

Review

Phenotyping Common Bean Under Drought Stress: High-Throughput Approaches for Enhanced Drought Tolerance

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Abstract: In the course of climate change, drought is becoming one of the most important abiotic stress factors in agroecosystems and significantly affects agricultural productivity. Common bean (*Phaseolus vulgaris* L.), one of the most important legumes with a high protein content for human consumption, is very sensitive to water deficit. Thus, it is important to understand the physiological and developmental effects of water deficit on the bean. Thanks to technological advances, traditional phenotyping methods have evolved towards high-throughput phenotyping (HTP), which utilizes various imaging technologies for rapid and non-destructive monitoring of plant traits. This review examines the effects of water deficit on bean morphology (roots, leaves, stems, and generative organs), physiology (photosynthesis, antioxidant activity, phytohormones), and gene expression. We will also describe the HTP techniques used to quantify this water deficit-induced response through different imaging techniques and evaluate their applicability for the generation of reliable phenotypic data and the selection of drought-tolerant genotypes for further breeding and genetic progress.

Keywords: drought; high-throughput phenotyping; morphology; genetic improvement



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1. Introduction

Climate change is leading to increasingly frequent occurrences of drought and other abiotic stress factors in agroecosystems. Drought is a complex ecological phenomenon that can be divided into several categories depending on its impact and consequences: meteorological drought, which is caused by a lack of precipitation; hydrological drought, caused by a decrease in the water levels in the surface and subsurface water layers; and agricultural drought, which causes plant stress due to low soil moisture [1], i.e., water deficit. Water deficit is the main cause of crop losses, leading to global food price instability and uncertainty.

Common bean (*Phaseolus vulgaris* L.) is a plant species that can adapt to various climatic conditions, so its cultivation is widespread [2]. Due to its high nutritional and economic value, it is considered one of the most important crops for direct human consumption [3]. Whether the beans are grown on small farms or on large cultivation areas, the lack of

investment in irrigation systems and infrastructure due to the high costs means that the plants are often exposed to unfavorable environmental conditions [4]. It is estimated that 60% of global bean production takes place in regions with water scarcity [5]. There are reports that water deficit leads to yield losses of up to 50%, especially in the flowering and pod-filling stages, which are the most drought-sensitive stages of plant development [6]. However, water deficit as well as any combination of abiotic stress factors can lead to a complete loss of yield, such as the combination of heat and drought [7].

Water deficit affects all major physiological and developmental processes of plants, such as respiration, photosynthesis, nutrient uptake, and root and shoot growth, leading to significant yield losses [8]. As drought exerts complex effects on the molecular, biochemical, physiological, and phenological processes of plants and their morphological development, understanding the plant phenotype under drought conditions is crucial to gaining insights into plant responses and adaptation to this stress.

Phenotyping refers to a quantitative description of plant characteristics (anatomical, ontogenetic, physiological, and biochemical) in its natural environment [9]. While traditional phenotyping methods have contributed to the understanding of plant traits, technological advancements in the last two decades have led to the development of high-throughput phenotyping (HTP).

High-throughput phenotyping (HTP) comprises non-destructive and rapid methods for monitoring and measuring multiple phenotypic traits related to growth, yield, and adaptation to biotic or abiotic stress. HTP integrates various disciplines, such as plant science, environmental science, engineering, imaging and sensor technologies, mathematics, statistics, and computation [10,11]. HTP typically involves the use of cameras, including visible (RGB), multispectral, hyperspectral, thermal, and chlorophyll fluorescence cameras and technologies such as lidar and 3D scanning [12–15]. These techniques accelerate and facilitate phenotyping research by providing precise insight into the physiological state of plants under different environmental conditions. They can efficiently detect morphological and biochemical changes and enable rapid data collection and processing [16]. They have also proven to be highly effective for the early detection of plant stress responses and are widely used under both controlled and field conditions [17].

All of the above HTP methods have been successfully used in bean phenotyping under controlled conditions and in the field. Researchers have used these powerful tools in selecting resistant bean genotypes, monitoring the effects of drought, selecting specific traits that contribute to drought resistance, or predicting the onset of drought [12,14,18].

Collected phenotypic data can be combined with genotypic data to expand the understanding of the genetic basis of drought tolerance and the adaptation mechanisms of beans through genome-wide association studies (GWASs) and the identification of quantitative trait loci (QTLs) [19]. By combining these powerful tools, we can successfully support breeding programs and create new drought-resistant genotypes.

In this review, we highlight the key morphological, physiological, and molecular responses and traits associated with drought tolerance in common bean. In addition, we summarize the effectiveness of different high-throughput phenotyping (HTP) methods for drought detection and their application in the selection of drought-tolerant genotypes of common bean.

In this review, we have included studies conducted under both controlled and field conditions, recognizing that experimental water deficit treatments often differ from naturally occurring drought, which is typically a complex interplay of factors such as soil moisture decline, high temperatures, vapor pressure deficit, and radiation load. Nevertheless, all cited studies share a common objective—to induce plant responses to water deficit to better understand the physiological, morphological, or molecular traits associated

with drought tolerance. While not all experiments reflect the precise water regimes of major common bean production regions, they provide valuable insights into how different genotypes respond to water deficits. This broader approach is essential given the high diversity in common bean germplasm, where genotypic variation in phenology and stress response can influence both the expression and detectability of drought-adaptive traits. The phenotyping methods and traits discussed here are thus considered within a comparative framework that seeks to identify robust indicators of drought tolerance across environments and genetic backgrounds.

2. Key Developmental, Morphological, Physiological, and Molecular Responses to Drought Stress in Common Bean

There are considerable morphological and physiological differences between the various morphotypes of common bean, leading to different levels of tolerance to drought [20]. Since it was independently domesticated at least twice, there are two major gene pools in the cultivated common bean: the Mesoamerican and the Andean [21]. Certain genotypes from these pools may have developed specific traits that contribute to drought tolerance. The superior performance of these genotypes under drought is usually associated with increased biomass accumulation. Increased canopy biomass accumulation is related to a deeper and more vigorous root system that facilitates the uptake of soil moisture. These traits, in combination with the efficient remobilization of photosynthates from the vegetative structures for pod production and grain filling, will lead to higher yields under water deficit conditions [20]. Tepary bean (*Phaseolus acutifolius* L.), a minor crop closely related to common bean, has been used as a model plant for studying the drought tolerance of beans since the 1980s [22]. A recent breakthrough is the development of *P. vulgaris* × *P. acutifolius* hybrids. The hybrids combine the desirable seed characteristics of *P. vulgaris* with the drought resistance of *P. acutifolius* and are therefore a promising candidate for breeding drought-tolerant bean genotypes [23]. The drought tolerance of tepary bean is attributed to several traits, including extensive fine root formation, efficient water utilization, small leaves that minimize transpiration losses, osmotic adaptation, high sink strength, and enhanced mobilization of photoassimilates for pod and seed development [24]. All of these traits that contribute to drought tolerance are the result of a complex interplay involving a series of responses at morphological, physiological, and molecular levels (gene activation, regulation of photosynthesis, osmotic adjustment, synthesis of protective macromolecules and antioxidants) [25]. In the following chapters, we will outline the impact of drought stress on the morphological, physiological, and molecular aspects of beans and the HTP methods which can be utilized for quantification of these drought-induced responses. At the end of the chapter, we summarize the morphological, physiological, and molecular responses of bean to drought stress in Figure 1.

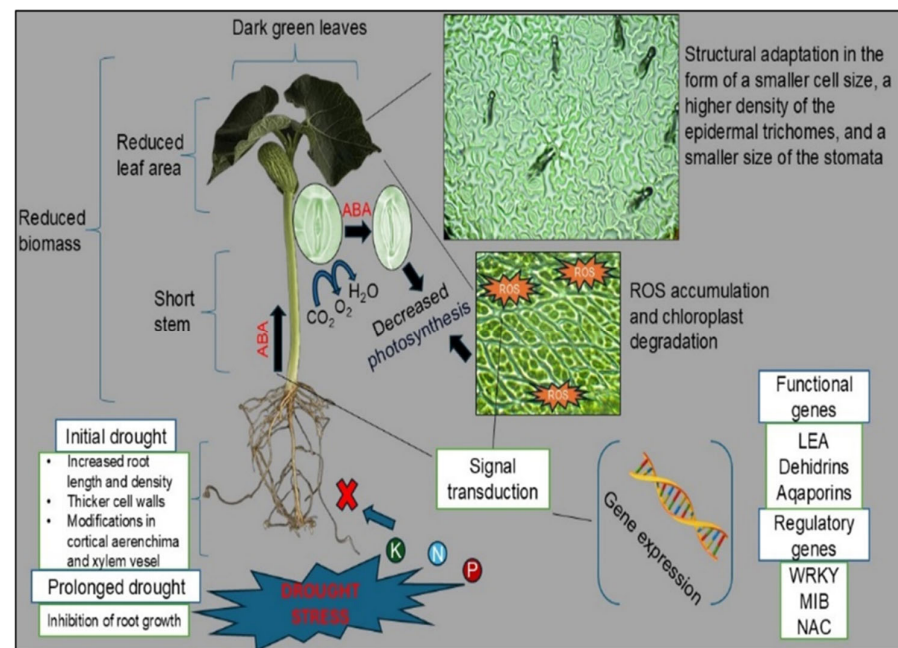


Figure 1. The structural adaptations of bean shoots and roots to drought stress with physiological responses based on molecular reactions and gene expression.

2.1. Root Morphology

The root system is the primary factor in the plant's water uptake due to its spatial architecture and hydraulic conductance [26]. The root system is crucial for plant responses and adaptations to drought. Some plant species can increase their root growth in the early phase of drought stress, allowing them to uptake water from deeper soil layers [27]. Many authors have found a positive correlation between root architecture plasticity and the degree of drought tolerance in legumes [27–29]. Legumes like chickpeas (*Cicer arietinum* L.), peas (*Pisum sativum* L.), and soybean (*Glycine max* [L.] Merr.) exhibit adaptive root traits under drought conditions. These include increased root length, density, deeper roots, and changes in vascular anatomy [30,31]. Root anatomical features such as thicker cell walls, increased sclerenchyma production, and more medullary rays contribute to drought tolerance [31]. Root cortical aerenchyma, xylem vessel modifications, and endodermal suberization can improve water acquisition in drying soils [32].

A study by the Centro Internacional de Agricultura Tropical (CIAT) found that drought-tolerant bean genotypes have deeper root growth. However, their benefits are limited when soil conditions restrict root growth, such as low pH and high aluminum saturation [33]. Furthermore, studies on grafting have been particularly informative. The results indicate that root traits are of major importance in determining the drought response of common bean, and that, conversely, shoot traits are of much less importance. However, the response of specific genotypes varies greatly with the environment [34]. These results are mainly due to the different characteristics of the experimental sites. One soil was the fertile Mollisol, while the other was Oxisol with low pH and aluminum saturation.

Depending on the duration, drought can reduce root growth in beans. However, in the recovery phase, root growth can resume and help the plants to recover [35]. The main drivers of spatial plasticity of root architecture traits in beans are increased root diameter, surface area, and volume in the deeper soil layers. A larger root diameter of tap and basal roots helps penetrate deeper soil layers. At the same time, a larger surface area and volume allow plants to increase the area explored by a given root mass and improve water uptake from deeper layers [29]. However, excessive root development can lead to an imbalance between above- and belowground biomass, which limits light absorption

and carbon assimilation, thus reducing plant productivity [36]. Therefore, in addition to root development, it is important to consider the different adaptation mechanisms of the aboveground organs to understand plant ability to adapt to drought. An example of this is *Phaseolus acutifolius* L. with its fine root architecture and smaller leaves compared to common bean, or even better, an advanced *P. vulgaris* × *P. acutifolius* hybrid, such as INB 47 with its balanced root-to-shoot ratio and stable yield under drought stress [23].

2.2. Stem Morphology

Drought leads to the changes in the internal structure and then in the external appearance/shape of the stem [37]. Stem thickness, diameter, height, color, and overall functionality are affected under water deficit conditions, resulting in reduced structural and physiological performance [38,39]. Water deficit reduced the stem height in common beans with different growth habits (indeterminate upright cultivar and bushy determinate upright cultivar) [39]. The color of common bean stems also changes under drought conditions, which is associated with stem wilting. Drought-tolerant bean genotypes are able to maintain the green color of their stems compared to susceptible genotypes. Thus, greener stems are an indication of drought tolerance, as plants with greener stems recover more effectively after rewatering [38]. Water deficit affects the phloem transport of the assimilates from the source to the reproductive organs (sink), causing them to accumulate in the source leaves and stems [40]. The accumulation of assimilates, such as soluble sugars and starch in the stem, can be beneficial under drought conditions, as a higher concentration of assimilates lowers the water potential in the phloem, facilitating water influx from the xylem. This process expands the stem's soft tissues and helps to maintain turgor pressure [41].

2.3. Leaf Morphology

During drought, the turgor pressure in the cells decreases [42]. Cell growth is directly influenced by turgor, and when it decreases, the cell membrane becomes thicker, the cell wall is less elastic, and the cytoplasm is more concentrated [37]. The inhibition of mitosis and the disruption of cell growth lead to a reduction in leaf area and plant height [43]. Many authors have reported such results in beans grown under drought [6,35,44]. Drought significantly reduces common beans' leaflet blade thickness (40%), palisade thickness (43%), spongy tissue (11%), midvein length (35%), midvein width (41%), phloem thickness (38%), xylem thickness (33%), and vessel diameter (30%) [45]. Decreased turgor causes leaf wilting, a passive form of leaf movement, which prevents excessive water loss during drought [46]. On the other hand, heliotropic movements of leaves are active forms of adaptation that reduce the amount of absorbed light and, thus, excessive heating of leaves. Bean plants orientate their leaves more frequently to reduce midday stress [47]. These include the ability of leaves to turn in the opposite direction to the light source or to point their edges directly towards the light source [46]. Pastenes et al. [48] identified paraheliotropism as an important trait of bean plants to reduce light interception, avoid photoinhibition and protect their photosystems. This leaf shading adaptation helps to reduce overall transpiration but significantly affects overall biomass production and plant functionality [37].

Under drought, plants can form a waxy layer on their leaves, develop more epidermal trichomes, reduce stomatal size, and increase cuticle thickness to minimize water loss and enhance drought tolerance. These morphological adaptations reduce excessive transpiration and increase light reflection from the leaf surface [49,50]. The ideal drought-tolerant common bean plants could exhibit specific leaf adaptations, including epicuticular wax crystalloids, a thick cuticle, a higher density of longer trichomes, and a lower density of smaller stomata [49].

2.4. Generative Organs

Flowering and pollination are the most drought-sensitive development phases in the plant's life cycle. In addition, drought intensity and duration influence the onset and duration of flowering and flower development [51]. Negative changes in the flower itself relate to the sterility of the pollen grain, fewer pollen grains, and volatiles in the flower, which can influence the attractiveness of flowers to pollinators [52]. In common beans, drought conditions lead to morphological changes in the flowers, including premature senescence and shedding, while changes in the pods are characterized by inhibited elongation, a reduced diameter, and the abortion of young pods. Drought has been reported to significantly reduce the number of flowers, with Nuñez Barrios et al. [44] reporting a 50% reduction in pod set [39,44] and a 40% decrease in grain yield [39,53].

To cope with the negative effects of drought, some bean genotypes can shorten their life cycle by increasing their metabolic activity. In the study by Soureshjani et al. [54], two bean genotypes were exposed to different levels of drought. While the drought significantly reduced the yield of both genotypes, the genotype that shortened its life cycle by reducing the number of days from flowering to maturity under drought conditions achieved a higher yield.

Drought also affects the vigor and germination rate of common bean seeds. It disrupts seed metabolism and alters endogenous hormone levels, resulting in lower soluble sugar content, impaired respiration, and decreased energy production for seed germination. These effects contribute significantly to production losses and have a negative impact on seed germination and early seedling survival [55]. Wu et al. [56] reported five times lower bean seed germination vigor and a two times lower germination rate under drought compared to control conditions.

2.5. Stomatal Conductance and Transpiration

The stomata are responsible for regulating the uptake and assimilation of CO₂ and optimizing transpiration [57]. Therefore, the function of stomata in regulating transpiration becomes particularly important under conditions of water scarcity. Plants that are well adapted to drought close their stomata before reaching plant dehydration [58]. The guard cells are extremely sensitive to changes in water availability. Once stimulated (such as changes in water potential, ABA signaling, and the efflux of potassium ions), the stomata limit water diffusion and thus regulate the rate of gas exchange and photosynthesis [58]. For this reason, size, density, and stomatal conductance are closely related to the plant's tolerance to drought [24,59]. In the study by Polania et al. [24], both tepary bean and common bean genotypes exhibited a reduction in stomatal size across leaves from the lower, middle, and upper sections under drought conditions. This adaptation enables the plants to regulate the stomata's opening and closing more effectively, thus improving carbon utilization while minimizing water loss. By measuring stomatal conductance, it is possible to quantify drought stress and select drought-tolerant genotypes. Drought-tolerant genotypes can maintain higher stomatal conductance, stable gas exchange, and higher photosynthetic rate under dry conditions compared to sensitive genotypes [60]. Gonçalves et al. [61] studied drought tolerance in an extensive collection of common bean genotypes and found that genotypes with higher stomatal conductance also exhibited higher yields under drought conditions. This indicates that stomatal conductance could be used as a reliable trait for the early selection of drought-tolerant bean genotypes. Polania et al. [62] analyzed 36 bean genotypes under field conditions and identified six drought-tolerant genotypes that were termed "water savers" and showed a positive correlation between stomatal conductance, water use efficiency, and yield. The authors also described

common bean tolerance mechanisms, including early stomatal closure, reduced stomatal development, and restricted biomass accumulation to conserve soil water.

Decreased CO₂ uptake caused by stomatal regulation leads to an imbalance in the intercellular (mesophyll) CO₂ concentration. In addition to stomatal regulation, the characteristics of the leaf mesophyll play a significant role in facilitating CO₂ diffusion to the carboxylation site [8]. As reported in the chapter on leaf morphology, the leaf thickness of beans decreases under drought conditions [45]. The reduction in leaf thickness (especially the mesophyll) represents the adaptation that facilitates the diffusion of CO₂ in the leaf to the carboxylation site [8].

2.6. Photosynthetic Pigments

Photosynthetic pigments are responsible for the absorption of photosynthetically active radiation (PAR), which is converted into chemical energy in the process of photosynthesis. The content of photosynthetic pigments is positively correlated with the intensity of photosynthesis [63]. In contrast, a decreasing pigment content is a typical symptom of drought stress due to oxidative stress or photooxidation, which decreases photosynthesis [64]. Drought stress alters the ratio of chlorophyll a and b and the carotenoid content. By reducing the content of photosynthetic pigments, photosynthesis's efficiency declines, which in turn reduces the plant's energy production and its ability to survive and adapt under stressful conditions [65]. Since photosynthetic pigments are sensitive to drought stress, their content can be a reliable indicator of a plant's tolerance and adaptability to drought. Plants that can maintain a high chlorophyll content under drought conditions can utilize light energy more efficiently and are considered more drought-tolerant [66]. In some cases, reducing chlorophyll content can be a good strategy to protect the plant from excessive overheating, which often occurs under dry conditions [65]. The HTP technique, such as chlorophyll fluorescence imaging, provides a comprehensive insight into the distribution of light energy. Its absorption, reflection, or loss in the form of heat can be an excellent indicator of how plants utilize light energy [67]. This topic is covered in more detail in Section 3.

Despite these facts, studies on the effects of drought on the photosynthetic pigments of beans provide contradictory results. For example, several authors found a significant reduction in common beans' chlorophyll content under drought conditions [68,69], which was related to drought-induced oxidative stress [69]. On the other hand, Sánchez-Reinoso et al. [70] found that drought increased chlorophyll content (a, b, and total chlorophyll content) in one bean genotype, while no significant changes were observed in the other studied genotypes. Asfaw et al. [71] also found an increase in chlorophyll content (SPAD readings) in beans under dry conditions. Their work was based on the finding of quantitative trait loci (QTLs) associated with bean drought tolerance in a recombinant inbred line population derived from crossing drought-susceptible and drought-tolerant cultivars grown under different drought stress conditions. Due to the increased SPAD values under drought conditions, these authors consider the identification of QTLs associated with chlorophyll content a less useful trait for drought tolerance in beans. This finding was supported by the fact that bean plants develop small, dark green-colored leaves with confinement of the cells under drought conditions [5]. Asfaw et al. [71] attributed increased SPAD values in dry environments to drought stress-induced chlorophyll concentration within smaller leaf areas. Similar results were reported by Rasti Sani et al. [72] and Javornik et al. [18], who found an increase in the chlorophyll content index in bean genotypes under drought treatments. However, the chlorophyll content of bean plants changes throughout their life cycle, with an initial increase in chlorophyll levels in the cotyledons up to 13 days, followed by a decline as the plant matures [73]. Therefore, the described contrasting effects

of drought on the chlorophyll content of common beans could be influenced by the plant or leaf developmental stage at which the drought stress occurs [68] and the intensity and duration of drought.

2.7. Light Reaction and Calvin Cycle

Drought restricts CO₂ diffusion through stomata and the leaf mesophyll, reducing CO₂ concentration at the carboxylation site and consequently increasing photorespiration. Thus, stomata closure is the primary limitation of photosynthesis at the onset of drought. However, after mild drought exposure, the consumption of ATP during photorespiration and the impairment of ATP synthesis will limit ribulose biphosphate (RuBP) regeneration in the Calvin cycle. In the case of prolonged and severe drought, excessive light energy damages the photosystems and causes photoinhibition [74].

Prolonged drought significantly reduces photochemical efficiency, which is associated with damage to the D1 protein of the PSII complex and reduces the maximum efficiency of PSII (F_v/F_m) [75]. The adaptive adjustments during the light reactions rely on mechanisms such as the activation of the water–water cycle, the xanthophyll cycle, and the dissipation of excess absorbed light energy, primarily as heat [76]. The xanthophyll cycle deactivates the excited state of chlorophyll, releases excess light energy in the form of heat, and prevents the excessive production of reactive oxygen species (ROS) [77]. The water–water cycle reduces the transport of electrons between photosystems and shortens the lifetime of photoproduced superoxide and hydrogen peroxide to suppress the production of hydroxyl radicals and their harmful interactions with target molecules in the chloroplasts [78].

Mladenov et al. [79] examined the impact of drought on three bean cultivars and 23 mutant lines, revealing disruptions in photosystem II (PSII) activity. Drought impaired PSII efficiency by reducing the conversion of light energy into chemical energy. This PSII inactivation was likely caused by the reduced plastoquinone acceptor (Q–A) due to the decreased electron flow through PSII. These changes highlight the drought-induced damage to the photosynthetic machinery, severely limiting the plant's ability to efficiently capture and utilize light energy [80].

Drought in beans reduces the amount of oxygen-evolving enhancer proteins (OEEs) and chlorophyll a/b-binding proteins [81]. As an integral part of the photosynthetic machinery, OEEs are important for maintaining the functionality of PSII. OEE1 contributes to the stabilization of the oxygen-evolving complex (OEC) and supports the light-driven reactions of PSII, while OEE2 is directly involved in catalyzing the water-splitting reaction that generates electrons, protons, and molecular oxygen [82]. In addition, chlorophyll a/b-binding proteins, which are key components of the light-harvesting complex (LHC) in the chloroplast, play essential roles in light energy capture, electron transport, water oxidation, and O₂ production [83]. These results suggest that drought in common bean affects light reactions from the disruption of the LHC and the water-splitting system to the entire electron transport chain (ETC) and the final electron acceptor (NADP⁺). As a result of the inhibited light reactions, ATP and NADPH production is reduced, leading to reduced enzymatic activity in the Calvin cycle [81,84,85].

In addition, drought leads to a decrease in the content and activity of enzymes involved in the Calvin cycle and the pentose phosphate pathway, such as RuBisCO, transketolase, and ribulose phosphate 3-epimerase [86,87]. Boroujerdnia et al. [88] (2020) found that many genes in common beans associated with the Calvin cycle were downregulated under drought. In some cases, overexpression of Calvin cycle enzymes can improve photosynthetic performance under drought. Mladenov et al. [79] (2023) reported that the most drought-tolerant bean mutant line, which exhibited the highest productivity under drought conditions, showed overexpression of two RuBisCO isoforms. This overexpression

was associated with the slightest disruption of photosynthetic light reactions compared to other mutant lines, indicating a link between enhanced Calvin cycle activity and resilience to drought.

2.8. Osmotic Adjustment

Osmotic adjustment is a cellular and molecular mechanism that enables plants to maintain turgor pressure and sustain physiological processes under drought conditions, thereby enhancing their tolerance. This includes the active accumulation of osmolytes under conditions of decreased water potential in the cells [89]. The most important role in osmoregulation is played by inorganic ions (Na^+ , K^+ , Ca^{2+} , and Cl^-) and organic osmolytes, such as amino acids, proteins, carbohydrates, and sugars [90]. Osmotic adjustment stabilizes cell structures at low water potential, improves root growth, and delays leaf senescence and death. Osmotic adjustment also protects photosynthesis by maintaining turgor pressure in the guard cells and enhances leaf mesophyll conductivity [91]. Different osmotic substances have different functions in osmotic adjustment, and not all osmotically active substances contribute equally to turgor formation [92]. The osmotic regulation of inorganic ions is closely related to the operation of ion pumps. For example, sodium (Na^+), potassium (K^+), and hydrogen (H^+) pumps can regulate the concentration of inorganic substances inside and outside the cell and thus change the cell's osmotic potential [93].

Amede et al. [92] studied the correlation between drought-induced solute accumulation and drought tolerance in various grain legumes, including faba bean (*Vicia faba* L.), pea, chickpea, and common bean. Despite the lowest accumulation of solutes among the legumes, common bean maintained the highest turgor under drought stress, probably due to efficient stomatal regulation. The drought tolerance of common bean was driven by maintaining a higher water potential with minimal osmotic adjustment. The predominant osmolytes in common bean were cations and anions, particularly calcium (Ca^{2+}) and nitrate (NO_3^-). The study also emphasizes that different legumes use different mechanisms of osmotic adaptation to cope with drought stress.

One of the most important and highly studied osmolytes is proline. The increase in proline concentration is a widespread response to drought, cold, and salt stress in plants [94]. The hydrophobic part of proline can bind to proteins, while its hydrophilic part can bind to water molecules, allowing for the hydration of proteins and thus increasing their solubility and preventing their denaturation. Proline protects enzymes and cell structures and regulates cells' redox potential and pH [46]. Sánchez-Reinoso et al. [95] found increased proline concentrations in drought-tolerant common bean under drought conditions. They suggested that assessing proline content can be an effective, rapid, and economically viable method for identifying drought-tolerant genotypes.

2.9. Antioxidant Activity

Oxidative stress occurs when there is an imbalance between the production of reactive oxygen species (ROS) and the ability of the biological system to remove reactive intermediates and detoxify or repair the resulting damage [96]. ROS include hydrogen peroxide (H_2O_2), hydroxyl radicals ($\bullet\text{OH}$), superoxide anions ($\text{O}_2\bullet^-$), singlet oxygen ($^1\text{O}_2$), and alkyl radicals ($\text{RO}\bullet$), which damage macromolecules and cellular structures [97]. Increased ROS production under drought occurs during redox processes and electron transfer in chloroplasts, peroxisomes, mitochondria, the endoplasmic reticulum, plasma membranes, and cell walls [98]. Impairment of the functions of certain parts of the cell leads to a cascade reaction of disruption of the membrane structure, membrane proteins, and enzymatic processes, an increase in membrane permeability, a loss of ions from the cells, and the destruction of chlorophyll, leading to metabolic disorders and death of the cell and the

plant [99]. ROS can also interact with purines, pyrimidines, and deoxyribose in DNA molecules, leading to DNA breakage and degradation, causing genetic material damage or alteration [99].

Enzymatic and non-enzymatic components regulate the protective mechanisms against ROS in cells, and it has been shown that maintaining a higher concentration of antioxidants and antioxidant enzymes is an adaptive stress response [25]. The balance between the production of ROS and the action of antioxidant enzymes is crucial for preventing cell damage [91]. Antioxidant enzymes include catalase (CAT), superoxide dismutase (SOD), peroxidase (POD), glutathione peroxidase (GPX), ascorbate peroxidase (APX), dehydroascorbate reductase (DHAR), monodehydroascorbate reductase (MDHAR), and glutathione reductase (GR). Non-enzymatic antioxidants include glucose, ascorbate, tocopherols, carotenoids, phenols, and ascorbic acid [100]. Non-enzymatic antioxidants maintain the integrity of the phospholipid membrane during oxidative stress, while antioxidant enzymes can directly remove ROS from the organism and are involved in the synthesis of non-enzymatic antioxidants [101].

Symptoms caused by drought in beans, such as accelerated senescence and reduced chlorophyll content, are associated with the action of ROS [69,102]. Drought increases H_2O_2 and $\bullet OH$ production in beans, increasing lipid peroxidation and membrane damage. The tolerant genotypes have higher antioxidant activity (ascorbate peroxidase and catalase) and a lower accumulation of H_2O_2 and $\bullet OH$, contributing to the preservation of lipid membranes [103]. There is a strong correlation between abscisic acid (ABA) expression and antioxidant activity. Tolerant genotypes tend to exhibit higher concentrations of antioxidant enzymes and ABA [104]. In this context, ABA may serve as a crucial signaling molecule in plants under stress, enhancing the expression of genes involved in antioxidant defense and stimulating the production of the enzymes APX and SOD [105].

2.10. Phytohormones

Phytohormones regulate and control all aspects of plant growth and development and, therefore, play a crucial role in mediating plant responses to abiotic stress. With the onset of drought, the activity of phytohormones and their concentration in plant tissue changes. In particular, the concentrations of gibberellins, cytokinins, and auxins tend to decrease, while the concentrations of ethylene and abscisic acid (ABA) increase within the plant organism [106]. Interactions between ABA and other phytohormones are crucial for optimizing plant reactions under drought [107]. Low soil water potential induces the synthesis of ABA in plant roots [108]. ABA is then transported through the xylem to the leaves, where it causes stomatal closure, alters the plant's water potential, and rapidly limits leaf growth [107]. ABA signaling occurs via binding to specific receptors, including pyrabactin resistance (PYR), PYR1-like (PYL), or regulatory components of the ABA receptor (RCAR). This interaction inhibits type 2C protein phosphatases (PP2Cs), activating SnRK2 protein kinases. The activated SnRK2 kinases initiate signaling pathways that regulate stomatal closure [109]. This process begins with regulating ion channels, such as SLAC1 and SLAH3 (S-type anion channels), which facilitate the efflux of anions from the guard cells. At the same time, it promotes potassium (K^+) efflux while inhibiting K^+ influx [110]. This leads to a loss of osmotic potential in the guard cells, reducing their turgor pressure and causing stomatal closing. In addition to ion channel regulation, ABA triggers ROS production, enhancing calcium (Ca^{2+}) signaling in the guard cells. Increased cytosolic Ca^{2+} activates additional ion channels, further amplifying guard cell turgor pressure loss [110,111]. Moreover, the ABA signaling pathway interacts with other signaling molecules, such as nitric oxide (NO) and sphingosine-1-phosphate (S1P), which modulate and often amplify its effects on stomatal movement [110,111].

Other hormones, including jasmonic acid (JA), ethylene, cytokinins, and gibberellins, also contribute to drought tolerance mechanisms [112,113]. JA influences ABA biosynthesis and signaling, and JA interacts with ABA to enhance stomatal closure and antioxidant defenses [114].

Ethylene has a dual function: it promotes leaf senescence while regulating stomatal closure and root growth [115]. Cytokinins and gibberellins are downregulated during drought to conserve resources and promote root growth [116]. In some cases, an increase in cytokinin in the xylem has been observed during drought, allowing for better stimulation of stomatal opening and reducing the plant's sensitivity to ABA [37]. During drought, ABA promotes root growth by modulating auxin transport, thus improving the plant's ability to access water [117].

Wang [118] demonstrated that drought-tolerant bean genotypes have higher levels of key endogenous hormones and osmotic regulating substances compared to sensitive genotypes. Tolerant genotypes showed a higher accumulation of ABA, proline, and soluble sugars compared to sensitive genotypes. Plant hormone signaling pathways such as mitogen-activated protein kinase (MAPK) are more strongly regulated in tolerant bean genotypes [119]. Using single-nucleotide polymorphism (SNP) markers, Labastida et al. [120] could detect ABA and gibberellin signaling pathways in beans. These signaling pathways are important for the stay-green strategy, which enables plants to maintain photosynthetic activity and delay senescence under water-limiting conditions, thereby improving survival and productivity.

2.11. Molecular Response

Gene activation and gene expression control all morphological, physiological, and biochemical changes described above during drought. Transcription factors such as MYB, WRKY, DREB, and NAC play a central role in modulating these responses. They coordinate the transcription of genes responsible for osmoprotection, hormonal signaling, and stomatal control [121]. For instance, *PvMYB60*, a member of the MYB family, has been identified as a key regulator of stomatal opening and closing in beans, directly influencing water retention. Given its role in drought tolerance, manipulating *PvMYB60* could significantly enhance bean drought tolerance [122].

Gene activation during stress is specifically linked to ABA signaling. During drought, ABA influences both molecular and physiological responses. Genes involved in ABA biosynthesis, such as those encoding the enzyme 9-cis-epoxycarotenoid dioxygenase (NCED), are crucial for the plant's response to drought [102,123]. In drought-tolerant genotypes, lower expression of NCED reduces the overproduction of ABA, thus balancing stress responses and growth requirements. ABA also mediates nutrient remobilization during organ senescence, ensuring resource allocation to younger tissues. This process is less pronounced in drought-tolerant genotypes, where transcriptional regulation by *PvWRKY70* delays senescence and promotes nitrogen retention [102,124]. Such transcriptional regulation enables the plant to utilize nitrogen better and maintain productivity under drought. In addition, the *Asr* (abscisic acid-, stress-, ripening-induced) gene family is an example of the complex genetic mechanisms underlying drought adaptation [125]. In beans, overexpression of *Asr1* increases amino acid levels and the expression of other genes, probably through its DNA-binding activity. One of these genes, *PvSR1*, encodes a proline-rich protein that strengthens the integrity of the cell wall, a crucial trait for maintaining cell structure during dehydration [126].

Another important gene family comprises the aquaporins, which facilitate water transport through the cell membranes. Increased expression of *PvTIP2;3* in roots and *PvPIP2;5* in leaves improved water retention and reduced transpiration in drought-stressed

beans [127,128]. These findings emphasize the role of aquaporins in maintaining cellular hydration under water-limiting conditions. In addition, genes related to membrane and protein protection and the uptake and transport of water and ions have been identified, including aquaporins, RING-type E3 ubiquitin transferases, antioxidant enzymes such as glutathione S-transferase (GSTs) and Cytochrome P450 (CYPs), and thioredoxins (TRX) [129].

While many genes may be activated in response to drought, actual protein levels can vary due to post-transcriptional regulatory mechanisms. Proteins involved in photosynthesis, energy metabolism, and stress mitigation exhibit significant changes in abundance in common beans under drought. Key photosynthetic proteins such as RuBisCO and carbonic anhydrase are reduced during drought to save energy and adjust photosynthetic activity [130]. Conversely, stress-related proteins, including SOD and APX, are upregulated, mitigating oxidative damage caused by ROS [86]. Some proteins are also involved in maintaining cellular integrity and stability during stress. For example, heat shock proteins, particularly the 70 kDa chaperone, ensure proper protein folding under drought, preventing the accumulation of misfolded proteins [130]. Other stress-responsive proteins, such as dehydrins and small heat shock proteins, also accumulate during drought [79]. Meanwhile, cysteine and serine proteases regulate protein turnover by degrading damaged proteins and enabling cellular homeostasis [131].

2.12. Bean Phenology

The phenology of the bean is strongly influenced by drought, so traits such as days to flowering, seed filling, harvest maturity, etc., are particularly researched as they are good predictors of the bean's adaptation to drought and its escape mechanisms [54,132]. These traits can also be used for mass screening of ideal genotypes [133]. In most production regions, bean crops mature earlier than other crops, allowing the species to escape water deficits [28]. The escape mechanism involves increased metabolic activity and accelerated plant growth to speed up the completion of the life cycle before the onset of an intense drought period [46]. Drought escape is most successful when vegetative and reproductive growth are accompanied by a period of higher soil water availability before the onset of drought. Legumes with a successful drought escape mechanism retain higher water potential in tissues by improving water uptake and reducing water loss [53]. There are also reports that photoperiod sensitivity is adaptive in certain bean-growing regions (e.g., in the Mexican highlands) and that superior genotypes accelerate grain filling and maturation processes under water deficits [5].

All this makes research into drought tolerance difficult. While differences in phenology can be adaptive, they also pose a challenge for practical phenotyping, as it is difficult to compare physiological responses when genotypes differ across growth stages despite being exposed to a similar pattern of water deficits. One solution to such research difficulties could be multi-location experiments in the context of multi-environment phenotyping trials aimed at understanding genotype $\times$ environment interactions in different agroecological zones [134].

3. The Role of High-Throughput Phenotyping Techniques in Common Bean Breeding for Drought Tolerance

The described drought-induced changes and adaptations highlight the complexity of plant responses under drought stress. Therefore, research aimed at understanding the effects of drought, as well as efforts focusing on the selection and breeding of drought-tolerant genotypes, should encompass a wide range of morphological and physiological responses, i.e., they should investigate and quantify the entire plant phenotype.

The process of quantitatively describing a plant's observable traits (phenotype) resulting from genotype–environment interactions is known as plant phenotyping. It includes morphological, physiological, and biochemical traits measured at the whole-plant or individual-organ level [9,135]. Traditional manual plant phenotyping methods are increasingly being replaced by non-destructive, image-based approaches to high-throughput phenotyping (HTP) [136].

Traditional phenotyping of drought-related traits is time-consuming, labor-intensive, often destructive, and less accurate, making it statistically unreliable [136]. High-throughput phenotyping increases the precision of phenotypic trait detection in combination with reduced labor through automation, remote control, and image analysis programs (Figure 2) [137].

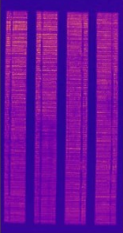
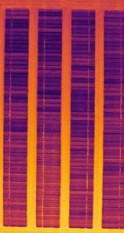
Color imaging (RGB)	Multispectral/Hyperspectral imaging	Thermal imaging	Porometer/ Fluorometer	Chlorophyll fluorescence imaging	3D cameras/LIDAR
Wavelengths 380 – 780 nm	Wavelengths 380 – 2500 nm	Wavelengths 9 – 14 μ m		Wavelengths 600 – 800 nm	
Capturing images of plants using cameras that detect light within the visible spectrum	Multispectral 3 – 10 bands Hyperspectral >100 narrow bands (5 – 20 nm)	Measures infrared radiation emitted by plants in the long-wave infrared.	Water vapour flow rate at ambient conditions *sometimes combined with chlorophyll fluorescence	Reemission of the light energy from the excited chlorophyll in the red and far-red regions of the spectrum.	Utilize various technologies: stereo vision, structured light, laser scanning, laser pulses
Purpose: detection of subtle changes in color that may indicate stress. Measures various growth parameters such as biomass, leaf area, and growth rates.	Capture a spectral reflectance in (visible, NIR, VIS, SWIR, LWMR) and used for calculation of different vegetation indices. Purpose: Advanced analysis of plant composition and detection of various stress factors.	Purpose: Allows rapid assessment of plant surface temperature, which serves as a proxy for stomatal conductance and water status.	Purpose: Measurement of stomatal conductance and transpiration. *optionally it can be combined with chlorophyll fluorescence	Purpose: Quantification of the efficiency of plant photosystems and photochemistry which provides information on the health of the plant and its response to stress.	Purpose: Precise measurements of plant structure, including leaf area, stem height, canopy volume, and overall architecture.
Morphology, Spectral reflectance/vegetation indices		Canopy temperature	Stomatal conductance	Photochemical efficiency	Morphology
					
Handheld multispectral and hyperspectral sensors	Drones (equipped with various sensors and imaging systems)		Handheld porometer and fluorometer	Chlorophyll fluorescence imaging chamber	Multispectral 3D scanner

Figure 2. High-throughput phenotyping devices and examples of their use in crop phenotyping.

Using HTP to quantify drought responses in common beans enhances our understanding of the fundamental physiological processes and mechanisms underlying drought tolerance. Applying HTP to common bean germplasm under drought conditions also facilitates the selection of drought-tolerant genotypes and the identification of beneficial genes. In the following chapters, we will present modern HTP techniques and their application in common bean phenotyping.

3.1. RGB Imaging

Cameras that project color images, or RGB cameras, are used for imaging in the visible part of the spectrum, i.e., the wavelengths of light (380–780 nm) that the human eye perceives as colors [138]. Spectral images are based on the interaction between plants and photons that plant tissue can reflect, absorb, and transmit [139]. RGB cameras contain three primary color channels—red, green, and blue—which, when combined, create a color image/2D image [140]. Their cost-effectiveness and versatility, either indoors (greenhouses, plant growth chambers, etc.) or in the field, make them popular with many researchers. In addition, the adaptability of RGB sensors to different plant species and environmental conditions makes them the most versatile tool for phenotyping in agriculture [141]. Images created by reflection in the visible part of the spectrum are primarily used to measure plant architecture. Still, they are also used to measure biomass, leaf surface area, plant color, growth dynamics, senescence, yield, and root architecture and to detect various diseases

and deformities that may be related to the plant's response to certain stress factors [14,142]. RGB cameras can be easily incorporated into various devices, such as mobile devices and aerial vehicles [141]. Numerous image processing and analysis methods have been developed to analyze and extract certain phenotypic characteristics from RGB images. When analyzing phenotypic traits, segmentation, i.e., the separation of objects (areas of interest for analysis) from the background, is an important step. Segmentation of objects is used in all types of image generation and processing methods (RGB imaging, multi-spectral/hyperspectral imaging, chlorophyll fluorescence imaging, etc.). It can be based on simple techniques such as distinguishing the color of the object from the background to sophisticated artificial intelligence algorithms based on color indices and pixels of objects [143]. Software for image analysis is mainly based on detecting variations in the image (changes in texture, edges, and lines), which enables the detection of modifications/changes in the structure of the plant. Integrated color-based algorithms are usually used in the software to detect stress-related changes in the color (especially of the leaves), saturation, or brightness of the plants. Analyses of leaf texture can also indicate specific stresses [140]. Since the effects of water deficit are manifested by numerous external changes in the plant (reduction in leaf area/biomass, changes in color, plant height, root architecture, etc.), RGB imaging is proving to be one of the best HTP methods for detecting and quantifying drought-induced changes in the plant [144].

An HTP platform equipped with RGB camera imaging that generates images from three angles (0° , 90° , and 180°) was used to evaluate the phenotypic variation of two bean cultivars under drought [145]. The study demonstrated the potential of using a digital RGB imaging HTP platform to evaluate the drought tolerance of common bean cultivars. Image analysis enabled quantification of the stay-green trait related to drought tolerance through enhanced chlorophyll retention and delayed senescence under drought treatment.

Verheyen et al. [14] used the HTP system equipped with RGB, multispectral, and hyperspectral cameras to evaluate the drought tolerance of 151 bean genotypes based on five phenotypic traits: biomass, water use efficiency, relative water content, chlorophyll content, and root/shoot mass ratio. The HTP system consisted of a conveyor belt that brought each plant to a camera system that captured six side images of each plant. The same camera system in the bottom view was used to determine the projected root area at the bottom of the transparent container as root biomass. The HTP system determined numerous phenotypic differences in drought tolerance among tested bean genotypes. The results highlight the potential of using HTP systems to accelerate breeding programs by identifying genotypes with superior drought tolerance traits.

From the above, we can conclude that RGB imaging is the most cost-effective and efficient method for monitoring bean biomass and phenology [14,23]. It is also a very effective technique for observing color changes that can be caused by drought. The background of why color changes occur and the changes in plant composition may be better suited to other techniques, such as hyperspectral or multispectral imaging.

Despite their widespread use, RGB cameras also have limitations. For example, image processing algorithms cannot easily detect subtle changes in leaf color or texture [146]. RGB sensors are also limited by external factors such as lighting conditions, shadows, and reflections, which can affect the accuracy of the sensors and the interpretation of the physiological state of the plants [140]. As technologies evolve, the shortcomings of RGB cameras and image processing are complemented and combinations of RGB imaging with saturation pulse (illumination to measure chlorophyll fluorescence) and multispectral sensors are increasingly being used to extend the applicability of these techniques and gain better insight into physiological responses [9].

3.2. Multispectral and Hyperspectral Imaging

Multispectral cameras capture images in a limited number of discrete wavelength ranges of the electromagnetic spectrum, usually 3 to 10 bands. They often include bands in the visible spectrum (380–780 nm), but also some wavelengths that lie in the near-infrared region of the spectrum (NIR; 700–1300 nm) [147]. Hyperspectral cameras enable the capture of images in much narrower spectral bands, often hundreds to thousands of narrow wavelength bands. The bandwidth of the individual spectral band is usually only 10–20 nm, which allows for a detailed and precise analysis of the recorded object. In addition to the visible part of the spectrum (VIS), hyperspectral cameras also capture the near-infrared (NIR) and short-wave infrared (SWIR) regions of the electromagnetic spectrum [148]. This technology provides extensive information about the characteristic spectral signatures of the photographed plant.

The spectral reflectance of a leaf is influenced by several factors, including the content of chlorophyll and other pigments (carotenoids and anthocyanins), the water content, the structural properties of the leaf (arrangement and density of cells, the presence of hairs or wax), and damage caused by biotic and abiotic stress [149,150]. Photosynthetic pigments absorb light highly in the blue and red parts of the visible spectrum and cause a characteristic reflection peak in the green range (around 550 nm) [150,151]. Water strongly absorbs wavelengths in the near-infrared range (around 970 nm and 1200 nm), which leads to a decrease in reflectance at these wavelengths [152]. Other plant pigments, such as carotenoids and anthocyanins, can also influence the spectral reflectance of leaves, especially in the visible and near-infrared range [153]. Cellulose absorbs photons in a broad spectrum of 2200 and 2500 nm [146]. Healthy vegetation is characterized by a substantial increase in reflectance in the so-called red edge region, which is due to the transition between the strong absorption of red light (600–700 nm) by photosynthetic pigments and the high reflectance of NIR light (700–780 nm) by leaf cell structures [154]. The red edge can serve as an indicator of plant vitality and the biological status of plants [155]. Changes in the red edge can respond to various stress factors, such as nutrient deficiency and water deficit stress [156].

The study by Thenkabail et al. [157] utilized field hyperspectral measurements (350–2500 nm) and two Hyperion satellite images to analyze the spectral signatures of eight major crops at different stages of development and different agroecological zones over a decade (2000–2010). The research identified 33 optimal hyperspectral narrow bands (HNBS) and hyperspectral vegetation indices (HVIs) that significantly improved crop classification and assessment of biophysical traits, including biomass, leaf area index (LAI), and grain yield. These findings demonstrate the applicability of hyperspectral and multispectral analysis as reliable tools for monitoring crop health and productivity in different agroecological zones.

Multispectral and hyperspectral imaging have an advantage over RGB technology because they can detect more subtle changes in reflectance, especially in the early stages of stress [144]. Multispectral sensors are widely used in remote sensing from the ground (robots, vehicles, HTP platforms) and from the air (satellites and unmanned aerial vehicles) [158,159]. There is an increasing number of low-cost portable multispectral devices that are successfully used to monitor various stresses on smaller surfaces [160]. Handheld devices have better spatial resolution than airborne and satellite-based sensors. However, the limiting factor of such devices is the required data acquisition time and the inability to cover larger areas [161]. In both aspects of research (remote and manual), multispectral sensors collect a large amount of data that require knowledge and specialized software for processing and analysis [162].

The data obtained on the spectral reflectance of plants are used to calculate different vegetation indices (Table 1). Each vegetation index is based on the ratio and/or difference

in the reflectance of certain electromagnetic spectrum bands, i.e., each index is predefined and determined by the reflected wavelengths [161]. Vegetation indices indicate the health status of plants and can be specific to a particular biotic or abiotic stress (Table 1). There are many vegetation indices, but the most commonly used vegetation index for assessing drought stress is the Normalized Difference Vegetation Index (NDVI) (Figure 3) [163]. For assessing water deficit stress, indices derived from the ratio and difference in reflectance in the visible (VIS), near-infrared (NIR), and shortwave infrared (SWIR) spectral regions are commonly utilized [164]. Besides the NDVI, some of the commonly used indices to assess drought stress are the Green Normalized Difference Vegetation Index (GNDVI), the Water Band Index (WBI), the Moisture Stress Index (MSI), and the Optimized Soil-Adjusted Vegetation Index (OSAVI) [12,165–167]. The Drought Severity Index (DSI) showed superior performance in detecting agricultural drought [168], while the Normalized Difference Drought Index (NDDI) showed high sensitivity to precipitation in rice paddy fields [169]. As drought affects pigment content, indices related to the pigment content, such as the anthocyanin index (ARI) and the chlorophyll index (CHI), can be used for assessing drought tolerance [170]. The effectiveness of these indices may vary depending on the type of land cover, the climatic conditions, and the specific characteristics of the drought [171]. However, recent studies suggest that combined vegetation indices may be more effective for drought monitoring. Sankaran et al. [172] successfully used the GNDVI and the average canopy area to predict bean yield under drought conditions. The experimental plots with beans were monitored for two years across different phenophases using an unmanned aerial vehicle (UAV) equipped with a multispectral camera. The authors concluded that the GNDVI and canopy area positively correlate with plant health, earlier growth, and higher yield potential, which can be used to select drought-tolerant genotypes. A similar result was obtained by Lipovac et al. [12], who used a UAV equipped with a multispectral camera and a combination of vegetation indices, the NDVI, GNDVI and Modified Chlorophyll Absorption in Reflectance Index (MCARI1), to predict drought stress and yield in beans. The NDVI and the MACARI1 have proven to be particularly useful for early drought detection. However, as shown by Behmann et al. [173], the leaf inclination angles can cause unevenness in spectral reflectance and concomitant changes in calculated vegetation indexes such as the NDVI. This means that during spectral imaging and analysis, besides environmental effects such as winds, sunlight, atmospheric conditions, and imaging distance, one should also consider the effect of plant geometry on the spectral data.

Table 1. A list of frequently used vegetation indices and their applications in the assessment of plant health.

Index	Abbreviation	Equation	Utilization	Reference
Anthocyanin Index	ARI	$ARI = (R_{Green})^{-1} - (R_{FarRed})^{-1}$	Assessment of anthocyanin content	[174]
Chlorophyll Index	CHI	$CHI = (R_{Chl})^{-1} - (R_{NIR})^{-1}$	Assessment of chlorophyll content	[151]
Drought Severity Index	DSI	Calculation is based on the model which uses relatively fine-scale (1 km resolution) NDVI inputs from Moderate Resolution Imaging Spectroradiometer (MODIS)	Agricultural drought monitoring and early warning	[175]
Green Normalized Difference Vegetation Index	GNDVI	$GNDVI = (R_{NIR} - R_{Green}) / (R_{NIR} + R_{Green})$	Vegetation health assessment and yield prediction	[176]
Modified Chlorophyll Absorption in Reflectance Index	MCARI1	$MCAR1 = 1.2 \times (2.5 \times (R_{NIR} - R_{Red}) - 1.3 \times (R_{NIR} - R_{Green}))$	Assessment of vegetation health, biomass, and chlorophyll content	[177]

Table 1. Cont.

Index	Abbreviation	Equation	Utilization	Reference
Moisture Stress Index	MSI	$MSI = 1600 \text{ nm}/820 \text{ nm}$	Determines leaf and canopy water content	[178]
Normalized Difference Drought Index	NDDI	$NDDI = NDVI - NDWI/NDVI + NDWI$	More sensitive indicator of drought than the NDVI	[179]
Normalized Difference Water Index	NDWI	$NDWI = (860 \text{ nm} - 1240 \text{ nm})/(860 \text{ nm} + 1240 \text{ nm})$	Monitoring changes in the water content of plants	[180]
Optimized Soil-Adjusted Vegetation Index	OSAVI	$OSAVI = R_{NIR} - R_{Red}/R_{NIR} + R_{Red} + 0.16$	Assessment of vegetation health	[181]
Normalized Difference Vegetation Index	NDVI	$NDVI = (R_{NIR} - R_{Red})/(R_{NIR} + R_{Red})$	Assessment of vegetation, phenophase, and biomass	[163]
Water Band Index	WBI	$WBI = 950 \text{ nm}/900 \text{ nm}$	Assessment of water stress and water use efficiency	[165]

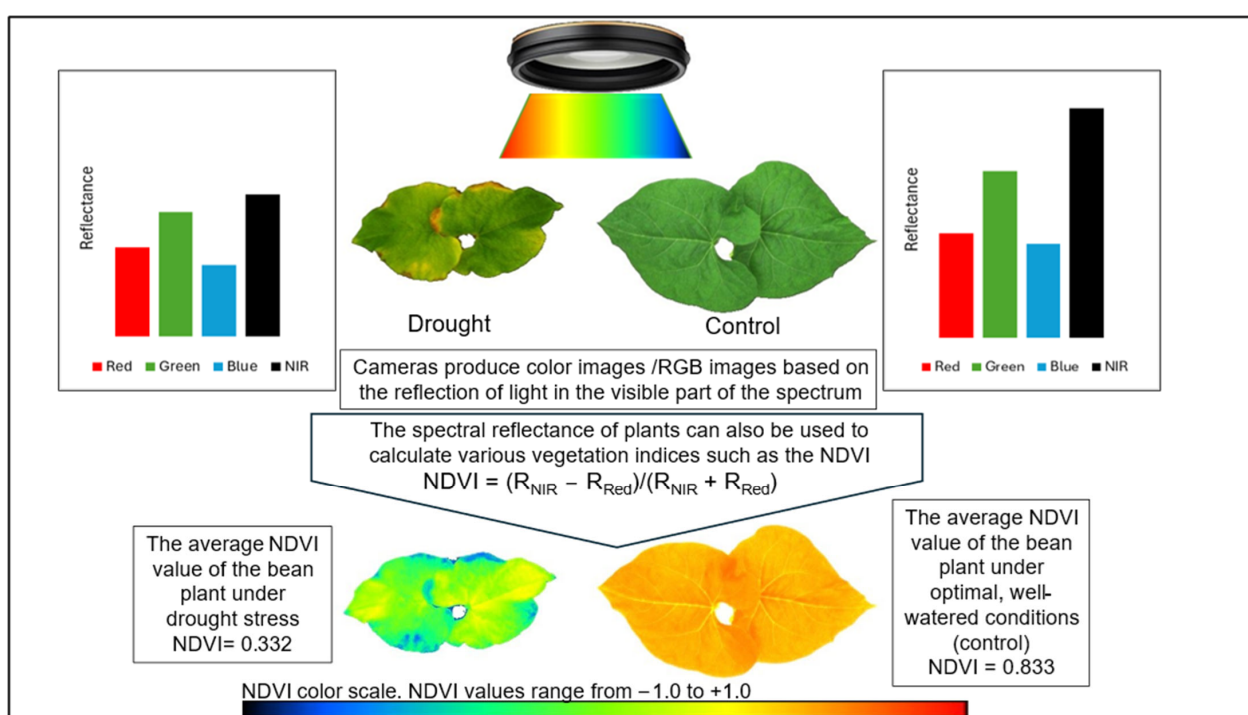


Figure 3. Example of multispectral imaging and Normalized Difference Vegetation Index (NDVI) calculation for assessing plant health.

Multispectral and hyperspectral imaging are proving to be extremely effective in detecting subtle changes in bean color associated with specific wavelengths. The vegetation indices derived from these specific wavelengths are associated with green, red, and NIR reflectance and the specific reflectance of chlorophyll. Thus, the NDVI, the GNDVI, and indices that can be associated with changes in photosynthetic pigment content, such as the CHI and MACAR1, are introduced as effective indices for observing changes in beans due to drought.

3.3. Chlorophyll Fluorescence Imaging

Chlorophyll fluorescence (CF) is a key indicator of photosynthetic activity in plants, and changes in CF are used as a diagnostic method to assess the state of the photosynthetic apparatus [182]. CF measurement represents a non-destructive analysis of the primary reactions of photosynthesis, providing information on the structure and functionality of the photosystems, the transfer of excitation energy, and the electron transport reactions

across the thylakoid membrane [183]. The analysis of chlorophyll fluorescence is based on the fact that the light energy absorbed by chlorophyll can be used to initiate photosynthesis (photochemical reactions), released as heat or re-emitted as long-wavelength light radiation, known as fluorescence. These three processes are interdependent, so any increase in one process leads to a decrease in the value of the other two [182]. Traditional point-based chlorophyll fluorescence measurements have their limitations, e.g., when measuring the heterogeneity of photosynthesis across the leaf or the whole plant. Chlorophyll fluorescence imaging allows for the analysis of spatial heterogeneity on the plant, i.e., the determination of stress-induced damage sites, and such a CF analysis technique has become one of the most important tools in HTP (Figure 4) [184]. As previously described, drought stress can damage D1 and D2 proteins in the reaction centers of the photosystem [75]. Also, stomatal closure reduces CO₂ assimilation, which can lead to an imbalance between the photochemical activity of PSII and the demand for ATP and NADPH [74]. This can subsequently promote the formation of ROS and lead to photoinhibition [185]. These disorders in photochemistry can be monitored and quantified using chlorophyll fluorescence protocols. By applying HTP CF imaging protocols, many different fluorescence coefficients can be calculated (see [182]). The most common and frequently used fluorescence coefficients for monitoring drought stress are listed in Table 2.

Table 2. A list of commonly used chlorophyll fluorescence coefficients, including abbreviations, the equation for calculation, and a reference.

Abbreviation	Trait	Equation
F_v/F_m	Maximum Efficiency of Photosystem II	$F_v/F_m = (F_m - F_0)/F_m$ [186]
F_q'/F_m'	Effective Quantum Yield of Photosystem II	$F_q'/F_m' = (F_m' - F_s')/F_m'$ [187]
rETR	Relative Electron Transport Rate	$ETR = F_q'/F_m' \times PPFD \times (0.5)$ [187]
NPQ	Non-Photochemical Quenching	$NPQ = (F_m - F_m')/F_m'$ [188]
qP	Coefficient of Photochemical Quenching	$qP = (F_m' - F_s)/F_v$ [189]
qN	Coefficient of Non-Photochemical Quenching	$qN = 1 - (F_m' - F_0')/(F_m - F_0)$ [189]

One of the most commonly used fluorescence coefficients in plant stress monitoring is the maximum efficiency of PSII (F_v/F_m) [67]. However, PSII is relatively insensitive to drought stress, with a noticeable decrease occurring only under severe and prolonged drought conditions [69,190]. Besides this, measurements of fluorescence kinetics are sensitive to drought stress, in particular parameters such as the effective quantum yield of PSII (F_q'/F_m'), the relative electron transport rate (rETR), and non-photochemical quenching (NPQ). Mathobo et al. [69] reported that drought stress in beans decreased the maximum chlorophyll fluorescence (F_m) and the coefficient of photochemical quenching (qP) and increased the coefficient of non-photochemical quenching (qN) and minimal chlorophyll fluorescence (F_0). Saglam et al. [191] used chlorophyll fluorescence parameters in combination with enzymatic activity to evaluate the drought tolerance of bean genotypes. F_q'/F_m' and qP were significantly reduced in the most sensitive genotype. Sánchez-Reinoso et al. [192] found the parameters F_v/F_m , NPQ, and rETR to be excellent drought stress indicators in different bean genotypes. In the study by Javornik et al. [18], the first CF coefficients that responded to water deficit were NPQ and the quantum yield of non-regulated

non-photochemical energy loss in PSII (ϕ_{no}), which represents the activation of the photo-protective process of chloroplasts to prevent overheating and maintain the photosynthetic process. These CF coefficients proved to be good indicators for early water deficit detection.

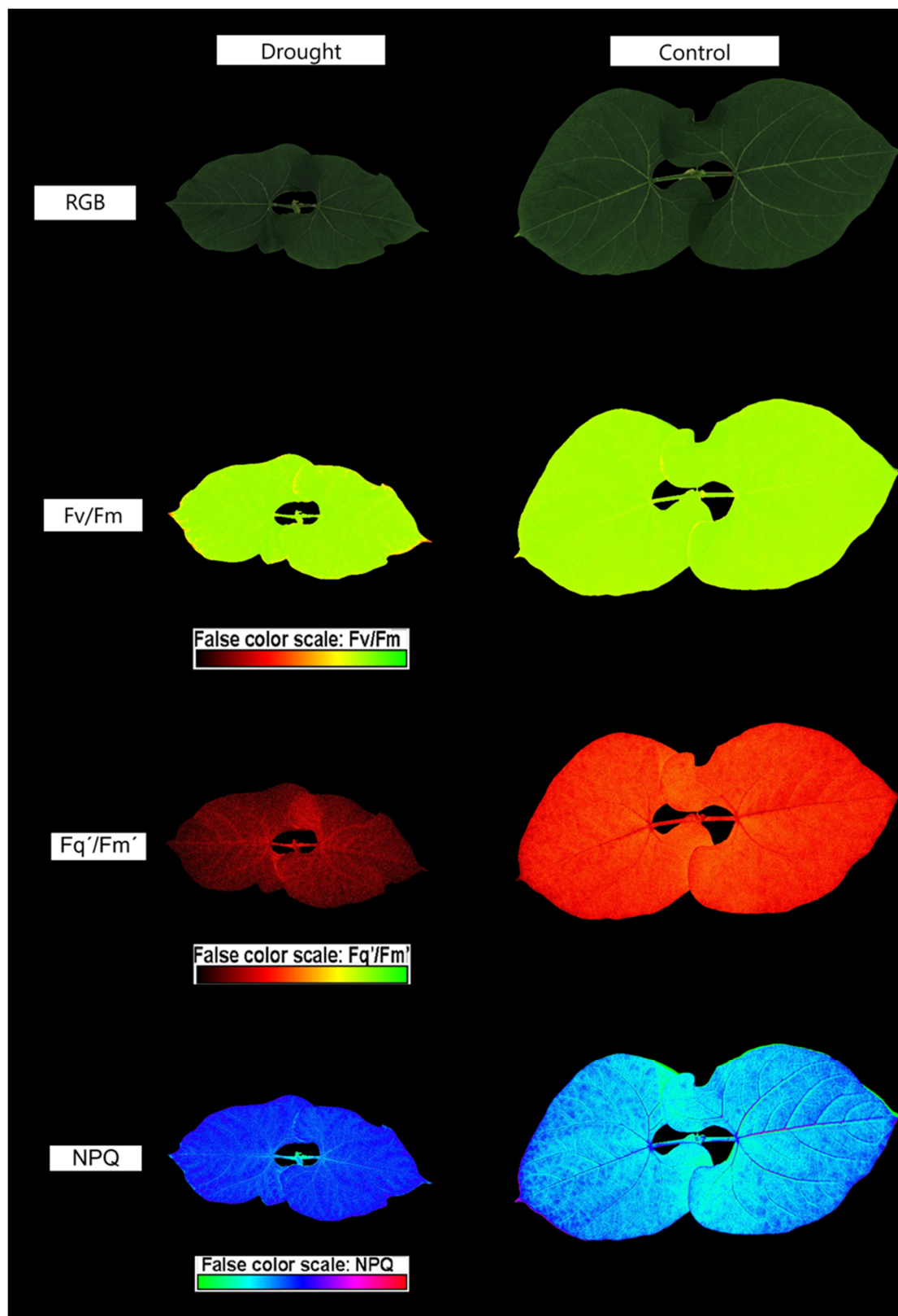


Figure 4. Chlorophyll fluorescence (CF) imaging as a tool for detecting drought effects in common bean plants. Compared to RGB imaging, which primarily detects size differences (leaf area), chlorophyll

fluorescence (CF) imaging allows for quantification of drought-induced photochemical inhibition. While the maximum efficiency of PSII (F_v/F_m) remains relatively unaffected by drought, the effective quantum yield of PSII (F_q'/F_m') decreases, and non-photochemical quenching (NPQ) increases under drought conditions.

CF traits, such as F_q'/F_m' and NPQ, best represent the changes and imbalances in the bean photosystems during drought. Although the F_v/F_m trait is presented in the literature as one of the most commonly used traits to evaluate the efficiency of photosystems under stress, changes in this trait only occur in beans under severe drought.

Although chlorophyll fluorescence imaging is a powerful tool used for HTP to study plant physiology and photosynthesis, its reliability and applicability under field conditions are limited by the necessary dark adaptation and its sensitivity to ambient light [193]. Therefore, controlled lighting environments or modulated systems are often used to reduce background noise, which can complicate field applications. Additionally, the interpretation of fluorescence results can be complex as changes can be due to multiple physiological processes. Furthermore, CF measurements do not provide spectral and morphological (structural) information about the plants. For this reason, modern HTP platforms combine CF imaging with other techniques such as RGB and/or multispectral imaging [194].

3.4. Three-Dimensional (3D) Imaging

Because water deficit has profound effects on plant morphology, quantification of morphological traits allows us to evaluate the impact of drought stress on plant development [195]. Also, the measurement of morphological traits is the basis for the characterization and further improvement in the selection of drought-tolerant genotypes. Therefore, the development of techniques to automatically obtain and analyze morphological data is of great importance for plant phenotyping and further plant improvements [196]. Three-dimensional imaging has become a transformative tool in plant phenotyping, enabling detailed analysis of plant morphology and physiology [197]. It enables non-destructive monitoring of plant development under different environmental conditions. Due to the geometric complexity and dynamic nature of the development of plant structures, image-based assessment of even very basic morphological characteristics of plants is a challenging technical and analytical task. Various methods for 3D imaging and reconstruction of the geometry of plants have been developed to quantify their three-dimensional structure accurately. Despite different acquisition approaches, all reconstruction methods of 3D objects provide a similar 3D representation in the form of a point cloud or triangular mesh [198]. Three-dimensional imaging techniques are typically divided into active and passive approaches [197].

Active methods include laser triangulation, LiDAR, and structured light systems that rely on controlled energy emissions to gather precise spatial information. These methods are ideal for accurately capturing plant architecture and fine structural features but rely on specialized and costly equipment. In contrast, passive methods such as structure-from-motion (SfM) and multi-view stereo (MVS) utilize natural light and rely on multiple overlapping 2D images taken from different angles to reconstruct 3D models. These methods are generally more affordable, but they often demand significant computational resources to achieve resolutions comparable to active systems (see [197] Harandi et al., 2023).

Three-dimensional imaging has proven to be an excellent technique for assessing morphological traits that are significantly affected by drought, such as biomass (digital plant volume), leaf area, plant height, number of flowers, and others [199]. Color changes in combination with plant morphological changes can serve as good indicators of water deficiency in plants [195]. Drought usually leads to morphological changes in plants earlier than changes in structure or pigment content, which generally manifest only after

prolonged drought [37]. Consequently, morphological changes can serve as early indicators of water scarcity.

The combination of 3D imaging with spectral data, such as multispectral imaging, further enhances its usefulness in plant phenotyping. Multispectral 3D models integrate geometric and spectral information, enabling the assessment of stress responses and physiological traits of plants. By mapping multispectral data and vegetation indices onto 3D plant models, researchers can analyze the spatial distribution of drought-induced changes, such as enhanced senescence and decreased chlorophyll content, while accounting for geometric distortions caused by plant architecture [173,197]. For example, Javornik et al. [18] used 3D multispectral scanning to monitor the effects of water deficit on common bean morphology. They observed that the reduction in leaf area and digital volume were the first morphological traits to respond to water deficit. This biomass and leaf area reduction reflected the plants' adaptive strategies to cope with water stress. In addition, significant changes in leaf angle and leaf inclination were also noted, further highlighting the plants' morphological adjustments under water deficit conditions. It is known that water deficit causes wilting of plants and, thus, changes in leaf angle [46]. However, these traits showed inconsistent results at different measurement times, indicating that water deficit does not solely affect these traits. Despite its advantages, 3D imaging in plant phenotyping faces challenges, including data processing complexity, high equipment costs, and environmental sensitivities during field applications. However, the ongoing advancements in hardware, algorithms, and computational methods address these limitations, making 3D imaging more accessible and efficient in HTP platforms [197]. An example of 3D multispectral scans of common bean are shown in Figure 5.

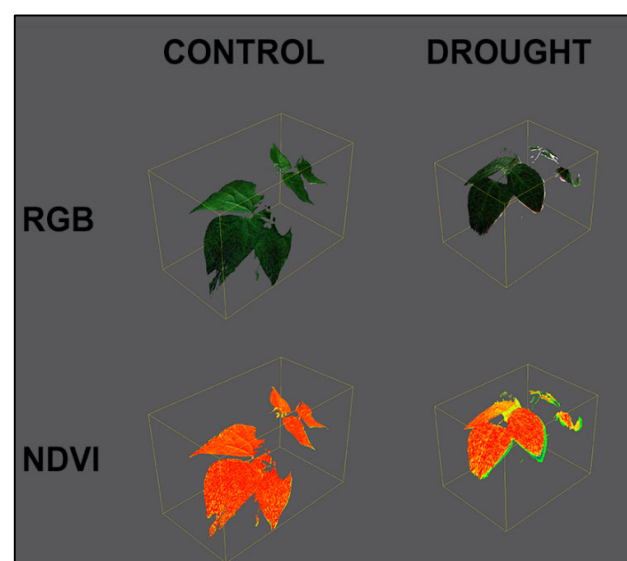


Figure 5. Example of 3D multispectral scanning of common bean under well-watered (control) and drought conditions: integrating morphological measurements with vegetation indices (such as NDVI).

3.5. Thermal Imaging

To avoid excessive water loss during drought, plants need good stomatal regulation. For this reason, measuring stomatal conductance proves to be one of the best techniques for assessing the response of plants during water deficit.

Thermal imaging, especially infrared thermography (IRT), detects and measures the infrared radiation emitted by objects or surfaces to create images based on temperature changes [200]. Thermal cameras detect long-wave infrared (LWIR) range radiation, typ-

ically between 9 and 14 μm , emitted by objects, which correlates with their temperature. This allows for the visualization of thermal profiles, where temperature variations are represented in grayscale or color-coded thermograms [201]. Thus, it can identify water-stressed plants by detecting higher leaf or canopy temperatures caused by reduced transpiration, which enables the monitoring of plant water status under drought conditions. Thermal indices derived from these measurements correlate well with stomatal conductance and can be used for irrigation scheduling and phenotyping drought-tolerant genotypes [202]. The main index derived from thermal imaging is the Crop Water Stress Index (CWSI) [203]. Higher CWSI values indicate greater water stress, allowing for the identification of drought-tolerant genotypes in various crops, including maize, wheat, lentil, and cotton [204–206].

Thermal imaging is particularly useful in large-scale monitoring in agriculture, where early detection of stress factors can lead to rapid intervention and better crop management [207]. Thus, combining thermal cameras with UAVs enables rapid screening of crop water status and yield prediction under water-limited conditions [205]. In common bean, thermal imaging combined with gas exchange analysis has been used to study stomatal heterogeneity's response to humidity and temperature variations [208]. On a larger scale, UAV-based remote sensing of canopy temperature has proven its effectiveness in assessing water stress, demonstrating the potential of thermal imaging for precision irrigation management in common beans [15].

Despite its advantages, IRT faces challenges with environmental fluctuations and mixed pixels, requiring careful data interpretation and integration with other phenotyping approaches [209]. Also, emissivity, ambient temperature, and surrounding infrared reflections can affect measurement accuracy [140].

In addition to thermal imaging, stomatal conductance can be measured using infrared gas analyzers (IRGAs) and porometers [210]. IRGA-based devices measure gas exchange (CO_2 and H_2O) from an acclimatized leaf in a controlled leaf chamber, while parameters quantify water vapor diffusion from the leaf to the surrounding environment under ambient conditions [210]. For this reason, IRGAs provide more precise and comprehensive gas exchange measurements but are time-consuming and not considered an HTP method. In contrast, porometers offer faster measurements, are often designed for manual use, and are easily portable, making them ideal for simple and quick field analyses [211]. Their ability to measure physiological traits such as stomatal conductance and transpiration, as well as the possibility of being equipped with additional sensors such as the saturation pulse to measure chlorophyll fluorescence, GPS, or barcode scanners for more accurate field measurements (e.g., LI-600 Porometer; LI-COR Biosciences, Lincoln, NE, USA), may contribute to considering them as HTP tools. However, with the further development of HTP platforms, the integration of parameters into these systems can be expected, further increasing their efficiency and applicability.

3.6. Root Phenotyping

Root plasticity plays a crucial role in acquiring soil resources, especially in a water-limited environment [212]. Therefore, studying root phenotypes is essential for understanding drought-induced responses and drought tolerance in common beans. Studies on common bean root traits highlight their significant contribution to improving drought resilience and productivity. For example, root length, branching pattern, and diameter traits have been strongly linked to enhanced water and nutrient uptake under drought stress [213]. Xylem conductivity and aquaporin activity improve water transport and drought resilience [214]. Also, increased nodule formation and nitrogen fixation capacity are essential for maintaining productivity in legumes under different abiotic stress [215].

Advances in root phenotyping technologies, particularly HTP, have facilitated the evaluation of these traits under controlled and field conditions (Table 3).

Conventional field-based techniques such as shovelomics, soil coring, trenching, and minirhizotrons provide a realistic representation of root traits under natural environmental conditions [216]. However, these methods are labor-intensive. Roots often need to be washed out of the soil, which risks damaging or loosening the roots and makes repeated measurements impossible. The variability in soil properties and climate further complicates their application. On the other hand, controlled systems, which include substrate-based setups such as pots, tubes, rhizoboxes, and chambers [217], are easier to manage and allow for rapid data collection. Additionally, soilless transparent media systems (e.g., agar plates, gels, hydroponics, and aeroponics) provide non-destructive and repeatable methods for root phenotyping. These systems simplify root imaging and analysis but lack field conditions and complex environmental conditions, while root growth is often limited by the container size [218].

Root phenotyping platforms are equipped with advanced imaging techniques and automated image analysis software that have revolutionized root phenotyping by enabling non-invasive analysis of root systems, often in 3D. In addition to transparent or soilless media, tomographic techniques such as X-ray computed tomography (μ CT) and magnetic resonance imaging (MRI) provide detailed 3D reconstructions of the root architecture of plants grown in soil [219,220].

Integrating conventional phenotyping with advanced HTP systems can improve the accuracy and agronomic applicability of root phenotyping in common beans. Field-based phenotyping methods provide ecological relevance, while controlled systems enable precise root phenotyping under uniform conditions. For example, automated tomographic systems or the RhizoTubes system [221] offer non-destructive and high-resolution analyses, making them valuable tools for research and breeding programs. In addition to direct root phenotyping, root trait selection can be complemented and supported by additional shoot phenotyping by measuring root traits via canopy temperature and various spectral imaging systems [14,222]. For example, some systems (equipped with RGB, multispectral, and hyperspectral cameras) can be used not only to measure bean shoot traits under drought conditions but also in the bottom view to determine the projected root area at the bottom of the transparent container as root biomass [14]. Recently, shoot trait measurements were used to estimate root depth [223]. Hanlon et al. [223] developed LEADER (Leaf Element Accumulation from Deep Roots), a novel method that correlates leaf elemental content, measured by XRF and ICP-OES, with root metrics and provides a practical alternative for studying deep rooting in different plant species and soils.

Table 3. Advantages and disadvantages of root phenotyping systems based on growth environment and growth media.

Environment	Media	Methods	Advantages	Disadvantages
Field Phenotyping	Soil	Shovelomics, soil coring/washing/breaking, trenching, minirhizotrons	- Plants grow under natural environmental conditions - Provides the most representative physiological response - Reflects realistic root development	- Labor-intensive - Requires multiple steps such as soil riddling and washing - Potential root damage and loss - Repeated measurements on the same plant are not possible - High variability due to soil and climate differences

Table 3. Cont.

Environment	Media	Methods	Advantages	Disadvantages
Laboratory/ Greenhouse Phenotyping	Substrate based systems	Pots, tubes, boxes, rhizoboxes, root chambers	- Easier experimental control and monitoring - Allows for more measurements in less time - Requires less root preparation before measurement - Lower risk of root damage during handling and extraction	- Root growth is restricted by container size - Possible root breakage during extraction and washing - Growth conditions are not fully representative of field conditions
	Soilless, transparent systems	Agar plates, gel-based systems, “pouch-and-wick” systems, hydroponics, aeroponics	- Provides easy root access - Eliminates the need for extensive root cleaning - Allows for repeated measurements on the same plant - Highly reproducible	- Lacks natural environmental influences on root development - Requires further validation for physiological relevance

4. Conclusion and Perspectives: Towards an Effective Phenotyping Strategy for Drought Tolerance in Common Bean

Developing drought-tolerant genotypes through genetic improvement is a crucial strategy to mitigate the adverse impacts of water deficit on crop production globally. In common bean, drought tolerance is a complex trait involving a dynamic interplay of morphological, physiological, and molecular mechanisms that collectively contribute to plant performance under water-limited conditions. These mechanisms may include traits such as root architecture, stomatal regulation, osmotic adjustment, and maintenance of photosynthetic efficiency. Among these, phenology is critical, particularly in environments where early flowering and maturation allow genotypes to escape terminal drought. However, this phenological diversity among genotypes presents a significant challenge for phenotyping, as differences in developmental stage complicate the interpretation of physiological responses to water deficit.

To address these challenges, phenotyping strategies must be embedded within multi-environment trials (METs) aimed at capturing genotype $\times$ environment ($G \times E$) interactions across contrasting agroecological zones. Within this framework, phenological tracking should be standardized and quantified using time-series RGB imaging, thermal indices, or stage-specific vegetation indices (e.g., NDVI trajectory analysis or growing degree day modeling) in order to enable fair comparisons across genotypes and environments.

Modern high-throughput phenotyping (HTP) platforms allow for non-destructive, precise, and automated measurements of plant responses to water deficit. However, no single method is sufficient to capture the full spectrum of drought-adaptive traits. A holistic phenotyping approach is therefore required, one that integrates multiple sensor types, such as RGB imaging for growth dynamics, IR thermography for stomatal behavior, multispectral indices for pigment content, and fluorescence for stress detection.

In the context of common bean, specific considerations—such as heliotropic leaf movement that interferes with thermal imaging—must be factored into protocol design. For example, thermal measurements should be conducted under appropriate light conditions or supported by image segmentation techniques that reduce soil background noise.

Controlled-environment HTP must be complemented by field-based phenotyping across multiple sites and seasons to ensure robustness and real-world applicability. This

validates sensor-derived traits and enhances the findings' relevance to breeding programs operating in water-limited environments.

Yet this multi-layered phenotyping approach generates vast and complex datasets, posing challenges in data handling, interpretation, and cross-study comparability. These challenges can be addressed by implementing machine learning (ML) and artificial intelligence (AI) tools that uncover patterns, model trait interactions, and improve predictive accuracy. Equally important is the standardization of phenotyping protocols, including data formats, metadata reporting, and sensor calibration, to enable meaningful meta-analyses and foster international collaboration.

Such integration will accelerate the discovery of robust, scalable phenotypic traits and enhance the selection of drought-adapted genotypes, contributing to greater crop resilience under climate variability.

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Abbreviations

The following abbreviations are used in this manuscript:

ABA	Abscisic acid
APX	Ascorbate peroxidase
ARI	Anthocyanin Index
ATP	Adenosine triphosphate
CAT	Catalase
CF	Chlorophyll fluorescence
CHI	Chlorophyll Index
CT	X-ray computed tomography
CYPs	Cytochrome P450
DHAR	Dehydroascorbate reductase
DSI	Drought Severity Index
ETC	Electron transport chain
F_0	Minimum chlorophyll fluorescence of dark-adapted plants
F_0'	Minimum fluorescence yield of illuminated plant
F_m	Maximum chlorophyll fluorescence of dark-adapted plants
F_m'	Maximum chlorophyll fluorescence of light-adapted plants
F_q'/F_m'	Effective Quantum Yield of Photosystem II
F_s'	Steady-state fluorescence yield
F_v/F_m	Maximum Efficiency of Photosystem II
GNDVI	Green Normalized Difference Vegetation Index

GPX	Glutathione peroxidase
GR	Glutathione reductase
GSTs	Glutathione S-transferase
GWAS	Genome-wide association studies
HNBS	Hyperspectral narrowbands
HTP	Hight-throughput phenotyping
HVIs	Hyperspectral vegetation indices
IRGA	Infrared gas analyzer
JA	Jasmonic acid
LAI	Leaf area index
LEADER	Leaf Element Accumulation from Deep Roots
LHC	Light-harvesting complex
LiDAR	Light Detection and Ranging
LWIR	Long-wave infrared
MAPK	Mitogen-activated protein kinase
MCARI1	Modified Chlorophyll Absorption in Reflectance Index
MDHAR	Monodehydroascorbate reductase
MRI	Magnetic resonance imaging
MSI	Moisture Stress Index
MVS	Multi-view stereo
NADPH	Nicotinamide adenine dinucleotide phosphate
NCED	9-cis-epoxycarotenoid dioxygenase
NDDI	Normalized Difference Drought Index
NDVI	Normalized Difference Vegetation Index
NDWI	Normalized Difference Water Index
NO	Nitric oxide
NPQ	Non-photochemical quenching
ϕ_{no}	Quantum yield of non-regulated non-photochemical energy loss in PSII
OEC	Oxygen-evolving complex
OEE	Oxygen-evolving enhancer
PAR	Photosynthetically active radiation
POD	Peroxidase
PYR	Pyrabactin resistance
qP	Coefficient of photochemical quenching
qN	Coefficient of non-photochemical quenching
rETR	Relative electron transport rate
RGB	Red–green–blue
ROS	Reactive oxygen species
RuBisCO	Ribulose-1,5-diphosphate carboxylase/oxygenase
RuBP	Ribulose biphosphate
SfM	Structure-from-motion
SNP	Single-nucleotide polymorphism
SOD	Superoxide dismutase
TRX	Thioredoxin
UAV	Unmanned aerial vehicle

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