contents, together with measured or representative soil reflectance and the sun-sensor geometry of image acquisition. Because direct inversion is ill-posed, simulated lookup tables can be coupled with Bayesian optimisation or machine- and deep-learning algorithms to constrain the solution and retrieve physiologically meaningful traits [150]. In sorghum breeding plots, an integrated deep-learning inversion approach predicted LAI with an R^2 of 0.84 and an RMSE of 0.65, and leaf chlorophyll Ca+b with an R^2 of 0.94 and an RMSE of $4.94 \mu\text{g cm}^{-2}$. Retrieved maximum carboxylation capacity (V_{cmax}) ranged from 45 to $75 \mu\text{mol m}^{-2} \text{s}^{-1}$ [89]. These findings demonstrate the potential of RTM-informed inversion for sorghum, although validation across contrasting genotypes, canopy structures, environments, and developmental stages remains necessary. As already mentioned, these trait dynamics such as LAI, pigment composition, and canopy water content are central to stay-green expression, transpiration efficiency, and radiation use efficiency in sorghum.

(ii) SCOPE model:

Another prominent radiative transfer model is Soil Canopy Observation, Photochemistry and Energy (SCOPE), a one-dimensional, vertically integrated model that couples radiative transfer with canopy energy balance processes [7]. Unlike purely optical radiative transfer models, SCOPE couples leaf and canopy radiative processes with photosynthesis, fluorescence emission, transpiration, and thermal energy balance, enabling the simultaneous simulation of reflectance, thermal radiance, and SIF [151,152]. The model calculates radiation transport through a multi-layer canopy as a function of solar and viewing geometry, leaf optical properties, and canopy structure, while the biochemical module is based on the photosynthesis formulations as described in [153,154] for C_3 and C_4 species respectively. This integration allows SCOPE to provide mechanistic links between canopy spectral signals and underlying physiological processes such as photosynthetic capacity, stomatal conductance and water stress. As a result, SCOPE has become an important tool for functional phenotyping, enabling retrieval of traits related to photosynthesis, canopy temperature and water use from optical, thermal and fluorescence observations. This makes RTM-based retrievals particularly pertinent to high-throughput phenotyping.

6.2. A Hybrid Approach of Remote Sensing and RTM for Phenotyping

Assimilation of RTM-derived traits into crop models has therefore emerged as a powerful strategy to bridge observation and simulation. For example, LAI retrieved through PROSAIL inversion has been assimilated into APSIM to improve wheat performance, demonstrating that RTM-based canopy traits can directly enhance crop model realism [155,156].

More recently, SCOPE-based retrieval of maximum carboxylation capacity (V_{cmax}) and SIF has enabled coupling of photosynthetic capacity with crop growth and carbon balance models in terrestrial systems at field scale [87,88]. These advances move phenotyping beyond greenness and structure toward true physiological parameterisation, allowing breeding programs to target radiation-use efficiency, transpiration efficiency and photosynthetic resilience as selectable traits. A seminal demonstration of this approach for sorghum and wheat breeding has been provided by the study [89] integrating hyperspectral sensing, PRO4SAIL, and SCOPE radiative transfer models, and machine-learning inversion for biochemical, structural, and photosynthetic trait retrieval in sorghum breeding populations. Using airborne hyperspectral imagery, their framework retrieved LAI, chlorophyll content, carotenoids,

anthocyanins, and V_{cmax} at the plot scale with high accuracy (R^2 up to 0.94 for chlorophyll and >0.78 for V_{cmax}) and further demonstrated that inclusion of modelled solar-induced fluorescence improved physiological trait inversion under stress conditions. Another example of the utility of hybrid RTM–ML frameworks was provided by a study that estimated wheat grain protein content (GPC) across 6355 ha of commercial production systems using Sentinel-2 time-series data [157]. Through inversion of the PRO4SAIL model, key biophysical traits, including chlorophyll content, leaf water content, leaf dry matter, and LAI, were retrieved and subsequently used as inputs to machine-learning models. The gradient-boosting approach outperformed single-date models, demonstrating the advantage of exploiting temporal trait dynamics. Among the retrieved variables, leaf water content was identified as the most influential predictor of GPC under severe drought conditions, highlighting the capacity of RTM-derived traits to capture physiologically meaningful drivers of crop performance [157].

Overall, radiative transfer models add a theoretical backbone to high-throughput phenotyping. They allow estimation of canopy attributes like LAI, chlorophyll, photosynthetic parameters, and water content from spectral data with known confidence and they facilitate phenotype-to-process linkages by connecting what sensors see to what crop models simulate. For sorghum, where breeding increasingly targets physiological efficiency (RUE, transpiration efficiency, etc.), RTM-based phenotyping offers a powerful means to quantify those target traits across breeding populations and environments. Although substantial advances have been made over recent decades to develop scalable, non-destructive phenotyping tools for above-ground drought-adaptive traits, root function remains outside the optical RTM state vector and must be inferred through temporal coupling with soil water, crop growth, and validated root measurements.

7. From Canopy Dynamics to Root Function

Evidence, Limits, and Validation

Roots constitute the primary interface between crops and soil water, yet field-based root phenotyping remains constrained by labour, cost, and scalability [158]. Consequently, breeders have largely relied on indirect selection via canopy traits, despite strong evidence that root system architecture and functional root activity critically regulate drought resilience and yield stability in cereals, including sorghum [159]. Recent high-throughput field studies in sorghum have demonstrated that plasticity in functional root traits such as maximum rooting depth and root activity indices strongly influences yield stability across contrasting environments, confirming that root function is not only genetically variable but also a central driver of drought adaptation [141,160]. The development of scalable phenotyping tools for root traits has now become a major focus of current research [161], assessed four non-destructive methods, electrical resistance tomography (ERT), electromagnetic induction (EMI), penetrometer resistance, and neutron-probe measurements of soil water content to estimate wheat root activity based on soil-drying patterns across three growing seasons. Among these approaches, ERT and penetrometer resistance showed the strongest relationships with soil matric potential and were able to consistently differentiate between wheat genotypes. In contrast, EMI performed well only under moderate soil moisture conditions and was more suitable as a rapid screening tool. Overall, the study concluded that penetrometer resistance and ERT are the most reliable methods for high-throughput phenotyping of root activity, while EMI can be used for quick assessments when soil conditions are not excessively dry.

Canopy sensing can predict root traits only when a calibrated relationship exists between above-ground response and measured roots. In barley, Alahmad et al. trained models with depth-resolved roots from 20 genotypes and UAV vegetation indices, then predicted larger panels across two seasons. Validation R^2 ranged from 0.51 to 0.75,

predicted trait H^2 averaged 0.71–0.81 and the most informative indices changed between seasons [11]. This is strong cross-crop proof of concept, not a sorghum validation. In sorghum, a 2026 single-site study predicted partial root biomass sampled to 40 cm with $R^2 = 0.659$, but the design did not capture the crop's deeper root system and requires multi-environment replication [78].

The study by Lopes and Reynolds on wheat evaluated a Seri $\times$ Babax recombinant inbred wheat population under irrigated and late-season drought conditions and found that cooler canopy temperatures during grain filling accounted for approximately 60% of the yield variation under drought. Canopy temperature was strongly negatively correlated with root dry weight at 90–120 cm ($r = -0.76$) and positively correlated with root mass at 60–120 cm ($r \approx 0.99$), indicating that deeper rooting contributed to cooler canopies [162].

Together, these advances establish the conceptual foundation for multi-scale, hybrid phenotyping frameworks in which remotely sensed canopy traits, radiative transfer modelling, and crop growth simulation can be integrated to infer root function non-destructively. While this approach remains under-explored in sorghum, the availability of high-throughput functional root phenotyping platforms creates a compelling opportunity to develop scalable, physiology-driven pipelines for linking canopy signals to root system performance under drought.

8. Robust Phenotyping Approaches to Enhance the Selection of Elite Varieties

Genetic Architecture of Sensing-Derived Phenotypes

High-throughput phenotyping has fundamentally transformed the scale and resolution at which genetic analyses of drought adaptation can be conducted by enabling repeated, non-destructive measurement of physiologically relevant traits under field conditions. Unlike traditional phenotyping approaches, which rely on destructive sampling or subjective visual scoring and are therefore limited in temporal resolution and mapping power, remote sensing and model-assisted phenotyping allow canopy biochemical and photosynthetic traits to be treated as genetically analysable phenotypes. Hyperspectral sensing combined with radiative transfer modelling and machine learning has been particularly effective in this context. For example, a study demonstrated that key physiological traits in sorghum, including chlorophyll content, carotenoids, specific leaf nitrogen (SLN), leaf mass per area (LMA), and photosynthetic capacity parameters such as V_{cmax} , V_{pmax} , and J_{max} , can be accurately retrieved from canopy spectra using the partial least squares regression method (R^2 up to 0.93 for V_{pmax}) and exhibit moderate to high heritability ($H^2 \approx 0.5$), confirming their suitability for quantitative genetic analysis [90]. Importantly, when these predicted traits were used in GWAS, multiple quantitative trait loci were identified for photosynthetic capacity traits such as V_{cmax} and J_{max} , demonstrating that sensing-derived physiological phenotypes can be directly linked to underlying genetic architecture. Similar approaches in other cereals such as wheat further support this framework, where time-series vegetation indices (e.g., NDVI), canopy temperature and senescence metrics derived from UAV and satellite platforms have been successfully used as GWAS traits to identify loci associated with canopy development, expression of stay-green and yield stability under drought [163,164]. Although applications in sorghum remain relatively limited, studies using UAV-derived spectral and thermal traits have reported moderate to high genetic variance and significant associations with biomass and grain yield [35,165], indicating strong potential for integrating sensing-derived phenotypes into genomic analyses. Together, these advances demonstrate that high-throughput phenotyping can bridge physiology and genomics by

enabling the genetic dissection of dynamic, process-based traits relevant to drought adaptation.

9. Research Priorities for Advancing Drought Adaptation

Although the evidence presented in this review exemplifies significant advances in better understanding drought adaptation in sorghum, substantial knowledge gaps remain a key barrier to translating physiological insights into scalable breeding decisions. Much of the current literature is still dominated by canopy-level traits such as stay-green, leaf senescence scores, or biomass accumulation [166–168], while root system architecture, hydraulic function, and below-ground plasticity remain poorly characterised at population scale. Root traits are often measured destructively, in small subsets of genotypes, or under controlled conditions that fail to represent the complexity of field drought scenarios, resulting in limited integration of root function into breeding pipelines [169].

Remote sensing and proximal sensing technologies have expanded rapidly, yet their use has largely focused on canopy structure, greenness, and thermal responses, with relatively little emphasis on linking these signals to root activity, water uptake dynamics, and soil–plant hydraulic interactions. While radiative transfer models and machine-learning approaches have demonstrated strong potential for estimating canopy traits, their application for extracting mechanistic proxies of root function, radiation use efficiency, and stress resilience remains under-explored. Another critical gap lies in the limited temporal resolution of phenotyping strategies. The lack of harmonised multi-environment datasets combining canopy, root, environmental, and physiological measurements further constrains the development of transferable prediction models.

Addressing these gaps requires research priorities focused on:

- Developing non-destructive proxies for root and hydraulic traits [140,160,170],
- Integrating radiative transfer modelling with machine learning to retrieve physiologically meaningful parameters rather than purely statistical indices [88,89,148,155],
- Building temporally dense, multi-environment phenotyping datasets [171,172], and
- Embedding these approaches within breeding-relevant field trials to enable selection under realistic drought scenarios.

10. Towards Predictive, Data-Driven Breeding

Hybrid modelling strategies that combine process-based radiative transfer models with machine-learning algorithms offer a particularly powerful pathway for trait retrieval. Radiative transfer models provide biophysical interpretability, while machine-learning approaches enable the scaling of these models to large breeding populations and heterogeneous field environments [89]. This synergy allows the prediction of physiological traits that are otherwise difficult or impractical to measure directly, creating opportunities for high-throughput screening of drought resilience. Importantly, predictive breeding frameworks enable genotype performance to be evaluated not only under observed conditions but also under simulated drought scenarios, facilitating anticipatory selection for future climate variability [173,174]. When integrated with genomic information, these phenotyping pipelines provide a foundation for linking remotely sensed functional traits to genetic architecture, enabling genomic prediction models that are informed by plant physiology rather than purely statistical yield correlations [90].

Here we propose a novel integrated framework in Figures 7 and 8 as a conceptual synthesis for linking functional canopy-derived traits to root traits for enhanced drought resilience developed from the evidence reviewed in this paper.

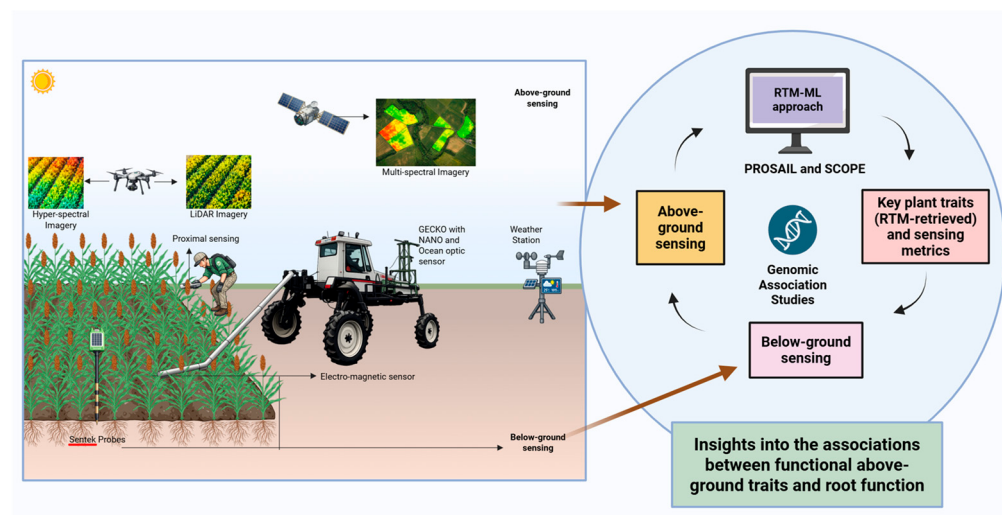


Figure 7. Hybrid sensing and modelling framework for linking above- and below-ground traits.

Sorghum-specific canopy-to-root phenotyping and breeding framework

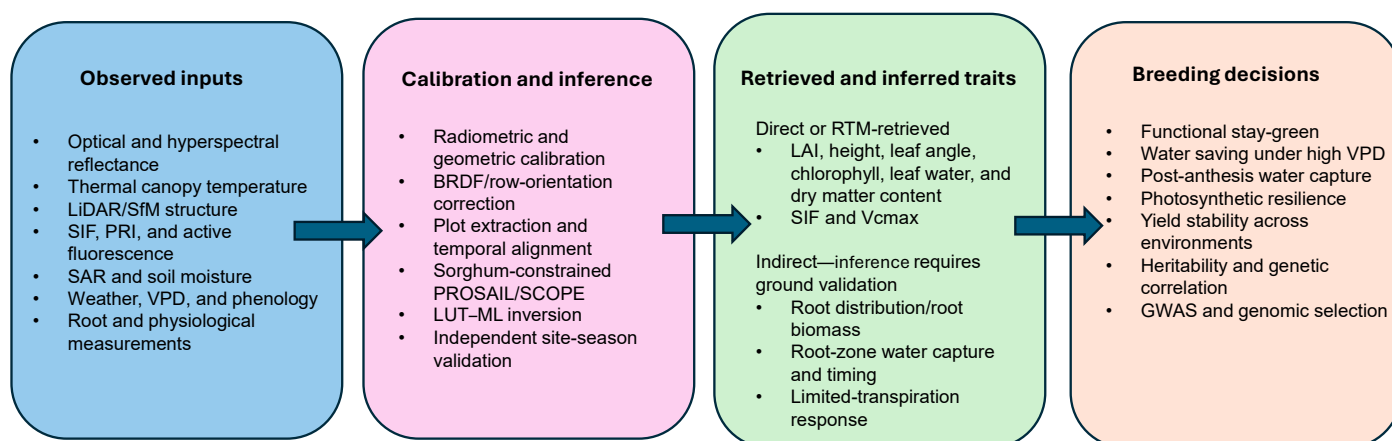


Figure 8. Sorghum-specific canopy-to-root phenotyping and breeding framework developed from the evidence synthesised in this review.

11. Conclusions and Future Directions

The transition towards holistic sensing and data-driven breeding therefore represents a fundamental shift in sorghum improvement, moving from phenotype description to physiological prediction. Overall, it allows the fusion of proximal and remote sensing from satellite, UAV, handheld, and subsurface sensors across multiple scales. Thus, it captures canopy, environmental, and soil-root signals, which are then combined with process-based modelling using radiative transfer models (e.g., PROSAIL, SCOPE). These models are embedded with machine-learning approaches to retrieve targeted morphological, biochemical, and physiological traits. It is anticipated that these sensing-derived traits can be readily integrated with genomic association studies to improve understanding of the functional relationships between canopy processes and root function for crop improvement. Future progress will depend less on adding more sensors than on multi-environment experimental design, uncertainty-aware inversion,

domain adaptation, and genetic validation of traits against yield stability in clearly defined target environments.

Finally, integrating high-resolution remote sensing, physics-based leaf-canopy modelling, and targeted trait retrieval is essential for establishing robust mechanistic phenotyping frameworks. This approach will enable the selection of drought-tolerant sorghum varieties with improved adaptive plasticity and yield stability under increasingly variable environments.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/rs18162676/s1>.

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Abbreviations

4SAIL	4SAIL canopy model (Scattering by Arbitrarily Inclined Leaves)
ABARES	Australian Bureau of Agricultural and Resource Economics and Sciences
ABS	Australian Bureau of Statistics
AGB	Above-Ground Biomass
APSIM	Agricultural Production Systems Simulator
ASD	Analytical Spectral Devices
ASTER	Advanced Spaceborne Thermal Emission and Reflection Radiometer
BLUP	Best Linear Unbiased Prediction
BRDF	Bidirectional Reflectance Distribution Function
CO ₂	Carbon dioxide
CRIedge	Carotenoid Reflectance Index (Red-edge)
CSI	Canopy Stress Index
CV	Coefficient of Variation
EM	Electromagnetic
EMI	Electromagnetic Induction
ERT	Electrical Resistance Tomography
ERTS-1	Earth Resources Technology Satellite-1 (Landsat-1)
EVI	Enhanced Vegetation Index
FAOSTAT	FAO Statistical Database (Food and Agriculture Organisation of the UN)

Fv/Fm	Maximum quantum efficiency of PSII (Fv; variable fluorescence, Fm; maximum fluorescence)
GECKO	Genotype and Environment Characterisation through Kinetic Observation
GPC	Grain Protein Content
GSD	Ground Sampling Distance
GWAS	Genome-Wide Association Studies
H ²	Broad-sense heritability
HS	Hyperspectral
HSU	Humboldt State University
HTP/HTTP	High-Throughput Phenotyping
IGC	International Grains Council
L8	Landsat 8
LAI	Leaf Area Index
LI-600	LI-COR LI-600 Porometer/Fluorometer system
LiDAR	Light Detection and Ranging
LMA	Leaf Mass per Area
LT	Limited Transpiration
MAE	Mean Absolute Error
ML	Machine Learning
MS	Multi-spectral
MSAVI	Modified Soil Adjusted Vegetation Index
MSI	Moisture Stress Index
NANO	NANO hyperspectral radiometer/sensor system
NASA	National Aeronautics and Space Administration
NDRE	Normalised Difference Red Edge Index
NDVI	Normalised Difference Vegetation Index
NDWI	Normalised Difference Water Index
NOAA	National Oceanic and Atmospheric Administration
nRMSE	Normalised Root Mean Square Error
OSAVI	Optimised Soil Adjusted Vegetation Index
PLSR	Partial Least Squares Regression
PNC	Plant Nitrogen Concentration
PRI	Photochemical Reflectance Index
PROSAIL	Coupled leaf-canopy reflectance model (PROSPECT + SAIL)
PROSPECT	Leaf optical properties model
PSII	Photosystem II
QLD	Queensland
QTL	Quantitative Trait Locus
R ²	Coefficient of determination
RF	Random Forest
RGB	Red, Green, Blue (imaging)
RMSE	Root Mean Square Error
RTM	Radiative Transfer Model
RUE	Radiation Use Efficiency
S2	Sentinel-2
SA2	Statistical Area Level 2
SAIL	Scattering by Arbitrarily Inclined Leaves (canopy reflectance model)
SCOPE	Soil Canopy Observation, Photochemistry and Energy fluxes model
SIF	Solar-Induced Fluorescence
SLN	Specific Leaf Nitrogen
SPAD/SPAD-502	Soil Plant Analysis Development chlorophyll meter
SVC	Spectra Vista Corporation
TIR	Thermal Infrared
TIROS-1	Television Infrared Observation Satellite-1
TIRS	Thermal Infrared Sensor (Landsat 8/9)
TVDI	Temperature-Vegetation Dryness Index
UAV	Unmanned Aerial Vehicle
UQ	The University of Queensland

US	United States (of America)
USGS	United States Geological Survey
VI _s	Vegetation Indices
VPD	Vapour Pressure Deficit
WDRVI	Wide Dynamic Range Vegetation Index
WI	Water Index
WUE	Water Use Efficiency

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