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Functional phenotyping: Understanding the dynamic response of plants to drought stress

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ABSTRACT

Drought stress, exacerbated by climate change, presents a critical global challenge characterized by increasingly severe and prolonged dehydration events. This phenomenon poses significant obstacles to both agricultural productivity and ecological stability. One promising strategy for addressing this issue involves functional phenotyping, a methodology that provides invaluable insights into the intricate responses of plants to water scarcity. A profound understanding of these responses is crucial for the advancement of drought-tolerant crop cultivars/species, the optimization of irrigation methodologies, and the implementation of effective water resource management practices in agriculture. This review underscores the potential of developing an ideal phenotyping tool that continuously monitors a plant's physiological profile in response to shifting environmental parameters. Such an approach enables the multifaceted characterization and assessment of various functional phenotypes and productivity levels. Through the application of functional phenotyping techniques, we stand to gain invaluable insights into plant behaviour, thereby contributing to the development of drought-tolerant crops and the establishment of sustainable agricultural systems.

1. Introduction

Drought, a prevalent and damaging environmental constraint, poses a significant threat to plant growth and crop productivity. The anticipated global temperature rise, coupled with the growing demand for water to sustain the increasing world population, further exacerbates the depletion of soil water reserves. Ensuring adequate crop yields in the face of escalating drought conditions has become an urgent priority [1–4]. The plant's response to drought stress is influenced by factors such as stress duration, severity, genotype, and developmental stage. Nonetheless, it is evident that drought stress primarily hampers cell division and expansion rates, leading to reduced leaf size, shorter stems, and diminished root systems. Moreover, nutrient uptake is compromised in drying soils due to alterations in the physiochemical composition and flow of xylem sap [1,2]. The impact of climate change on temperature and precipitation patterns is altering the water balance of ecosystems, resulting in prolonged drought periods in temperate regions, among other extreme weather events. Without effective measures, these countries may face severe water shortages that would impact both water and food security [1,3,4].

Initially, the development of drought-tolerant plants relied on conventional breeding techniques, which involved crossing promising genotypes and utilizing the natural genetic variation available. With advancements in genetics, new methods were devised to overcome the limitations of traditional breeding, including the ability to precisely edit genes at the single-base level [3,5]. Regardless of the specific techniques employed, it is essential to phenotype the modified plants. According to the classical equation "phenotype = genotype × environment," a mutation in a single gene can have diverse effects on the plant's phenotype [6,7]. Drought, manifested in diverse patterns such as intermittent or continuous periods of water scarcity, represents an opportunity to induce, investigate, and comprehend the adaptive phenotypic and, physiological mechanisms employed by plants [7,8].

The practical application of functional trait analysis to develop improved crop lines remains limited, with only a handful of instances reported. This constraint primarily arises from technical challenges in phenotyping functional traits at a population scale, which currently lags behind advancements in breeding techniques [9–11]. Consequently, there is an immediate need to intensify efforts in plant phenomics, directing a greater focus towards the phenotyping of functional traits. This emphasis is crucial to promptly address the existing genotype-to-phenotype knowledge gap in future breeding programs.

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Due to limitations in phenotyping techniques, noninvasive and high-throughput analyses of underlying functional traits significantly lag behind the observation of morphological features, which are more readily captured by imaging systems [12–15]. Consequently, there is a pressing need for tools to discern fundamental functional traits. Crop/-plant models present promising solutions for identifying robust functional traits across diverse environments for breeding purposes [10]. These models enable the deconstruction of complex phenotypes into probable sets of mechanisms, facilitating the identification of key functional traits for crop improvement. Additionally, they offer an alternative approach to quantifying the potential benefits of trait modification in targeted scenarios [16,17]. Negin et al. (2017) introduced the concept of functional phenotyping, a novel approach that characterizes plant functions across multiple scales. This methodology addresses crucial knowledge deficits bridging genomic information with external phenotypes for intricate traits.

The pioneering work on ’functional phenotyping’ by Negin et al., 2017 in their paper published in ’Functional Plant Biology.’ They were the first to articulate the concept of functional phenotyping for crop selection, emphasizing the necessity for a practical approach to agronomically characterize plant responses to the environment, particularly under stress conditions, distinct from traditional phenotyping methods. Furthermore, they delineated various crucial aspects unique to functional phenotyping, specifically for drought tolerance in pre-field screening. These essential components encompass: (i) identifying optimal conditions for phenotyping, specifying the environmental settings for experiments; (ii) defining relevant and effectively measurable traits for phenotyping; (iii) choosing appropriate methods for phenotyping; and (iv) translating acquired data into actionable knowledge for informed decision-making in practical field applications [13]. Prior to composing this review, the Connected Papers tool was employed to identify articles related to functional phenotyping and drought stress. A visual representation, in the form of a graph, was generated where articles sharing similarities were proximally positioned, with connecting lines denoting their relationships. This graph illustrates publications both cited and published within the field of functional phenotyping and drought stress. The size of each node in the graph corresponds to the number of citations received by the respective article, while the shade of color of the nodes indicates the publication year of each article (Fig. 1). The important element of this review revolves around the application of functional phenotyping platforms for monitoring plant conditions under drought stress. Through the utilization of these platforms, we can

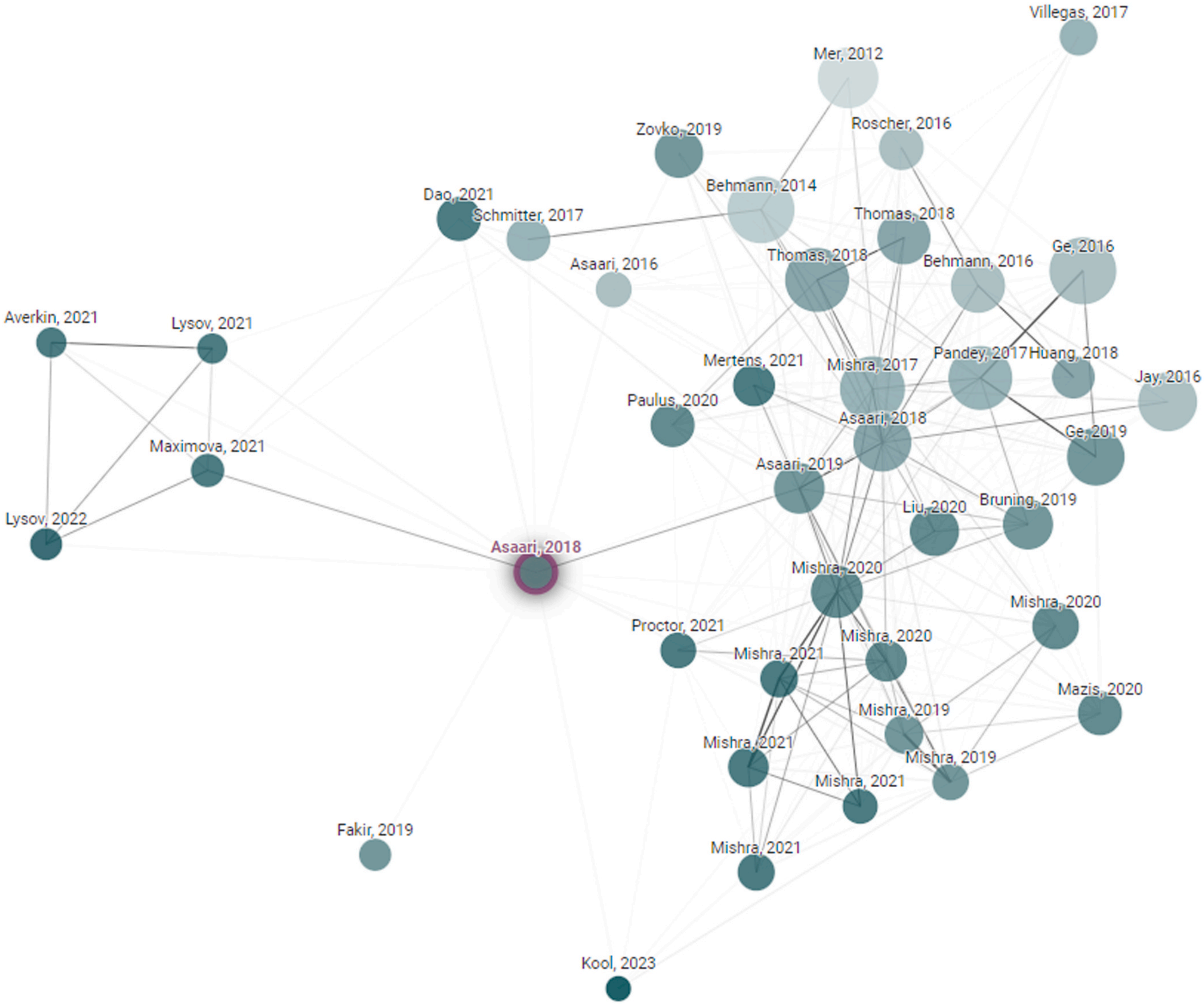

Fig. 1. The graph shows articles published and cited in field of functional phenotyping and drought stress. The size of each node in the graph indicated the number of citations an article has received, while the shade of color of the nodes represented the publication year of the article.

acquire a holistic comprehension of the adaptive mechanisms employed by plants. Moreover, employing various functional phenotyping approaches facilitates the creation of dependable predictive models for evaluating the drought tolerance of plants.

2. Plant drought stress and phenotyping

Plants exhibit diverse physiological, morphological, and biochemical traits as adaptive mechanisms in response to drought stress. These mechanisms allow them to cope with limited water availability and sustain their essential functions. Several studies have elucidated the different response and adaptive strategies employed by plants to combat abiotic water deficit stress. These strategies include, stomatal closure, drought escape and dehydration tolerance [18,19]. Drought stress triggers a range of physiological responses in plants, including stomatal closure to reduce water loss through transpiration, leading to decreased carbon dioxide uptake and photosynthesis. Additionally, drought stress often induces osmotic stress, resulting in cellular dehydration and altered ion balance [20–25]. Plants respond to drought stress at the molecular and biochemical levels by activating various stress-responsive genes and pathways. These include the synthesis of osmoprotectants such as proline and soluble sugars to maintain cellular turgor and protect cellular structures from damage [26–29]. Drought stress inhibits plant growth and development by affecting processes such as cell elongation, cell division, and flowering. Reduced water availability hampers nutrient uptake and transport, leading to stunted growth and delayed or aborted reproductive development [24,29,30]. Plants have evolved various mechanisms to adapt to drought stress, including morphological adaptations such as deep root systems to access groundwater, as well as biochemical and physiological adaptations to enhance water use efficiency and osmotic adjustment (Fig. 2) [7,27,29,31]. Functional phenotyping under drought stress involves evaluating plant traits and physiological processes to comprehend how plants cope with water scarcity. It quantifies performance-related traits like growth, development, and productivity under diverse environmental conditions, including drought. Various techniques such as imaging, spectroscopy, and physiological measurements aid in characterizing plant responses to drought stress across different scales, from molecular to whole-plant levels [16,32,33]. Studying plant water relations have traditionally relied on physiological parameters such as leaf gas exchange, canopy temperature, and spectral reflectance to assess water use efficiency. However, traditional methods, limited to specific leaf sections and time-consuming measurements, may not capture the overall plant response. In contrast, remote sensing techniques, such as infrared imaging, provide a rapid, straightforward, and cost-effective means to evaluate physiological traits in plants, offering a more comprehensive assessment of water-related characteristics [34–36]. In the process of phenotyping, we should prioritize key criteria (outlined in Table 1) to guide the planning and execution of functional phenotyping experiments. This entails selecting suitable experimental conditions, specifying the target trait, and opting for the most relevant phenotyping methods. These steps are essential for obtaining dependable and significant phenotypic data, facilitating subsequent analysis and informed decision-making.

Plant phenotyping is a rapidly advancing and wide-ranging area of research within the field of plant sciences. It involves the study of various characteristics of plants, and it is often carried out using specialized platforms that enable the simultaneous analysis of multiple plant features [37]. Phenotyping platforms are tools and systems designed to automate the process of measuring and analyzing the plant traits on a large scale. They typically combine various technologies, such as imaging, robotics, and sensors, to collect data on plant growth, physiology, and response to environmental factors [13,37]. These platforms are designed to rapidly screen large numbers of plants. They often use conveyor systems to move plants through imaging stations, where various sensors and cameras capture data on plant traits such as growth,

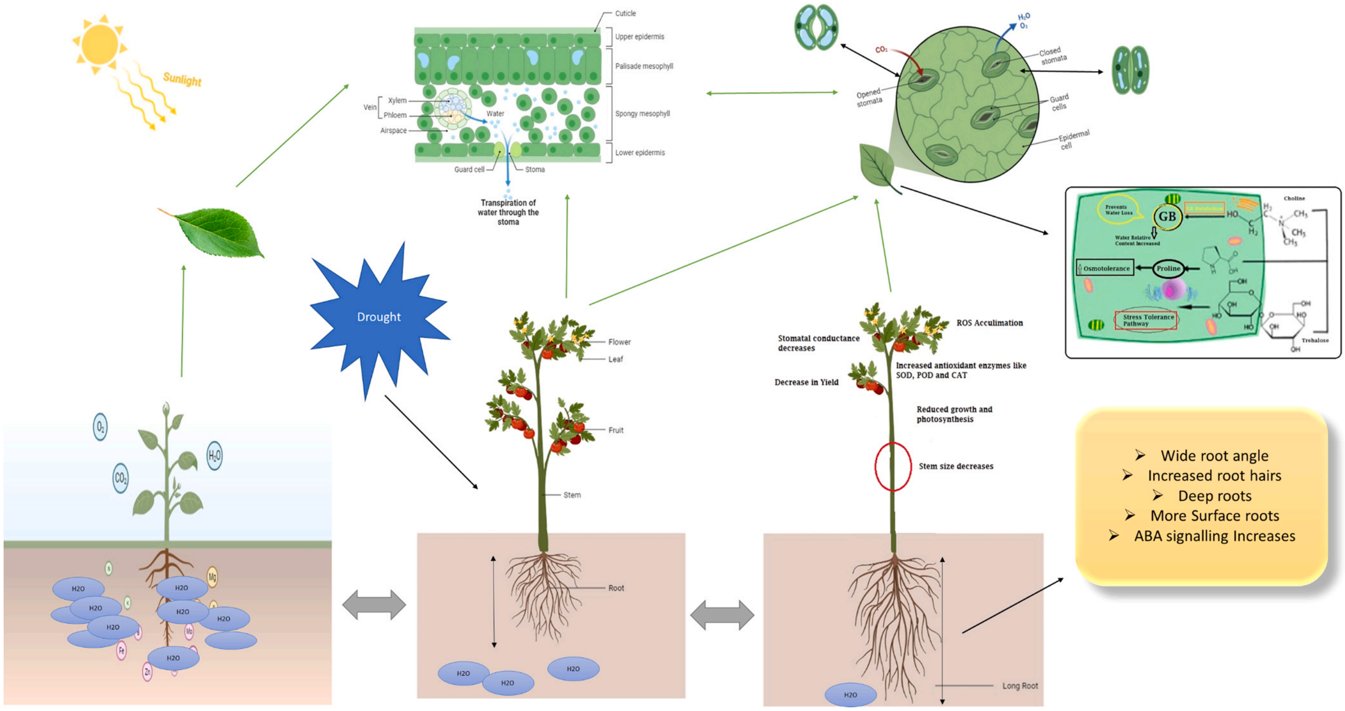

Fig. 2. The figure depicts plant adaptations to drought stress. It includes a representation of a plant thriving under optimal conditions with lush foliage, vigorous growth, and abundant flowering and fruiting. Additionally, it illustrates a drought-stressed plant with closed stomata to reduce transpiration and water loss. Osmotic adjustment is portrayed through the accumulation of compatible solutes like proline and soluble sugars to maintain cellular turgor. Root morphological adaptations, such as deeper root systems, enable access to groundwater reserves. Biochemical adaptations involve the activation of stress-responsive genes for osmoprotection and antioxidant defense. Water use efficiency enhancement mechanisms optimize water uptake, transport, and utilization in response to drought stress.

Table 1
Important criteria to effectively plan and execute for functional phenotyping experiments.

Component	Problem	Solution	Importance
Optimizing Phenotyping: Selecting Ideal Experimental Conditions	• It is difficult to define desired traits accurately with available different and inconsistent terminologies of desired traits. • It is hard to align treatment conditions with the expected environmental conditions in which the crop will grow.	• Clear definitions of agronomic crop tolerance should be formulated, considering the specific plant and goals of the study. • Multiple conditions should be assessed in cases where desired growth conditions are uncertain	• To determine the appropriate conditions (Where and When) to search for the desired trait.
Target Trait Definition for Phenotyping	• Conducting field trials in a high-throughput manner is challenging and costly. Field trials are considered the most reliable method for evaluating drought tolerance in crops, as they directly measure important traits. • Selecting plants that only perform well under stress conditions and testing more candidates with fewer field trials.	• Screening candidates can be performed using high-throughput methods and avoid selecting plants that only perform well under stressful conditions. • High-throughput measurements of plant behavior can be taken continuously which helps in screening for suitable traits.	• Capturing dynamic drought-tolerance traits through high-throughput techniques
Best method selection	• Improving drought tolerance in crops is a major challenge in breeding programs because it requires phenotyping of enormous number of plants. • Field experiments are difficult, so many screenings are done under controlled conditions, which may not reflect real field conditions.	• Technological advancements, such as remote-sensing methods like imaging and spectroscopy, have been used to overcome phenotyping bottlenecks. These methods measure various plant traits without causing damage, allowing multiple measurements throughout the growing season. • A multi-tier system has been proposed, where traits are screened using high-throughput systems to eliminate unsuitable plants rather than directly selecting the best performers.	• Pre-field screening for desired phenotypes can reduce the number of unsuitable plants and improve the chances of finding beneficial traits in field conditions. It is important to consider advanced technologies can capture measurement while keeping sensitivity and frequency of valuable data.
From Data to Decision: Practical Knowledge Extraction	• Although raw data can simply be converted into useful information, translating this information into meaningful knowledge that can help us understand how plants behave in different environments and select promising candidates for field trials is a challenge.	• Automated systems in future may provide a comprehensive set of a plant's physiological data. • Hypothetical models can be created to interpret this data in a way that allows us to understand how plants respond to specific conditions.	• Conversion of massive amounts of data into meaningful knowledge helps us understand how each plant responds to stress in its own unique way, based on its characteristics and physiological state.

leaf area, biomass, and chlorophyll content. Whereas, Imaging-based platforms rely on advanced imaging technologies, such as RGB (red, green, blue) and hyperspectral cameras to capture detailed information about plant traits [37–39].

Functional phenotyping permits the real-time monitoring of critical plant physiological processes, encompassing photosynthesis, stomatal conductance, water use efficiency, nutrient uptake, and hormonal signaling (as illustrated in Fig. 3). This real-time monitoring affords us for valuable insights into the temporal dynamics of stress adaptation, yielding a more comprehensive comprehension of how plants respond and adapt to challenging abiotic stress conditions. [13,40]. Various phenotyping platforms have been developed to investigate plant responses to abiotic stress [33,41]. In the case of drought stress, functional phenotyping allows for the precise characterization of stress levels based on parameters like 'theta crit' and facilitates quantitative understanding of plant responses. However, when utilizing pot-based functional phenotyping platforms, it is essential to exercise caution to avoid potential experimental artifacts that may arise from the pot effect. By taking necessary precautions, such artifacts can be eliminated, ensuring highly accurate results comparable to those obtained from studies conducted in gas-exchange chambers [13,42].

Mobile phenotyping platforms are designed for field-based studies. They often include robotic systems mounted on vehicles or drones, allowing for non-destructive and large-scale data collection across different locations and crop varieties. Controlled Environment Platforms provide tightly controlled growth conditions, such as temperature, humidity, light intensity, and CO_2 levels. These are frequently employed in controlled growth chambers or greenhouses and can scale up to large-scale field-based platforms to investigate plant responses to particular environmental conditions or stressors [35,43,44]. Platforms such as weighing lysimeters and gravimetric arrays provide non-destructive and non-invasive methods for continuously monitoring plant water relations. These systems can effectively capture dynamic environmental conditions like radiation, temperature, relative humidity, and vapor pressure deficit. Their advancements enable precise and comprehensive characterization of plant responses to water-related factors. Another sophisticated system, the Plantarray by Plant-DiTech, is renowned for creating specific drought scenarios and measuring various functional traits such as whole-plant transpiration and stomatal conductance. Additional platforms like the automated Drought Simulator Phenotyping Platform, HTP-telemetric phenotypic screening platforms, and Bioristor are also recognized for their capabilities in assessing plant responses to drought stress [12,40,41,43,45–52].

3. Direct and indirect functional phenotypic measurements

Functional phenotyping serves as a tool to directly evaluate plant physiological responses under varying environmental conditions. This encompasses direct measurements like transpiration rates, photosynthetic efficiency, stomatal conductance, growth rate assessments, nutrient uptake assays, and water-use efficiency (WUE) parameters [32,53]. Conversely, indirect functional phenotyping involves methods that deduce plant physiological status through indirect means, such as thermal imaging of the plant. These indirect techniques often employ optical methods to gather insights about the plant's health and its response to environmental changes. Examples include root architecture analysis, leaf morphology assessments, chlorophyll content estimation, and remote sensing imagery [16,54,55]. The latter method indirectly evaluates plant functional traits like canopy structure, biomass accumulation, or photosynthetic activity using satellite or drone-based remote sensing technologies. Analysis of remote sensing data enables the derivation of indices such as NDVI (Normalized Difference Vegetation Index) or PRI (Photochemical Reflectance Index) to infer the plant's functional status [16,40,54].

3.1. *Remote-sensing techniques*

Remote sensing techniques, such as multispectral imaging, thermal

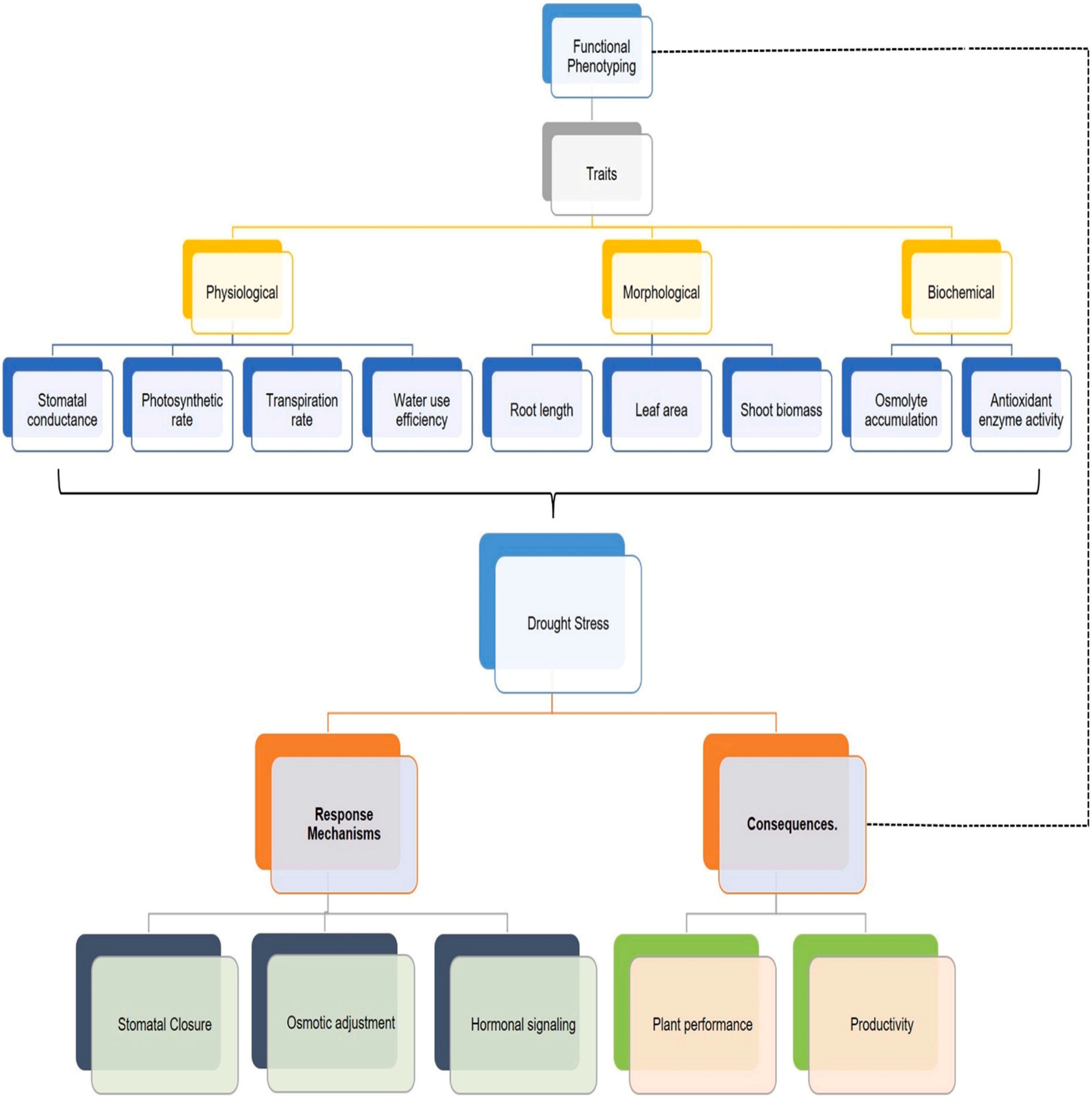

Fig. 3. Functional phenotyping is a comprehensive approach to assess plant responses to drought stress and improve drought resilience. It involves measuring various morphological, physiological, and biochemical traits in plants affected by drought. These traits include osmotic adjustment and stomatal closure, which help plants conserve water. Functional phenotyping allows us to identify specific traits and mechanisms associated with drought tolerance, aiding breeding efforts to develop more drought-tolerant crop varieties.

sensing, light detection and ranging (LiDAR), and vegetation indices, play a crucial role in monitoring crop growth, detecting stress, optimizing resource management, and aiding decision-making in agriculture by measuring different important phenotypic traits (Fig. 4) [56–59].

Multispectral imaging captures crop images in narrow spectral bands, providing valuable information on vegetation indices like normalized difference vegetation index (NDVI), indicating plant health, biomass, and growth stage. Thermal sensing measures crop thermal radiation, aiding in assessing water stress, detecting irrigation issues, and estimating water requirements [60–62]. LiDAR utilizes laser pulses to generate detailed 3D crop structure data, facilitating the study of crop height, canopy density, and biomass estimation [56,63]. Vegetation indices derived from remote sensing data, including NDVI, enhanced vegetation index (EVI), and soil-adjusted vegetation index (SAVI) offer quantitative measures of vegetation vigor and health [58,64]. These techniques empower us to make informed decisions on irrigation, fertilization, and disease control, ultimately enhancing crop productivity and sustainable agricultural practices.

Hyperspectral imaging is an advanced remote sensing technique that combines imaging and spectroscopy to capture and analyze the spectral signature of an object or scene across a wide range of wavelengths.

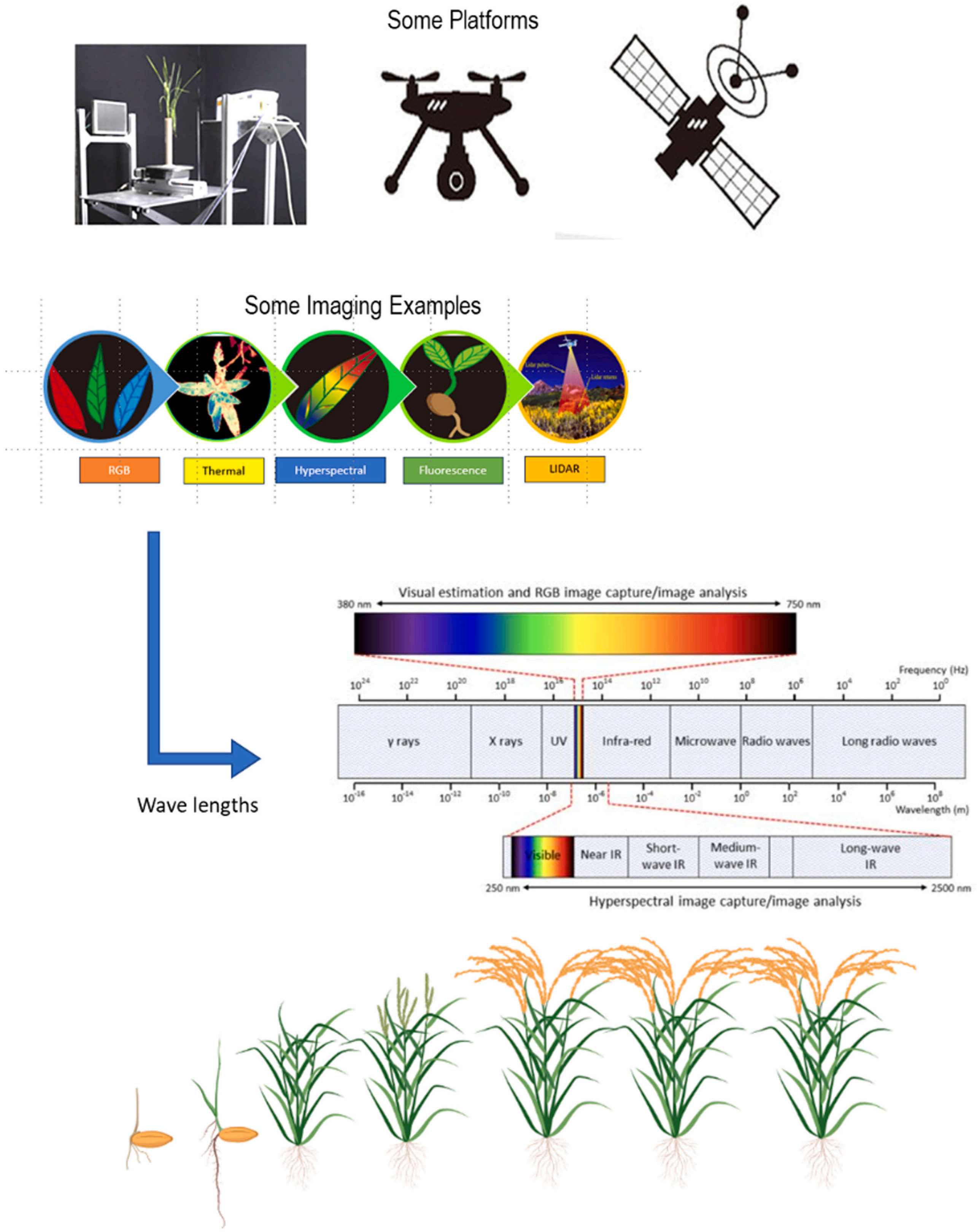

Fig. 4. The figure illustrates the use of advanced imaging technologies in imaging-based platforms to capture detailed information about plant traits.

Unlike traditional imaging methods that provide visual information only, hyperspectral imaging offers detailed spectral information for each pixel in an image [43]. This capability allows for the detection and characterization of subtle variations in plant responses to abiotic stress. Proximal hyperspectral sensing, in particular, involves capturing images with comprehensive spectral information for each pixel, covering a broad range of wavelengths. By utilizing proximal hyperspectral sensing, we can examine various plant processes in detail [65]. These include factors like leaf pigments, nutrient content, water status, photosynthetic activity, and stress responses. The high spatial resolution of this technique enables precise characterization of individual plant components such as leaves, stems, and fruits [34,66].

3.1.1. Hyperspectral imaging in drought Stress monitoring

Hyperspectral imaging has proven valuable in detecting drought stress in various crops by analyzing the spectral reflectance patterns associated with changes in leaf water content, stomatal conductance, and photosynthetic efficiency. Several notable studies have employed hyperspectral indices such as the normalized difference vegetation index (NDVI), water index (WI), and leaf water index (LWI) to evaluate drought stress in crops like wheat [67,68] and maize [69]. Detecting water stress at an early stage is crucial to prevent crop losses, as water stress can reach an irreversible state before visible symptoms appear [61]. Hyperspectral imaging, with its continuous spectral data, offers the potential to gain a deeper understanding of plant responses to water stress.

The use of hyperspectral technology was investigated for classifying soybean genotypes under varying water availability conditions throughout different stages of plant development. They found that the first three principal components, primarily in the shortwave infrared (SWIR) wavelengths, accounted for 94% of the spectral variance among soybean genotypes [70]. By employing a stepwise process, they identified up to 138 spectral bands that could effectively discriminate between soybean genotypes based on their response to water availability. Such information can contribute to understanding the mechanisms underlying plant responses to water stress and aid in the development of drought-tolerant crop varieties [70]. In another study, the application of hyperspectral data was investigated for early drought detection and assessment of leaf photosynthetic properties in citrus trees grown under greenhouse conditions. [71]. A study focusing on early-stage metabolism-driven responses to drought, even before visible signs of stress are noticeable in plants was conducted by burnett et al. They examined the physiology, biochemistry, and spectral responses of six different plant species grown under drought conditions in a greenhouse. They developed Partial Least Squares (PLS) models to predict metabolite content, achieving validation R2 values ranging from 0.49 to 0.87. To differentiate between watered plants and those affected by drought, the study employed Linear Discriminant Analysis (LDA) and PLS-Discriminant Analysis (PLS-DA) based on spectral characteristics and traits [72].

3.1.2. Chlorophyll fluorescence imaging

Chlorophyll fluorescence measurements have proven to be effective in detecting the physiological effects induced by a wide range of stressors [73]. By assessing the response of the photosynthetic machinery to these stressors, chlorophyll fluorescence measurements provide valuable insights into the overall health and performance of plants under challenging environmental conditions [74]. Unlike conventional analysis methods, chlorophyll fluorescence imaging allows for the capture and analysis of photosynthetic operation and regulation across the entire leaf surface. This imaging approach has introduced new opportunities for investigating the dynamic physiological processes of photosynthesis that cannot be discerned through traditional chlorophyll fluorescence analysis methods have contributed to the advancement and application of chlorophyll fluorescence imaging in plant research [75–77]. A cutting-edge robotic field scanning phenotyping platform was developed by Newcomb and Shakoor, 2022, specifically designed for conducting genetic studies on photosynthetic traits. This platform is equipped with a high-throughput chlorophyll fluorescence imaging system, allowing for efficient data collection in field trials. One of the key features of this platform is its ability to capture and analyze chlorophyll fluorescence in dark-adapted plants. By measuring the variable to maximum fluorescence ratio (Fv/Fm), they can assess the health and performance of plants' photosynthetic systems. The automated chlorophyll fluorescence imaging system integrated into the robotic field scanner enables rapid and non-destructive data collection. It captures fluorescence images of plants within field plots, providing a comprehensive view of the photosynthetic activity across the entire trial area [78].

3.1.3. Thermal Imaging

There has been a growing integration of thermal imaging with other imaging techniques. According to evaluations by Roitsch and Sperschneider, thermal infrared (TIR) cameras have been integrated with sensors like RGB, multi-, or hyperspectral cameras in phenotyping platforms. In order to develop reliable approaches for early diagnosis in agricultural fields, scientists can discover geographical and temporal trends by integrating TIR data with other pertinent vegetative indices (VIs). [79,80]. To identify a stress-specific signature, it is essential to do a preliminary examination of a particular plant-stressor interaction. Understanding these signs is crucial for appropriate interpretation since each plant stressor may have unique thermal properties. Complementary imaging methods together yield complicated and useful information [57].

Proximal sensing cameras can be mounted on static stands, small to medium-sized robots, or high-throughput platforms. The spatial and temporal resolution varies based on the sensor used and the revisiting frequency of satellites over a specific region. [81,82]. Thermal infrared (TIR) imaging is used to closely monitor drought stress, which can seriously harm crops. TIR imaging is essential to assisting farmers create accurate water management and scheduling plans. While most study on the effects of drought stress has been done in crop fields, several studies have additionally been conducted on plants cultivated under controlled (lab) conditions [81,83].

Thermography is not only useful for evaluating physiological variables related to plant water status but also for assessing production parameters. Several studies have demonstrated the correlation between thermal stress indices and grain yield in cereals like spring barley, maize, and wheat under various water conditions [57,84,85]. This suggests that thermography can be a valuable tool for predicting grain yield in these crops. The Crop Water Stress Index (CWSI) has proven to be a reliable predictor of garlic bulb biomass under different water availability levels. By assessing canopy temperature, thermography provides valuable insights into the water stress levels experienced by garlic plants, which directly impact bulb development and biomass accumulation [86].

3.1.4. Satellite imaging

An emerging trend in high-throughput phenotyping (HTP) is the integration of satellite imagery for monitoring agricultural plots and trials. Satellite imaging payloads have been utilized since the 1970 s to collect landscape-level information on crop growth, biochemical status, and phenology, offering high temporal resolution [87]. Comparisons between satellite and unmanned aerial vehicle (UAV) imagery have shown strong correlations in crops like wheat and field beans. However, in cases where satellite resolutions do not provide the desired level of detail for small plot trials, several techniques can be employed to enhance spatial resolution and improve the usability of lower-resolution data. These techniques include sub-pixel mapping, pan-sharpening, and the application of machine learning (ML) algorithms [88,89].

Satellite imagery, despite its limitations in capturing critical developmental stages due to factors like coverage frequency and cloud cover, can complement other high-throughput phenotyping (HTP) strategies such as UAV or ground-based measurements, providing adjustments with high temporal consistency. Comparisons between satellite and UAV imagery have shown strong correlations in crops like wheat and field beans, indicating their complementary nature[89,90]. To address the limitations of satellite resolutions for small plot trials, various techniques can be employed to enhance spatial resolution. Sub-pixel mapping using super-resolution models, traditional pan-sharpening methods, and the application of machine learning algorithms have been explored to improve the usability of lower-resolution data sources [88, 91]. While phenotyping offers numerous benefits, it also comes with certain challenges that are outlined in the Table 2 for discussion.

4. Recent advancements and platforms in functional phenotyping

In recent times, several high-throughput phenotyping platforms have emerged to address the difficulties associated with accurately phenotyping quantitative physiological traits (QPTs). These platforms, such as weighing lysimeters and gravimetric arrays, offer non-destructive and non-invasive systems for simultaneous and continuous monitoring of plant water relations. They can effectively capture dynamic environmental conditions, including radiation, temperature, relative humidity, and vapor pressure deficit. These advancements allow for more precise and comprehensive characterization of plant responses to water-related factors. [45,50]. The progress in phenotyping technologies, along with functional mapping methods, opens up new opportunities to comprehend the genetic foundations of plant responses to drought and identify crucial QPTs associated with drought tolerance. Through unraveling the underlying genetic mechanisms, we can devise improved breeding strategies to enhance drought tolerance in crop plants, ultimately bolstering global food security [92,93]. The impact of a specific quantitative physiological trait (QPT) on crop yield can vary depending on the severity and duration of drought conditions. For instance, low stomatal conductance is advantageous during severe drought as it reduces water loss, but it can be detrimental under mild drought by limiting photosynthesis. The phenotypic plasticity of QPTs in plants plays a crucial role in their adaptability to different environments, making it an important breeding trait for food security. However, accurately phenotyping yield-related QPTs presents challenges due to their dynamic nature. To overcome these challenges, a robust phenotyping system is needed that can continuously and simultaneously monitor plant physiological traits in response to changing environmental conditions, particularly those related to the soil-plant-atmosphere continuum (SPAC).[94,95]; [94,96,97].

Table 2
The challenges and limitations associated with advanced phenotyping.

S. No	Type of challenge	Description
1	Complexity	Phenotyping different traits accurately and comprehensively requires accounting for the interactions and dependencies between many factors, which poses significant challenges in experimental design, data collection, and data analysis.
2	Trait Selection	Choosing relevant and informative traits is crucial but challenging. Furthermore, standardizing phenotyping protocols is essential to ensure consistency and comparability of results.
3	Non-invasive and Measurement	Developing techniques that can accurately capture detailed phenotypic information, especially at the cellular or subcellular level, remains challenging
4	Large Scale data Management	The generation of large-scale phenotypic datasets poses challenges in data management, storage, and analysis. Standardization of data formats, metadata, and ontologies is crucial for facilitating data sharing, collaboration, and comparative analyses
5	Controlled Environment to Field Conditions	The translation of phenotyping results obtained from controlled environments, such as growth chambers or greenhouses, to field conditions poses challenges due to the inherent complexity and variability of field environments
6	Cost and Accessibility	Many advanced phenotyping technologies and infrastructure can be costly, limiting their accessibility to us and breeders, particularly in resource-limited settings

Another challenge involves closing the knowledge gap between phenotypes and genotypes in order to effectively handle the extensive data on quantitative physiological traits obtained from pedigreed or natural populations. It is crucial to identify precise quantitative trait loci (QTLs) and comprehend the genetic interactions that drive phenotypic variations. Traditional genetic mapping methods typically rely on static data collected at a single time point, which may not fully capture the dynamic nature of QTL effects [98–100]. To overcome these challenges, there is a need for advanced methodologies that can integrate dynamic phenotypic data with genotypic information. Such approaches would enable the identification of time-varying QTLs and provide insights into the underlying genetic mechanisms driving phenotypic variations over time. An example of a platform that addresses these challenges is the Functional Phenomics Platform (FPP), which enables the continuous measurement of various plant-related factors as well as ambient conditions, encompassing soil and atmosphere parameters. These platforms provide a comprehensive and real-time monitoring system for studying and understanding the complex interactions between plants and their environment [40].

Functional mapping (FM) a mathematical approach that integrates the dynamic pathways involved in phenotypic formation. By utilizing mathematical equations, FM can uncover the quantitative trait loci (QTLs) that govern rate-limiting processes and quantify the changes in their genetic effects over time or space [51]. FM provides a comprehensive understanding of the genetic basis of complex traits and their temporal or spatial variations. By combining genetic and physiological information, FM reveals the underlying genetic architecture of quantitative traits and how they respond to changing environmental conditions. In the context of drought stress, FM can be particularly valuable. By integrating data from high-throughput phenotyping platforms with genetic information, FM allows for the identification of specific QTLs that are responsible for the dynamic phenotypic changes observed under drought stress [37,51]. In a research study that specifically investigated an introgression line population of tomatoes exposed to progressive drought stress and subsequent recovery, the combination of Functional Phenomics Platform (FPP) and Functional Mapping (FM) proved to be a valuable approach in unraveling the genetic basis of weight-normalized transpiration rate (E), which is a dynamic trait [46]. By employing FPP, which allowed for continuous measurement of E, and applying the principles of FM, the plant scientist were able to uncover the genetic factors responsible for the variations observed in E throughout the duration of the drought stress and subsequent recovery period [51]. This integrated approach provided a deeper understanding of how genetic factors influence the dynamics of E under drought conditions. It allowed them to identify specific genomic regions, known as quantitative trait loci (QTLs) that were associated with variations in E during different stages of the stress and recovery process [40,46].

This joint framework of FPP and FM has the potential to shed light on the genetic factors and underlying mechanisms involved in trait dynamics. By analyzing the continuous and integrated data, we can identify key genetic components associated with the variations in traits over time or in response to specific stressors [46,52]. It can be applied to a wide range of physiological processes and stress responses, allowing us to investigate diverse aspects of plant biology and improve crop performance under challenging environmental conditions [37,40].

4.1. Automated drought simulator phenotyping platform

In a study acquired drought tolerance (ADT) traits in two rice cultivars were examined, one which is drought susceptible (IR64) and another is drought tolerant (Apo), as well as a drought-tolerant wheat cultivar named Weebill. To induce soil moisture stress and capture above-ground vegetative traits accurately, they utilized a novel phenomic platform equipped with an automated irrigation system. This platform allowed precise control over soil moisture levels, enabling them to simulate drought conditions and monitor the resulting effects on plant growth and development. This system enabled the gradual progression of drought stress by employing software-controlled automated irrigation, ensuring consistent soil moisture levels regardless of variations in transpiration rates [101]. Another system known for its sophisticated ability to create specific drought scenarios as well as to measure many functional traits (whole-plant transpiration and stomatal conductance, etc.) is Plantarray (by Plant-DiTech). This system is capable of tailoring stress levels to each plant in a feedback-irrigation algorithm, considering its size and conditions, by integrating plant transpiration, soil sensing, and target weight adjustments in dynamic environments [47].

The implementation of this approach provided an accurate method for assessing ADT traits in the plants. The phenomic platform with its automated irrigation system emerged as a valuable tool in imposing and monitoring drought stress conditions with precision. It enabled to examine ADT (Above-ground Dry Biomass) traits during the vegetative stage of plants. Also, the Plantarray system measures the actual plant biomass continuously and simultaneously for all plants. Therefore, the platform facilitated the generation of specific and comparable stress conditions, enhancing the reliability and reproducibility of the experimental results. [101].

4.2. HTP-telemetric phenotypic screening platforms

The automated measurement and transmission of data from distant sources to a central receiving station via telemetry technology is essential for easing data recording and analysis. A nondestructive High-Throughput (HTP) telemetric device that combines several weighing lysimeters and environmental sensors for effective data gathering and processing is shown in a recent work by Dalal et al. (2020). This platform eliminates the need for image analysis by allowing the computation of several metrics in real-time, including whole-plant biomass gain, transpiration rates, stomatal conductance, root fluxes, and water-use efficiency (WUE). In particular, for controlled environment phenotyping research targeted at greenhouse drought stress investigations, real-time data processing improves the translation of data into usable knowledge. The telemetry platform offers several benefits, including scalability, easy installation, and minimal infrastructure requirements in growth facilities. It operates on a sensor-based system without moving parts, resulting in relatively low maintenance costs both in terms of initial investment and long-term upkeep. For instance, the cost of a 20-unit gravimetric system with feedback fertigation systems, a meteorological station, and software is comparable to that of a single portable gas-exchange system from a leading brand [48].

4.3. Bioristor

In 2019, Michela Janni and her team introduced a pioneering in vivo sensing device called the bioristor, which is an organic electrochemical transistor (OECT) sensor. This sensor was successfully integrated into the stem of tomato plants, enabling continuous monitoring of the plant's physiological state throughout its life cycle. The bioristor demonstrated its effectiveness in detecting changes in ion concentration within the plant's sap under drought conditions, providing immediate detection of drought stress and activation of defense responses (Janni et al., 2019). By combining the bioristor data with a high-throughput phenotyping platform, it showcased the complementary nature of these methods in studying mechanisms related to drought stress. These experiments represent a significant advancement in in vivo sensing technology applied to tomato plants. The bioristor offers several advantages for precision agriculture and high-throughput phenotyping of drought response, including continuous monitoring of plant physiology, minimal invasiveness, low cost, and easily interpretable data. Overall, the bioristor holds great promise as a valuable tool for studying and addressing drought stress in agricultural settings [49].

4.4. The functional phenotyping plant array 3.0 platform

In a 2019 study conducted by Ahan Dalal and colleagues, they utilized the Plantarray 3.0 platform (Plant-Ditech), a functional phenotyping system, to monitor plant performance throughout their experiment. This platform allowed them to control the irrigation schedule and quantity, enabling high-throughput physiological functional phenotyping. The system consisted of 72 units equipped with highly sensitive load cells that served as weighing lysimeters [47]. These load cells were temperature-compensated and connected to personalized controllers that collected data and controlled irrigation for each individual plant. To achieve precise irrigation, each pot had its own independent controller, which facilitated tight feedback irrigation based on the plant's transpiration rate. The controllers were interconnected, allowing for serial data collection and transmission to a server. Each pot, containing a single plant, was placed on a load cell for weighing purposes (more information in the "Experimental Setup" section). The collected data were analyzed using SPAC analytics, an online web-based software provided by Plant-Ditech. This software enabled real-time data visualization and analysis of the information gathered from the Plantarray system.

The utilization of the setup provided several advantages, including the ability to monitor water-related dynamics and plant-environment responses with high precision throughout the entire life cycle of the plant. The use of the phenomic platform with an automated irrigation system facilitated the implementation of a randomized experimental design with multiple independent treatment scenarios for each plant. This design minimized artificial disturbances arising from plant immobility or other objects, ensuring robust experimental conditions. Additionally, the study introduced two novel resilience-related traits: transpiration recovery rate and night water reabsorption. These traits were accurately measured using the High-Throughput Field Phenotyping System (HFPS) incorporated in the phenomic platform. The HFPS enabled efficient and precise measurements of these traits, providing valuable insights into the plants' capacity to recover from drought stress and their ability to reabsorb water during the night. These novel traits contribute to a better understanding of plant resilience mechanisms under drought conditions. The study provided valuable insights into the pre-field phenotyping of plants/crops using these biostimulants, emphasizing the significance of assessing their physiological mechanisms of action before their application in the field [47].

5. Conclusion

Identifying physiological markers that can effectively and easily select parental inbred lines and hybrids is crucial for improving breeding processes and developing plant varieties with drought stress tolerance. These markers need to be easily measurable, quickly assessed, and genetically heritable. The approach of integrating functional physiological phenotyping and functional genomics in studying plant responses to drought holds great potential for breeders. It enables the dynamic study of how plants react to drought stress and the discovery of crucial traits linked to tolerance. Furthermore, the relationship between agricultural productivity and physicochemical variables presents a chance to create effective algorithms for crop modeling, early yield forecasting, and predicting yield losses due to drought.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

No data was used for the research described in the article.

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