***Review Article***

**LEGUMES: BREEDING STRATEGIES AND ADAPTIVE TRAITS FOR DROUGHT TOLERANCE**

**Abstract**

Legume crops such as chickpea, cowpea, common bean, lima bean, mung bean, faba bean, and lentil are vital to global agriculture due to their nutritional value, environmental benefits, and role in sustainable farming systems. Rich in protein, fiber, and micronutrients, legumes support low-input farming, particularly in arid and semi-arid regions. However, their productivity is increasingly affected by drought and other climate-related stresses.This review synthesizes current knowledge on breeding strategies and adaptive traits that enhance drought tolerance in legumes. Key traits contributing to water-use efficiency and yield stability under stress include early flowering, stay-green phenotype, deep rooting, enhanced root hydraulic conductivity, and strong antioxidant defence. Physiological indicators such as canopy temperature depression, chlorophyll retention, relative water content, and membrane stability also play crucial roles. The review emphasizes the importance of genotypic variability and trait heritability across legume species, which serve as resources for developing climate-resilient varieties. While conventional breeding methods such as pedigree and recurrent selection have driven past progress, modern approaches like marker-assisted selection, genomic selection, GWAS, and CRISPR-based gene editing are now accelerating genetic improvement. Despite these advancements, challenges remain, including limited multi-environment testing, underuse of wild germplasm, inadequate phenotyping tools for complex traits, and poor adoption of improved cultivars. Addressing these requires a systems-based breeding framework that combines genomics, high-throughput phenotyping, and participatory approaches. Integrating adaptive traits with innovative breeding tools will enable the development of drought-resilient, high-yielding, and nutritionally rich legume cultivars, supporting food security and sustainable agriculture in a changing climate.

**Key words:** Drought tolerance, Legume breeding, Water use efficiency, Marker assisted selection (MAS), Genomic selection (GS)

**Introduction**

Legumes such as chickpea, lima bean, cowpea, common bean, mung bean, faba bean and lentil are crucial crops important for their high protein content and nutritional value. Globally, legumes are grown on approximately 70 million hectares of land, with an annual production of around 30 million metric tons. In India, legumes are extensively cultivated, covering about 12 million hectares and yielding approximately 10 million metric tons. These legumes play a significant role in improving soil fertility through nitrogen fixation, enhancing dietary protein intake and providing sustainable crop options for farmers (Pierre J. F., 2024). However, legume production faces considerable challenges, particularly in drought-prone and irrigated environments. Legume production faces major constraints from biotic and abiotic stresses. Biotic stresses, including insect herbivory, viral infections and bacterial pathogens, significantly impact productivity and food security (Akram *et al*., 2021). Pests and diseases like Helicoverpa, Ascochyta blight, and Fusarium blight cause up to 20% annual yield losses (Dhaliwal *et al*., 2020; Singh *et al*., 2022). Abiotic stresses such as drought, extreme temperatures, salinity and waterlogging lead to 51–82% global yield losses annually (Oshunsanya *et al*., 2019), with drought being the most severe, reducing photosynthesis, nutrient uptake and overall productivity. Drought stress can severely affect growth and yield, while issues such as waterlogging and salinity are common in irrigated areas. Recent studies emphasize the source necessity to develop drought-tolerant and high-yielding legume varieties to address these environmental challenges. Breeding efforts, supported by advances in genetic research, are key to overcoming these barriers. Identification of genes linked to drought tolerance and improved nitrogen fixation has been a significant development, with molecular breeding techniques offering promising solutions. These efforts are essential for ensuring food security and promoting sustainability in the face of climate change and other environmental pressures. Thus, breeding resilient, legumes is vital for enhancing productivity and supporting sustainable agriculture worldwide.

**Traits Performance in Legumes under Drought Conditions**

Drought is a major abiotic stress affecting legume production worldwide, especially in rainfed and semi-arid regions. Legumes are particularly sensitive to drought during reproductive development, which significantly impacts grain yield and seed quality. Understanding trait performance under water-deficit conditions is critical for breeding drought-resilient legume cultivars. A suite of morpho-physiological and yield-related traits collectively contribute to legume adaptation under drought stress, and their expression often varies with genotype, phenology, and stress intensity and timing. The Impact of drought stress in different traits are described detail in table 1.

1. **Yield Stability and Reproductive Resilience**

Yield stability under drought is a cornerstone trait for legume improvement. Drought stress predominantly reduces pod number and seed count rather than seed size, indicating that reproductive success, more than individual seed development, is the limiting factor (Kumar *et al.*., 2021). Drought-tolerant genotypes-such as early-maturing chickpea lines—often exhibit a drought escape mechanism by accelerating development, or a drought avoidance mechanism by conserving soil moisture during the vegetative phase to support reproductive success. Traits such as pod setting efficiency, seed filling duration, and harvest index become critical in determining final yield under moisture stress. Cowpea, for instance, demonstrates superior reproductive plasticity and yield retention under terminal drought, attributed to its stable harvest index and low water demand (Muchero *et al.*, 2008).

1. **Water Use Efficiency (WUE)**:

WUE is a central physiological trait for drought adaptation, representing the ratio of biomass or yield to water consumed. Drought-resilient legumes exhibit genotypic variation in WUE, enabling some cultivars to produce more biomass or yield per unit of water transpired. For instance, certain chickpea and common bean genotypes show enhanced WUE under deficit irrigation by optimizing stomatal regulation, reducing transpiration, and maintaining photosynthetic activity (Tavara *et al.*, 2018). Key physiological determinants of WUE include stomatal resistance, leaf area index (LAI), and transpiration efficiency. Moreover, indirect selection for WUE through traits like carbon isotope discrimination (Δ¹³C) has shown promise in legumes such as lentil and chickpea.

1. **Biomass and Canopy Dynamics**

Biomass accumulation under drought is often linked with root vigor and canopy architecture. High shoot biomass under stress, while maintaining reproductive output, is a distinguishing feature of drought-tolerant lines. Canopy conductance, a measure of stomatal behavior, is lower in tolerant genotypes, reflecting improved water conservation. The ability to sustain green leaf area under drought, or the "stay-green" trait, contributes to prolonged photosynthetic activity and assimilate partitioning to reproductive organs. This trait is associated not only with improved yield under drought but also with enhanced resistance to foliar diseases (Sivasakthi *et al*., 2019).

1. **Root System Architecture and Hydraulic Conductance**

Root traits are pivotal for water acquisition under drought conditions. Traits such as root depth, density, and root hydraulic conductivity determine the capacity of legumes to access moisture from deeper soil layers. A higher root/shoot ratio is often favored under drought as it reflects investment in water acquisition over shoot growth. In particular, genotypes with water-saving strategies such as controlled transpiration at high vapor pressure deficits and increased reliance on apoplastic water transport—show greater drought tolerance. Sivasakthi *et al* (2020) demonstrated that chickpea genotypes with efficient root hydraulics and root pressure generation maintained better water uptake and biomass production under progressive soil drying.

1. **Physiological and Biochemical Traits**

Drought resilience in legumes is also underpinned by a range of physiological and biochemical markers. Chlorophyll retention, as part of the stay-green phenotype, is indicative of sustained photosynthetic function under stress. Higher levels of soluble proteins and antioxidant enzymes (e.g., superoxide dismutase, catalase, and peroxidase) have been linked with better oxidative stress mitigation and membrane stability under drought conditions (Fogaca *et al.*, 2023). These biochemical traits often reflect the plant's metabolic capacity to endure prolonged water stress and contribute to maintaining cellular homeostasis.

1. **Integrative Trait Selection for Breeding**

The expression and stability of these adaptive traits vary across environments and developmental stages. Hence, a multi-trait approach integrating phenology, morphology, physiology, and root architecture is essential for breeding drought-resilient legume varieties. Modern breeding programs increasingly combine high-throughput phenotyping, genomic tools (e.g., QTL mapping, GWAS), and physiological trait selection to identify elite genotypes. Nonetheless, challenges such as limited multi-environment testing, narrow genetic base in breeding populations, and poor integration of root traits in phenotyping platforms persist.

|  |  |  |
| --- | --- | --- |
| **Trait/Process Affected** | **Impact of Drought Stress** | **References** |
| Nutrient Uptake and WUE | Reduces nutrient absorption and water use efficiency | Conesa *et al.*, 2016 |
| Cell Growth and Leaf Development | Impairs cell expansion and leaf morphology | Chowdhury *et al.*, 2016 |
| Photosynthesis | Inhibits photosynthetic efficiency, alters gas exchange, reduces carbon assimilation | Conesa *et al*., 2016 |
| Leaf Area and Turgor Pressure | Decreases leaf surface area and cellular turgor | Chowdhury *et al.*, 2016 |
| Oxidative Stress | Increases reactive oxygen species, leading to oxidative damage | Conesa *et al.*, 2016 |
| Reproductive Development | Reduces flowering, pod set, and seed development due to impaired assimilate partitioning | Sehgal *et al.*, 2019 |
| Pollen Viability | Causes pollen sterility, abortion, and abnormal morphology | Fang *et al.*, 2010 |
| Photosynthesis in Reproductive Phase | Reduces translocation and photosynthetic rate during seed development | Sehgal *et al.*, 2019 |
| Protein and Oil Content in Seeds | Lowers total protein and oil yield; in some cases, protein content increases while oil content declines | Farooq *et al.*, 2018; |
| Yield Loss | Overall reduction in productivity due to metabolic disruptions and impaired physiological processes | He *et al..*, 2017 |

**Table 1: Impact of drought stress in different traits**

**Key Traits for Improving Productivity and Drought Tolerance in Legumes**

Drought stress is one of the most critical constraints to legume productivity worldwide, particularly in rainfed systems. To enhance drought resilience and ensure sustainable productivity, recent research has emphasized the importance of identifying and utilizing key morpho-physiological and agronomic traits with high genetic variability and heritability. These traits serve as the foundation for breeding climate-resilient legume cultivars. The role of drought tolerance in different traits are given in detail in table 2.

1. **Genetic Variability and Trait Heritability**

Several studies have demonstrated significant genetic variation in legume crops for yield-contributing and drought-responsive traits. In chickpea, high heritability coupled with substantial genetic advance was observed for traits such as plant height, number of pods per plant, 100-seed weight, and seed yield per plant, indicating their potential utility in selection for drought tolerance (Basavaraja *et al.*, 2021; Meena *et al.*, 2021). Similarly, Ketema *et al.* (2022) reported high heritability for plant height, pod length, and seed yield in common bean, suggesting these traits are strongly controlled by genetic factors and could be effectively exploited in breeding programs. In cowpea, Swathi *et al.* (2024) reported strong genetic control for pod-related traits, emphasizing their importance for improving yield under both irrigated and water-deficient conditions.

1. **Physiological Indicators of Drought Tolerance**

Drought tolerance in legumes is also associated with physiological traits that reflect the plant’s capacity to maintain functionality under stress. Canopy temperature depression (CTD) and chlorophyll content have emerged as reliable physiological indicators of drought adaptation (Karimizadeh *et al.*, 2021). Raju *et al.* (2021) highlighted the role of pod and seed numbers as critical contributors to grain yield under drought, supporting the importance of reproductive resilience. Sachdeva *et al.* (2022) reported a significant yield loss (~33.23%) in chickpea under drought stress, emphasizing the need for selecting tolerant genotypes. Traits such as relative water content (RWC), membrane stability index (MSI), and chlorophyll index were associated with superior drought performance, demonstrating their relevance in breeding programs focused on physiological resilience.

1. **Trait Correlation and Principal Component Analysis (PCA)**

Correlation and PCA-based studies have been pivotal in identifying trait interrelationships and composite selection indices for legume improvement. Basavaraja *et al.* (2021) and Meena *et al.* (2021) revealed strong positive correlations between seed yield and agronomic traits such as branches per plant, biological yield, and harvest index in chickpea. Likewise, Raju *et al.* (2021) and Ketema *et al.* (2022) confirmed the consistent association of biological yield and harvest index with seed yield in chickpea and common bean, respectively. PCA analyses conducted by Girgel (2021) and Karimizadeh *et al.* (2021) underscored the significance of seed weight, chlorophyll content, and flowering time as major components contributing to drought tolerance and overall productivity across legume species.

**Table 2: Role of drought tolerance in different traits**

|  |  |  |
| --- | --- | --- |
| **Trait/Mechanism** | **Functional Role in Drought Tolerance** | **References** |
| Soluble Proteins and Antioxidant Enzymes | Enhance cellular defense mechanisms and mitigate oxidative damage | Fogaca *et al.*, 2023 |
| Root Traits (Hydraulics, Architecture) | Improve water uptake efficiency; deeper roots and better root/shoot ratio aid drought adaptation | Sivasakthi *et al.*, 2020 |
| Stay-Green Trait | Prolongs chlorophyll retention and photosynthetic activity during terminal drought | Sivasakthi *et al.*, 2019 |
| Water Use Efficiency (WUE), Stomatal Traits | Genotypic variation in WUE, stomatal resistance, and leaf area index confers adaptability under limited water | Nemeskéri *et al.*, 2018; Tavera *et al.*, 2018 |
| Root System Plasticity | Increases root length, spread, and density under drought, especially in small-leaf legumes | Varshney *et al.*, 2018 |
| Osmotic Adjustment | Facilitates water uptake by lowering osmotic potential in roots | Vadez *et al.*, 2008 |
| Stomatal Regulation | Promotes stomatal closure to reduce transpirational water loss and maintain leaf hydration | Vadez *et al.*, 2008 |
| Turgor Pressure Maintenance | Maintains cellular hydration under drought by reducing epidermal water loss | Sinclair and Ludlow, 1986 |

**Crop Adaptive Strategies for Drought Tolerance in Legumes: Insights from Common Beans, Cowpea, Chickpea, and Lima Beans**

Drought stress remains a critical constraint to legume productivity in rainfed systems globally. However, considerable progress has been made in identifying adaptive traits and drought-tolerant genotypes across major legumes through physiological, morphological, and agronomic evaluations. This section synthesizes key findings from recent studies that explored adaptive responses and genetic variability in common bean, cowpea, chickpea, and lima bean, offering actionable insights for breeding climate-resilient legume varieties.

**Common Bean (*Phaseolus vulgaris* L.)**

Common beans demonstrate substantial diversity in response to drought, particularly in terms of water use efficiency (WUE), photosynthesis, and root traits.

* Androcioli *et al.* (2020) compared multiple genotypes under water-deficit conditions and identified BAT 477 as a promising drought-tolerant line due to superior photosynthetic efficiency, stomatal conductance, and intrinsic WUE, making it ideal for breeding programs. In contrast, IAPAR 81 exhibited poor performance under stress, highlighting genotype-dependent variability.
* Basavaraja *et al.* (2021) evaluated germplasm accessions such as EC400414 and EC540173, revealing broad genetic variability in traits like plant height, pod number, seed yield, and relative water content (RWC). This diversity underscores the potential of underutilized germplasm in enhancing drought resilience.

**Key adaptive traits:** High WUE, sustained photosynthetic rate, and stability in yield-related traits under drought.

**Cowpea (*Vigna unguiculata* L.)**

Cowpea is naturally adapted to arid environments and exhibits significant phenotypic plasticity under drought stress.

* Ayala *et al.* (2020) highlighted genotypes such as LC-021-016 and LC-036-016, which maintained high photosynthetic activity, canopy temperature regulation, and total biomass under limited water availability.
* Ravelombola *et al.* (2020) conducted a large-scale screening of 331 genotypes, identifying 21 highly drought-tolerant lines, including PI583550, through evaluations of chlorophyll fluorescence, leaf wilting, and yield stability.
* Ezin *et al.* (2021) demonstrated the drought adaptability of local landraces like Kpodjiguegue, which retained productivity under both vegetative and reproductive stage drought, affirming the value of indigenous germplasm.

**Key adaptive traits:** Early maturity, chlorophyll retention, canopy temperature depression (CTD), and biomass accumulation under stress.

**Chickpea (*Cicer arietinum* L.)**

Chickpea, traditionally grown in semi-arid regions, exhibits substantial intraspecific variation in drought tolerance linked to root traits, osmotic adjustment, and transpiration efficiency.

* Tiwari *et al.* (2023) identified drought-resilient genotypes such as ICC4958 and JG11, characterized by deep rooting, sustained transpiration efficiency, and stable pod set under terminal drought.
* Shah *et al.* (2020) evaluated multiple breeding lines and highlighted D0091–10 as a genotype with superior drought tolerance due to its chlorophyll stability index, membrane integrity, and pod number retention.
* These findings are consistent with earlier reports linking stay-green traits, canopy cooling, and WUE with chickpea yield stability under limited moisture.

**Key adaptive traits:** Deep root systems, stay-green phenotype, high transpiration efficiency, and reproductive resilience.

**Lima Bean (*Phaseolus lunatus* L.)**

Although underutilized globally, lima beans possess inherent drought adaptation mechanisms, especially among traditional landraces.

* Martínez-Nieto *et al.* (2022) evaluated both landraces and commercial varieties, revealing distinct strategies for drought avoidance and tolerance at seedling, flowering, and pod-filling stages. Landraces maintained higher relative water content, root mass ratio, and delayed senescence, contributing to improved yield under water deficit.
* These genotypes also showed variability in leaf gas exchange, osmotic adjustment, and reproductive success, supporting their use in marginal environments with erratic rainfall.

**Key adaptive traits:** Enhanced root allocation, osmotic regulation, delayed leaf senescence, and stress-resilient reproductive development.

**Breeding Strategies for Legumes: Integrating Traditional and Modern Approaches for Drought Resilience and Productivity**

Breeding strategies for legumes have evolved from conventional selection methods to encompass advanced molecular and biotechnological tools, enabling the efficient development of high-yielding, drought-tolerant, and disease-resistant varieties. Given the vulnerability of legumes to abiotic stresses such as drought, the integration of traditional and modern breeding approaches is crucial for securing legume productivity in climate-stressed environments.

**1. Conventional Breeding Approaches**

Conventional methods remain foundational in legume breeding, especially for initial trait identification and varietal improvement in resource-limited settings. Some of the grain legumes with drought resistance have been developed using conventional breeding methods, highlighting major breeding achievements and targeted traits are in detailed in table 3.

* Mass Selection and Pedigree Breeding: These are widely applied to develop drought-tolerant varieties based on observable phenotypic traits such as early maturity, seed yield, canopy temperature depression, and root depth. For example, several high-yielding and drought-tolerant chickpea and cowpea varieties have been developed using pedigree selection in India and sub-Saharan Africa.
* Recurrent Selection and Hybridization: Crossbreeding of elite parents followed by recurrent selection helps accumulate desirable traits. These approaches, although time-consuming and labor-intensive, are effective in combining yield potential with stress tolerance.
* Participatory Breeding: Involving farmers in the selection process enhances the adoption of locally adapted varieties. This is particularly effective in marginal environments where genotype-by-environment interactions are significant.

However, conventional approaches are constrained by long breeding cycles, lower selection accuracy for complex traits, and environmental variability that often masks genetic potential.

**2. Marker-Assisted Selection (MAS)**

MAS has significantly improved the efficiency of legume breeding by enabling indirect selection based on linked molecular markers.

* Chickpea: MAS has been employed to introgress drought tolerance QTLs such as “QTL-hotspot” from ICC4958 into elite cultivars, improving root traits and water-use efficiency.
* Cowpea: Markers linked to traits like delayed leaf senescence, pod number, and seedling vigor have enhanced selection for terminal drought tolerance.
* Mung Bean and Lentil: MAS is used to select for disease resistance (e.g., powdery mildew in mung bean and Fusarium wilt in lentil), alongside yield stability under drought.

MAS shortens breeding cycles and enhances precision, particularly for traits with moderate to high heritability and well-characterized QTLs. Some of the Quantitative trait loci (QTLs) have been identified across various grain legumes, each associated with distinct traits are detailed in table 4.

**3. Genomic Selection (GS)**

GS leverages genome-wide markers to predict breeding values, allowing the selection of genotypes with complex quantitative traits like drought tolerance, yield stability, and multi-stress resistance.

* Advantages: GS enables early generation selection without phenotyping, increasing the genetic gain per unit time.
* Applications in Legumes: GS has been implemented in chickpea and lentil for predicting grain yield and drought response, using genomic prediction models with high accuracy. For example, GS has outperformed MAS in scenarios where drought tolerance is controlled by many small-effect loci.

As genomic resources expand (e.g., reference genomes and SNP panels), GS is expected to become a central component of breeding pipelines for legumes.

**4. Genomics and Gene Editing Tools**

Advanced genomics and biotechnological tools are unlocking new frontiers in legume improvement. Some of the Candidate genes for drought tolerance identified from a variety of grain legumes are presented in table 5.

* Transcriptomics and GWAS: These approaches identify novel drought-responsive genes and alleles across diverse germplasm collections. In chickpea, transcriptomic studies have revealed key regulators of ABA biosynthesis and root architecture under drought stress.
* CRISPR/Cas9: Gene editing technologies allow precise modifications in key drought-regulatory genes. Although in early stages for legumes, successful examples include editing of genes related to flowering time and stress signaling pathways (Jaganathan *et al.*, 2018).
* Speed Breeding and Doubled Haploids: These tools accelerate generation turnover and reduce breeding cycle duration, particularly when combined with genomic selection.

**5. Crop-Specific Breeding Advances**

**Mung Bean (*Vigna radiata*):**

* Focus on yield improvement, heat and drought tolerance, and resistance to powdery mildew and bacterial blight.
* Use of MAS and tissue culture to accelerate varietal release (Nair *et al..*, 2019).

**Faba Bean (*Vicia faba*):**

* Breeding targets include resistance to Ascochyta blight, enhanced nitrogen fixation, and yield stability under diverse environments.
* Development of mapping populations and QTL identification for flowering time and disease resistance traits.

**Lentil (*Lens culinaris*):**

* Emphasis on improving yield, terminal drought tolerance, and disease resistance (especially Fusarium wilt and rust).
* Application of GWAS and GS for identifying drought-responsive genotypes and shortening breeding cycles.

**Table 3:** **Grain legumes with drought resistance have been developed using conventional breeding methods, highlighting major breeding achievements and targeted traits**

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Legumes** | **Development Method** | **Achievement in Breeding** | **Targeted traits** | **References** |
| Chickpea  (*Cicer arietinum*) | * Line-source, * Drought-susceptibility index (DSI) | * Drought-escaping germplasm selection * Drought-avoidant germplasm selection * Drought-tolerant germplasm selection | * Low leaf conductance * Smaller leaf canopy * Soil water extraction * Early maturing * Deeper, more extensive root system * Increased yield during terminal drought | Berger, J.D. *et al.*, 2011  Zaman-Allah, M *et al.*, 2011  Vadez, V. *et al.*, 2012 |
| Pigeon pea (*Cajanus cajan*) | * Drought-susceptibility index (DSI) | * Drought-tolerant cultivated germplasm selection | * Polycarpic flowering habit * Deep root * Osmotic adjustment * Photosynthetic maintenance | Odeny, D.A. 2007 |
| Faba bean  (*Vicia faba*) | * Cytoplasmic genetic male sterility (CGMS) | * Drought-escaping and drought-tolerant germplasm selection | * Lower plant height * Higher WUE * Lower leaf temperature * Higher water content | Khazaei, H. *et al.*, 2013 |
| Common bean  (*Phaseolus vulgaris*) | * Recurrent selection * Advanced backcrossing * Double cross * Backcrossing | * Drought-escaping germplasm selection * Drought-avoidant germplasm selection * Drought-tolerant germplasm selection | * High grain output * High photosynthate remobilization * Early maturing * Deep roots * Stomatal control | Beebe, S.E. *et al.*, 2008  Blair, M.W. 2006  Devi, M.J. *et al.*, 2013 |

**Table 4: Quantitative trait loci (QTLs) have been identified across various grain legumes, each associated with distinct traits**

|  |  |  |  |
| --- | --- | --- | --- |
| **Grain Legumes** | **QTL Name** | **Characteristics** | **References** |
| Soybean  (*Glycine max*) | FR\_Gm01, FR\_Gm03, FR\_Gm04, FR\_Gm08, FR\_Gm20 | Fibrous rooting/surface area | Abdel-Haleem *et al.*, 2011 |
| SA\_Gm06, TRL\_Gm06, RDL3\_Gm07, TRL\_Gm08 | Root length | Manavalan *et al.,* 2015 |
| Cowpea  (*Vigna unguiculata*) | Mat-1, Mat-2 | Maturity | Muchero *et al.*, 2009 |
| Chickpea  (*Cicer arietinum*) | TR-50, SCEA19, TAA-58 | Grain weight | Hamwieh *et al.*, 2013 |
| H6C-07, H5G-01, H6C-07, H1B-04 | Grain yield |
| TA-113, TR-58, H6C-07, H1F-21 5 | Harvest index |
| Pigeon pea  (*Cajanus cajan*) | QTL-RF-1, QTL-RF-2, QTL-RF-3, QTL-RF-4 | Fertility restoration | Saxena *et al.*, 2011 |
| Pea (*Pisum sativum*) | rl1, rl2, rl3 | Root length | Fondevilla *et al.*, 2011 |

**Table 5: Candidate genes for drought tolerance identified from a variety of grain legumes**

|  |  |  |  |
| --- | --- | --- | --- |
| **Grain Legumes** | **Identified Gene** | **Functions** | **References** |
| Chickpea (*Cicer arietinum*) | MyB, AP2/ERF, XPB1 | Transcription factors | Deokar *et al.*, 2011 |
| DREB2A | Nayak *et al.*, 2009 |
| MYB, WRKY, bZIP | Hiremath *et al.*, 2011 |
| Mung bean (*Vigna radiata*) | codA | Improve abiotic-stress tolerance | Baloda and Madanpotra., 2017 |
| VrWRKY | Enhance abiotic-stress tolerance | Srivastava *et al.*, 2018 |
| VrbZIP | Drought-responsive gene | Wang *et al.*, 2018 |
| Broad bean (*Vicia faba*) | VfPIP1 | Aquaporin/water transport | Cui *et al.*, 2008 |
| Common bean (*Phaseolus vulgaris*) | DREB2B | Non-ABA dependent responses | Cortés *et al.*, 2012 |
| Asr1, Asr2 | ABA signaling pathway |
| PvLEA3 | Protein stabilization | Barrera-Figueroa *et al.*, 2008 |
| Soybean (*Glycine max*) | GmNAC, GmDREB, GmZIP, ERF089 | Transcription factors | Manavalan *et al.*, 2009 |
| DREB1A, rd29A | Bhatnagar-Mathur *et al.*, 2009 |
| GmBIN2 | Enhance tolerance to drought | Wang *et al.*, 2018 |
| GmCaM4 | Upregulate several drought-responsive genes | Yoo *et al.*, 2005 |
| CDPK | Enhance water permeability across the membrane | Guenther *et al.*, 2003 |
| GmHK, GmCLV1A, GmCLV1B, GmRLK1, GmRLK2, GmRLK3, GmRLK4 | Osmo sensor | Yamamoto *et al.*, 2000 |
| PgTIP1 | Confers drought tolerance | An *et al.*, 2018 |
| GmDREB2 | Enhance drought tolerance | Savitri and Fauziah 2018 and 2019 |
| GmRACK1 | Improve drought tolerance during vegetative growth | Li *et al.*, 2018 |
| AtABF3 | Improve drought tolerance | Kim *et al.*, 2018 |
| GmFDL19 | Enhance drought tolerance | Li *et al.*, 2017 |
| GmSK1 | Chen *et al.*, 2018 |
| Pigeon pea (Cajanus cajan) | CcM1522–CcM1821, CcM0047–CcM2332 | Improve drought tolerance | Saxena *et al.*, 2011 |
| MyB, WRKY, NF-Y | Transcription factors | Yang *et al.*, 2006 |
| Cowpea (Vigna unguiculata) | CPRD8, CPRD12, CPRD14, CPRD22, CPRD46 phospholipase D, VuPLD1, 9-cisepoxycarotenoid dioxygenase, VuNCED1 | ABA biosynthesis | Muchero *et al.*, 2010 |

**Breeding for Early Flowering in Legumes: A Strategic Trait for Drought Escape and Yield Stability**

**1. Introduction to Early Flowering as a Drought Escape Mechanism**

Drought is one of the most significant constraints limiting legume productivity, especially in rainfed and semi-arid regions. One of the most effective strategies for coping with terminal drought stress—common in these environments is drought escape through early flowering and maturity. Early flowering enables the crop to complete critical reproductive stages before the onset of severe water deficits, preserving grain yield and reproductive success.

In legumes, which are often cultivated under short growing seasons and erratic rainfall patterns, early flowering has emerged as a critical adaptive trait. Breeding programs have increasingly prioritized this trait to ensure crop establishment, timely flowering, and pod set before the depletion of soil moisture.

1. **Physiological and Agronomic Significance of Early Flowering**

* Drought Escape: Early flowering allows legumes to avoid the peak of water stress, particularly during the flowering and grain filling stages, which are highly sensitive to drought.
* Reproductive Assurance: By synchronizing flowering with favorable moisture conditions, early flowering genotypes improve pod formation, seed set, and harvest index under limited water availability.
* Heat Stress Avoidance: In regions where terminal drought is coupled with high temperatures, early flowering also helps the crop avoid heat-induced sterility during reproductive stages.
* Shorter Growth Duration: Early flowering varieties are often better suited for intercropping systems, residual moisture utilization, or post-rainy season sowing.

1. **Genetic Control of Early Flowering in Legumes**

Early flowering is a quantitative trait influenced by multiple genes and affected by environmental cues such as photoperiod and temperature. Significant progress has been made in mapping flowering-time loci in several legumes:

* **Chickpea (*Cicer arietinum*):**
  + The Efl (early flowering) locus and QTLs such as CaLG04\_EFL have been identified.
  + Genotypes like ICC 4958, JG 11, and DICC 79 exhibit early flowering and are integrated into drought breeding programs.
* **Cowpea (*Vigna unguiculata*):**
  + Early flowering is controlled by genes interacting with photoperiod sensitivity loci.
  + Breeding programs in West Africa and India utilize early-maturing genotypes like IT89KD-288 and LC-021-016.
* **Common Bean (*Phaseolus vulgaris*):**
  + The Ppd and Fin loci are associated with photoperiod sensitivity and flowering initiation.
  + Genotypes like BAT 477 exhibit early flowering and deeper rooting—an ideal combination for drought tolerance.
* **Lima Bean (*Phaseolus lunatus*):**
  + While less studied, landraces showing early flowering and determinate growth habit are prioritized in breeding for drought-prone environments (Martínez-Nieto *et al.*, 2022).

1. **Breeding Strategies Targeting Early Flowering**

Breeding for early flowering in legumes involves a multi-pronged approach combining conventional and molecular tools:

* **Phenotypic Selection:**
  + Field screening under rainfed conditions remains the first step for identifying early-flowering, drought-escaping genotypes.
  + Traits such as days to 50% flowering, days to maturity, and flowering-pod filling synchronization are used as selection indices.
* **Marker-Assisted Selection (MAS):**
  + Molecular markers linked to early flowering QTLs enable early-generation selection, particularly in chickpea and cowpea.
  + MAS has been used to introgress early flowering and root architecture QTLs into elite cultivars (e.g., introgression of QTL-hotspot in chickpea).
* **Genomic Selection (GS):**
  + GS models incorporating flowering time, biomass accumulation, and terminal drought stress response can accelerate selection in segregating populations.
* **Speed Breeding and Controlled Environments:**
  + Utilizing growth chambers and off-season nurseries facilitates rapid cycling and selection for early flowering genotypes.
  + This strategy is particularly useful for integrating early flowering with other adaptive traits like deep rooting or high water-use efficiency.
* **Participatory Breeding:**
  + Involving farmers in early selection stages helps identify early maturing varieties adapted to local rainfall patterns and cropping calendars.

1. **Challenges and Future Perspectives**

While early flowering confers advantages under drought-prone environments, trade-offs must be managed:

* Yield Potential: Extremely early genotypes may have reduced vegetative growth, leading to lower biomass and seed yield under favorable conditions.
* Photoperiod Sensitivity: Genotype x environment interaction for flowering time may limit wide adaptation.
* Integration with Other Traits: Combining early flowering with traits like deep rooting, stay-green, transpiration efficiency, and seed quality remains a key breeding goal.

**Future directions include:**

* Integrating phenomics to assess early flowering alongside whole-plant water relations.
* Exploiting wild relatives and landraces for novel alleles contributing to flowering plasticity.
* Employing CRISPR-Cas9 to modify flowering genes with high precision without linkage drag.

**2. Current Challenges and Future Prospects in Legume Breeding**

Legumes are crucial for global food security and sustainable agriculture due to their high protein content, nitrogen-fixing ability, and adaptability to marginal environments. However, the potential of legumes is often under-realized due to multiple breeding constraints, particularly under changing climate scenarios. Addressing these constraints is vital for developing climate-resilient, high-yielding, and nutritionally enriched legume varieties that can thrive under both abiotic and biotic stresses. The current challenges in legume breeding are described briefly:

1. **Limited Genetic Diversity and Germplasm Utilization**

A major bottleneck in legume breeding is the restricted use of genetically diverse and stress-adapted germplasm, especially under dual evaluation conditions (drought vs. irrigated). As Ye *et al.* (2018) noted, most breeding programs tend to evaluate genotypes under a single stress regime, which hampers the identification of stable, broadly adapted cultivars. Furthermore, wild relatives and landraces rich sources of novel alleles for stress tolerance—remain underexploited due to linkage drag and compatibility barriers.

1. **Inadequate Integration of Molecular Breeding Tools**

Despite substantial advances in genomics, the integration of marker-assisted selection (MAS), genomic selection (GS), and transcriptomics into mainstream legume breeding remains limited. This results in:

* Delayed selection cycles for complex traits like drought tolerance, root architecture, and yield stability.
* Underutilization of QTLs and genes identified for key traits in crops like chickpea, cowpea, and common bean.
* Inadequate marker-trait pipelines due to poor phenotyping and environmental characterization, limiting QTL validation and deployment.

1. **Complex Trait Architecture**

Drought tolerance, heat stress response, and nutrient-use efficiency are quantitative traits governed by multiple loci with strong genotype × environment (G×E) interactions. This complexity makes accurate selection difficult without large-scale, multi-location phenotyping, advanced statistical models, and long breeding cycles.

1. **Infrastructural and Capacity Gaps**

Breeding programs in many developing countries lack:

* High-throughput phenotyping (HTP) platforms for rapid trait assessment under stress conditions.
* Bioinformatics and data management capabilities to handle genomic datasets.
* Skilled personnel trained in modern breeding, genomics, and data integration approaches.

1. **Weak Seed Systems and Policy Support**

Even when improved cultivars are developed, poor seed dissemination, lack of farmer awareness, and weak policy frameworks restrict adoption and scaling of improved legume varieties.

**3. Future Prospects and Strategic Directions**

To overcome these challenges, legume breeding must adopt an integrated, multi-disciplinary approach that leverages both conventional and modern tools for climate-smart variety development.

1. **Harnessing Genomic Technologies**

Advanced genomics, transcriptomics, and genome-wide association studies (GWAS) can identify novel genes and markers for key traits such as:

* Drought and heat stress tolerance
* Pest and disease resistance
* Nutrient-use efficiency
* Tools such as next-generation sequencing (NGS), exome capture, SNP arrays, and CRISPR-Cas9 gene editing offer unprecedented precision and speed in trait discovery and deployment (Tyagi *et al.*, 2024).

1. **Enhancing Phenotyping Precision**

Adopting high-throughput phenotyping (HTP) tools (e.g., LeasyScan, UAVs, thermal and spectral imaging) is essential to capture dynamic plant responses under drought, heat, and combined stresses. These tools support the:

* Identification of component traits like transpiration efficiency, canopy temperature, stomatal regulation, and root traits.
* Trait-based breeding, allowing for effective marker-trait associations.

1. **Accelerating Breeding Cycles**

Combining speed breeding, doubled haploids, and rapid generation advance (RGA) techniques can shorten the time required for varietal development and release, particularly when integrated with genomic prediction models.

1. **Climate-Resilient Ideotype Design**

Breeding programs should focus on designing climate-resilient ideotypes by:

* Selecting genotypes with early flowering, deep rooting, stay-green traits, and recovery capacity after drought.
* Targeting specific adaptation for marginal environments using environmental characterization and target population of environments (TPEs) framework.

1. **Strengthening Pre-Breeding and Germplasm Enhancement**

Pre-breeding must focus on introgression of stress-resilience alleles from wild species and landraces into elite backgrounds. Novel gene pools and core collections must be developed and evaluated across diverse agro-ecological zones.

1. **Policy and Institutional Strengthening**

Robust legume improvement requires:

* Investment in breeding infrastructure, HTP, and data science.
* Cross-institutional partnerships (e.g., CGIAR, national programs, universities).
* Supportive seed systems, farmer engagement, and market linkages to ensure the adoption of improved varieties.

**Conclusion**

Legume crops are foundational to global food security, sustainable agriculture, and soil health, particularly in regions prone to erratic rainfall and marginal growing conditions. However, their production is severely constrained by drought and other environmental stresses, which reduce yield, impair reproductive development, and threaten their ecological benefits. Addressing these challenges through strategic breeding is essential to ensure resilient and productive legume-based systems.

This review highlights the multidimensional progress made in identifying adaptive traits, breeding strategies, and genetic resources for drought tolerance in legumes such as chickpea, cowpea, common bean, lima bean, faba bean, mung bean, and lentil. Adaptive traits including early flowering, deep rooting, high water-use efficiency (WUE), stay-green characteristics, and reproductive resilience have been consistently linked to drought tolerance and yield stability. Significant genetic variability for these traits exists across diverse germplasm, offering substantial potential for crop improvement.

Conventional breeding methods, such as mass and pedigree selection, continue to play a vital role in cultivar development, especially in resource-constrained environments. However, these approaches face limitations in speed and precision. The integration of modern genomics-assisted techniques—including marker-assisted selection (MAS), genomic selection (GS), genome-wide association studies (GWAS), and CRISPR-Cas9 gene editing—has accelerated the identification and deployment of key drought-responsive genes and QTLs across legumes. Coupling these tools with high-throughput phenotyping platforms and environmental characterization enhances the efficiency of trait-based selection, especially for complex traits influenced by genotype × environment interactions.

Despite this progress, significant challenges remain. These include limited utilization of wild and landrace germplasm, underrepresentation of dual-stress studies (irrigated vs. drought), poor integration of physiological traits in breeding programs, and infrastructural deficits in phenotyping and data science capacity. Furthermore, the adoption and scalability of improved cultivars are hindered by weak seed systems, fragmented policy support, and limited farmer engagement.

To overcome these barriers and ensure future-ready legume varieties, a multipronged strategy is needed:

* **Expand and diversify the germplasm base** by tapping into underutilized and wild genetic resources.
* **Strengthen trait dissection and ideotype development** focusing on climate resilience, nutritional quality, and agronomic suitability.
* **Integrate genomics and phenomics** for precision breeding, supported by robust bioinformatics pipelines.
* **Accelerate breeding cycles** through speed breeding, participatory approaches, and multi-environment testing.
* **Reinforce institutional and policy frameworks** to enable effective dissemination, adoption, and impact of improved legume technologies.

In an era of climate uncertainty and increasing global food demand, developing legume cultivars with stable performance under variable moisture regimes is both a scientific and socio-economic imperative. A future-oriented breeding paradigm- anchored in interdisciplinary collaboration, cutting-edge science, and farmer-centric innovation-will be key to unlocking the full potential of legumes as climate-smart crops that nourish both people and the planet.

**References:**

Abdel-Haleem, H., Lee, G. J. and Boerma, R. H. 2011. Identification of QTL for increased fibrous roots in soybean. Theoretical and applied genetics. 122: 935-946.

Akram, M., Kamaal, N., Pratap, A. and Singh, N. P. 2021. Resistance status of mungbean [*Vigna radiata* (L.) Wilczek] advanced breeding materials against mungbean yellow mosaic India virus. Archives of Phytopathology and Plant Protection. 54(19):2533-2546.

An, J., Cheng, C., Hu, Z., Chen, H., Cai, W. and Yu, B. 2018. The Panax ginseng PgTIP1 gene confers enhanced salt and drought tolerance to transgenic soybean plants by maintaining homeostasis of water, salt ions and ROS. Environmental and experimental botany. 155: 45-55.

Azeem, F., Bilal, A., Rana, M. A., Muhammad, A. A., Habibullah, N., Sabir, H. and Muhammad, A. 2019. Drought affects aquaporins gene expression in important pulse legume chickpea (*Cicer arietinum* L.). Pak. Journal. Botany. 51(1): 81-88.

Baloda, A. and Madanpotra, S. 2017. Transformation of mung bean plants for salt and drought tolerance by introducing a gene for an Osmo protectant glycine betaine. Journal of Plant Stress Physiology. 3: 5-11.

Barrera-Figueroa, B. E., Peña-Castro, J. M., Acosta-Gallegos, J. A., Ruiz-Medrano, R. and Xoconostle-Cázares, B. 2007. Isolation of dehydration-responsive genes in a drought tolerant common bean cultivar and expression of a group 3 late embryogenesis abundant mRNA in tolerant and susceptible bean cultivars. Functional plant biology. 34(4): 368-381.

Basavaraja, T., Manjunatha, L., Chandora, R., Gurumurthy, S. and Singh, N. P. 2021. Assessment of genetic variability, diversity and trait correlation analysis in common bean (*Phaseolus vulgaris* L.) genotypes. Legume Research-An International Journal. 44(3):252-260.

Beebe, S. E., Rao, I. M., Cajiao, C. and Grajales, M. 2008. Selection for drought resistance in common bean also improves yield in phosphorus limited and favorable environments. Crop Science. 48(2): 582-592.

Berger, J. D., Milroy, S. P., Turner, N. C., Siddique, K. H., Imtiaz, M. and Malhotra, R. 2011. Chickpea evolution has been selected for contrasting phenological mechanisms among different habitats. Euphytica, 180: 1-15.

Bhatnagar-Mathur, P., Vadez, V., Jyostna Devi, M., Lavanya, M., Vani, G. and Sharma, K. 2009. Genetic engineering of chickpea (*Cicer arietinum* L.) with the P5CSF129A gene for osmoregulation with implications on drought tolerance. Molecular Breeding. 23:591-606.

Blair, M. W., Iriarte, G. and Beebe, S. 2006. QTL analysis of yield traits in an advanced backcross population derived from a cultivated Andean× wild common bean (*Phaseolus vulgaris* L.) cross. Theoretical and Applied Genetics. 112: 1149-1163.

Cardona-Ayala, C., Cardona-Villadiego, C., Peñate-Pacheco, C., Araméndiz-Tatis, H and Espitia-Camacho, M. M. 2020. Growth, biomass distribution, gas exchange and chlorophyll fluorescence in cowpea (*Vigna unguiculata* (L.) Walp.) under drought conditions. Australian Journal of Crop Science. 14(2): 371-381.

Chen, Y., Chi, Y., Meng, Q., Wang, X. and Yu, D. 2018. GmSK1, an SKP1 homologue in soybean, is involved in the tolerance to salt and drought. Plant Physiology and Biochemistry. 127: 25-31.

Chowdhury, J. A., Karim, M. A., Khaliq, Q. A., Ahmed, A. U. and Khan, M. S. A. 2016. Effect of drought stress on gas exchange characteristics of four soybean genotypes. Bangladesh Journal of Agricultural Research. 41(2):195-205.

Conesa, M. R., De La Rosa, J. M., Domingo, R., Banon, S. and Pérez-Pastor, A. 2016. Changes induced by water stress on water relations, stomatal behaviour and morphology of table grapes *(cv. Crimson* *Seedles*s) grown in pots. Scientia Horticulturae. 202: 9-16.

Cortés, A. J., This, D., Chavarro, C., Madriñán, S. and Blair, M. W. 2012. Nucleotide diversity patterns at the drought-related DREB2 encoding genes in wild and cultivated common bean (*Phaseolus vulgaris* L.). Theoretical and Applied Genetics. 125: 1069-1085.

Cui, X. H., Hao, F. S., Chen, H., Chen, J. and Wang, X. C. 2008. Expression of the Vicia faba VfPIP1 gene in Arabidopsis thaliana plants improves their drought resistance. Journal of Plant Research. 121: 207-214.

Deokar, A. A., Kondawar, V., Jain, P. K., Karuppayil, S. M., Raju, N. L., Vadez, V. and Srinivasan, R. 2011. Comparative analysis of expressed sequence tags (ESTs) between drought-tolerant and-susceptible genotypes of chickpea under terminal drought stress. BMC plant biology. 11:1-20.

Devi, M. J., Sinclair, T. R., Beebe, S. E. and Rao, I. M. 2013. Comparison of common bean (P*haseolus vulgaris* L.) genotypes for nitrogen fixation tolerance to soil drying. Plant and Soil. 364: 29-37.

Dhaliwal, S. K., Salaria, P. and Kaushik, P. 2020. Revisiting and Enlisting Important QTLs Identified in French Bean (*Phaseolus vulgaris* L.): A Review. Preprints. 1(16):1-17

Ezin, V., Tosse, A. G. C., Chabi, I. B. and Ahanchede, A. 2021. Adaptation of cowpea (*Vigna unguiculata* L. Walp.) to water deficit during vegetative and reproductive phases using physiological and agronomic characters. International Journal of Agronomy. 6(1):1-12.

Fang, X., Turner, N. C., Yan, G., Li, F. and Siddique, K. H. 2010. Flower numbers, pod production, pollen viability, and pistil function are reduced and flower and pod abortion increased in chickpea (*Cicer arietinum* L.) under terminal drought. Journal of experimental botany. 61:335-345.

Farooq, M., Ullah, A., Lee, D. J., Alghamdi, S. S. and Siddique, K. H. 2018. Desi chickpea genotypes tolerate drought stress better than kabuli types by modulating germination metabolism, trehalose accumulation, and carbon assimilation. Plant Physiology and Biochemistry. 126: 47-54.

Fogaca, A. M., Castro, A. G., and Barbosa, E. A. A. 2023. Physiological and morphological responses of two beans common genotype to water stress at different phenological stages. Bioscience Journal. 39:1981-3163.

Fondevilla, S., Almeida, N. F., Satovic, Z., Rubiales, D., Vaz Patto, M. C., Cubero, J. I. and Torres, A. M. 2011. Identification of common genomic regions controlling resistance to Mycosphaerella pinodes, earliness and architectural traits in different pea genetic backgrounds. Euphytica. 182: 43-52.

Godoy Androcioli, L., Mariani Zeffa, D., Soares Alves, D., Pires Tomaz, J. and Moda-Cirino, V. 2020. Effect of water deficit on morpho-agronomic and physiological traits of common Bean genotypes with contrasting drought tolerance. Water. 12(1): 217.

Guenther, J. F., Chanmanivone, N., Galetovic, M. P., Wallace, I. S., Cobb, J. A. and Roberts, D. M. 2003. Phosphorylation of soybean nodulin 26 on serine 262 enhances water permeability and is regulated developmentally and by osmotic signals. The Plant Cell. 15(4): 981-991.

Halilou, O., Hamidou, F., Taya, B. K., Mahamane, S. and Vadez, V. 2015. Water use, transpiration efficiency and yield in cowpea (Vigna unguiculata) and peanut (Arachis hypogaea) across water regimes. Crop And Pasture Science. 66(7):715-728.

Hamwieh, A., Imtiaz, M. and Malhotra, R. S. 2013. Multi-environment QTL analyses for drought-related traits in a recombinant inbred population of chickpea (*Cicer arientinum* L.). Theoretical and Applied Genetics. 126: 1025-1038.

He, J., Du, Y. L., Wang, T., Turner, N. C., Yang, R. P., Jin, Y., Xi, Y., Zhang, C., Cui, T. and Fang, X. W. 2017. Conserved water use improves the yield performance of soybeans (*Glycine max* L.) under drought. Agricultural Water Management.179: 236 245.

Hiremath, P. J., Farmer, A., Cannon, S. B., Woodward, J., Kudapa, H., Tuteja, R. and Varshney, R. K. 2011. Large‐scale transcriptome analysis in chickpea (*Cicer arietinum* L.), an orphan legume crop of the semi‐arid tropics of Asia and Africa. Plant biotechnology journal. 9(8): 922-931.

Jaganathan, D., Ramasamy, K., Sellamuthu, G., Jayabalan, S. and Venkataraman, G. 2018. CRISPR for crop improvement: an update review. Frontiers in plant science.9: 985.

Jincya M., Prasad Rajendra Babu V., Jeyakumara P, Senthila A., Manivannan N., 2019. Evaluation of green gram genotypes for drought tolerance by PEG (polyethylene glycol) induced drought stress at seedling stage. Legume Research. 44(6): 684-691.

Karimizadeh, R., Keshavarzi, K., Karimpour, F. and Peyman, S. 2021. Analysis of screening tools for drought tolerance in chickpea (*Cicer arietinum* L.) genotypes. Agricultural Science Digest-A Research Journal. 41(4):531-541.

Ketema, W. and Geleta, N. 2022. Studies on genetic variability of common bean (*Phaseolus vulgaris* L.) varieties for yield and yield related traits in Western Ethiopia. International Journal of Applied Agricultural Sciences. 8(1): 41-49.

Khatun, M., Sarkar, S., Era, F. M., Islam, A. M., Anwar, M. P., Fahad, S. and Islam, A. A. 2021. Drought stress in grain legumes: Effects, tolerance mechanisms and management. Agronomy. 11(12):23-74.

Khazaei, H., Street, K., Santanen, A., Bari, A. and Stoddard, F. L. 2013. Do faba bean (*Vicia faba* L.) accessions from environments with contrasting seasonal moisture availabilities differ in stomatal characteristics and related traits. Genetic Resources and Crop Evolution. 60: 2343-2357.

Kim, H. J., Cho, H. S., Pak, J. H., Kwon, T., Lee, J. H., Kim, D. H. and Chung, Y. S. 2018. Confirmation of drought tolerance of ectopically expressed AtABF3 gene in soybean. Molecules and cells. 41(5): 413-422.

Kumar, J., Choudhary, A. K., Solanki, R. K. and Pratap, A. 2011. Towards marker‐assisted selection in pulses: a review. Plant breeding. 130(3):297-313.

Li, D. H., Chen, F. J., Li, H. Y., Li, W. and Guo, J. J. 2018. The soybean GmRACK1 gene plays a role in drought tolerance at vegetative stages. Russian Journal of Plant Physiology. 65: 541-552.

Li, Y., Chen, Q., Nan, H., Li, X., Lu, S., Zhao, X. and Cao, D. 2017. Overexpression of GmFDL19 enhances tolerance to drought and salt stresses in soybean. PLoS One. 12(6): e0179554.

Manavalan, L. P., Guttikonda, S. K., Phan Tran, L. S. and Nguyen, H. T. 2009. Physiological and molecular approaches to improve drought resistance in soybeans. Plant and cell physiology. 50(7): 1260-1276.

Manavalan, L. P., Prince, S. J., Musket, T. A., Chaky, J., Deshmukh, R., Vuong, T. D. and Nguyen, H. T. 2015. Identification of novel QTL governing root architectural traits in an interspecific soybean population. PLoS One.10(3): e0120490.

Martínez-Nieto, M. I., González-Orenga, S., Soriano, P., Prieto-Mossi, J., Larrea, E., Doménech-Carbó, A. and Mayoral, O. 2022. Are traditional lima bean (*Phaseolus lunatus* L.) landraces valuable to cope with climate change? The effects of drought on growth and biochemical stress markers. Agronomy. 12(7):1-20.

Meena, V. K., Verma, P., Tak, Y. and Meena, D. 2021. Genetic variability, correlation and path coefficient studies in chickpea (*Cicer arietinum* L.) genotypes in Southeastern Rajasthan. Biological Forum- An International Journal. 13(3a): 93-98.

Mondal, M. M., Fakir, M. S., Juraimi, A. S., Hakim, M. A., Islam, M. M. and Shamsuddoha A. T. 2011. Effect of water stress on growth and yield of mung beans (Vigna radiata L.). Australian Journal of Crop Science. 5: 945.

Muchero, W., Ehlers, J. D. and Roberts, P. A. 2010. Restriction site polymorphism-based candidate gene mapping for seedling drought tolerance in cowpea [*Vigna unguiculata* (L.) Walp.]. Theoretical and Applied Genetics. 120: 509-518.

Muchero, W., Ehlers, J. D., Close, T. J. and Roberts, P. A. 2009. Mapping QTL for drought stress-induced premature senescence and maturity in cowpea [*Vigna unguiculata* (L.) Walp.]. Theoretical and Applied Genetics. 118: 849-863.

Nair, R. M., Yang, R. Y., Easdown, W. J., Thavarajah, D., Thavarajah, P., Hughes, J. D. A. and Keatinge, J. D. H. 2013. Biofortification of mungbean (*Vigna radiata*) as a whole food to enhance human health. Journal of the Science of Food and Agriculture, 93(8), 1805-1813.

Nayak, S. N., Balaji, J., Upadhyaya, H. D., Hash, C. T., Kishor, P. K., Chattopadhyay, D. and Varshney, R. K. 2009. Isolation and sequence analysis of DREB2A homologues in three cereal and two legume species. Plant Science. 177(5): 460-467.

Nemeskéri, E., Molnár, K., Pék, Z. and Helyes, L. 2018. Effect of water supply on the water use-related physiological traits and yield of snap beans in dry seasons. Irrigation Science. 36:143-158.

Odeny, D. A. 2007. The potential of pigeonpea (*Cajanus cajan* L.) in Africa. In Natural resources forum. 31(4): 297-305.

Oshunsanya, S. O., Nwosu, N. J. and Li, Y. 2019. Abiotic stress in agricultural crops under climatic conditions. Sustainable Agriculture, Forest and Environmental Management, Springer.1(3):71-100.

Pierre, J. F. 2024. Legumes: Cornerstones of Global Food Security and Sustainable Agriculture. Intechopen:1006180.

Raju, A. C. and Lal, G. M. 2021. Correlation and path coefficient analysis for quantitative traits in chickpea (Cicer arietinum L). International Journal of Botany and Research. 11(2):15-22.

Ramamoorthy, P., Lakshmanan, K., Upadhyaya, H. D., Vadez, V. and Varshney, R. K. 2016. Shoot traits and their relevance in terminal drought tolerance of chickpea (*Cicer arietinum* L.). Field Crops Research. 197:10-27.

Rasti Sani, M., Ganjeali, A., Lahouti, M. and Mousavi Kouhi, S. M. 2018. Morphological and physiological responses of two common bean cultivars to drought stress. Journal of Plant Process and Function. 6(22):37-46.

Ravelombola, W., Shi, A., Chen, S., Xiong, H., Yang, Y., Cui, Q. and Mou, B. 2020. Evaluation of cowpea for drought tolerance at seedling stage. Euphytica. 216:1-19.

Sachdeva, S., Bharadwaj, C., Patil, B. S., Pal, M., Roorkiwal, M. and Varshney, R. K. 2022. Agronomic performance of chickpea affected by drought stress at different growth stages. Agronomy. 12(5): 995.

Samal I., Bhoi, T. K, Raj., M.N., Majhi., P. K., Murmu., S, Pradhan A.K and Guru., P. N. 2023. Underutilized legumes: nutrient status and advanced breeding approaches for qualitative and quantitative enhancement. Frontiers in Nutrition. 10:1110750.

Savitri, E. S. and Fauziah, S. M. 2018. Characterization of drought tolerance of GmDREB2 soybean mutants (*Glycine max* (L.) by ethyl methane sulfonate induction. In AIP conference proceedings. Vol. 2019: No. 1.

Saxena, K. B., Singh, G., Gupta, H. S., Mahajan, V., Kumar, R. V., Singh, B. and Sultana, R. 2011. Enhancing the livelihoods of Uttarakhand farmers by introducing pigeon pea cultivation in hilly areas. Journal of Food Legumes. 24(2): 128-132.

Sehgal, A., Sita, K., Bhandari, K., Kumar, S., Kumar, J., Vara Prasad, P. V. and Siddique, K. H. M. 2019. Influence of drought and heat stress applied independently or in combination during seed development, on qualitative and quantitative aspects of seeds of lentil (*Lens culinaris Medikus*) genotypes, differing in drought sensitivity. Plant, Cell and Environment. 42(1): 198-211.

Shah, T. M., Imran, M., Atta, B. M., Ashraf, M. Y., Hameed, A., Waqar, I. and Maqbool, M. A. 2020. Selection and screening of drought tolerant high yielding chickpea genotypes based on physio-biochemical indices and multi-environmental yield trials. BMC Plant Biology. 20:1-16.

Sinclair, T. R. and Ludlow, M. M. 1986. Influence of soil water supply on the plant water balance of four tropical grain legumes. Australian Journal of Plant Physiology.13:329–341.

Singh, R. K., Singh, C., Ambika, Chandana, B. S., Mahto, R. K., Patial, R. and Kumar, R. 2022. Exploring chickpea germplasm diversity for broadening the genetic base utilizing genomic resourses. Frontiers in Genetics.13:1-21.

Sivasakthi, K., Marques, E., Kalungwana, N. A., Carrasquilla-Garcia, N., Chang, P. L., Bergmann, E. M. and Penmetsa, R. V. 2019. Functional dissection of the chickpea (*Cicer arietinum* L.) stay-green phenotype associated with molecular variation at an ortholog of Mendel’s I gene for cotyledon color: implications for crop production and carotenoid biofortification. International journal of molecular sciences. 20(22):5562.

Sivasakthi, K., Tharanya, M., Zaman‐Allah, M., Kholová, J., Thirunalasundari, T. and Vadez, V. 2020. Transpiration difference under high evaporative demand in chickpea (*Cicer arietinum* L.) may be explained by differences in the water transport pathway in the root cylinder. Plant Biology. 22(5):769-780.

Srivastava, R., Kumar, S., Kobayashi, Y., Kusunoki, K., Tripathi, P., Kobayashi, Y. and Sahoo, L. 2018. Comparative genome-wide analysis of WRKY transcription factors in two Asian legume crops: Adzuki bean and Mung bean. Scientific reports.8(1):16971.

Swathi, S., Joseph, J., Sindhumole, P. and Mathew, D. 2024. Genetic variability and heritability studies in cowpea (Vigna unguiculata L. Walp.). Journal of Tropical Agriculture. 62(1): 14-21.

Tavera, V. M., Mancilla, C. L. A., Gallegos, J. A. A., Pimentel, J. G. R., Arriaga, A. I. M. and Ruiz Nieto, J. E. 2018. Mechanisms for water-use efficiency between bean cultivars tolerant to drought are different. Acta Scientiarum. Agronomy. 40: 39378.

Tiwari, P. N., Tiwari, S., Sapre, S., Tripathi, N., Payasi, D. K., Singh, M. and Tripathi, M. K. 2023. Prioritization of physio-biochemical selection indices and yield-attributing traits toward the acquisition of drought tolerance in chickpea (*Cicer arietinum* L.). Plants. 12(18): 1-21

Tyagi, A., Mir, Z. A., Almalki, M. A., Deshmukh, R. and Ali, S. 2024. Genomics-Assisted Breeding: A Powerful Breeding Approach for Improving Plant Growth and Stress Resilience. Agronomy. 14(6): 1128.

Vadez, V., Rao, S., Kholova, J., Krishnamurthy, L., Kashiwagi, J., Ratnakumar, P. and Basu, P. S. 2008. Root research for drought tolerance in legumes: Quo vadis? Journal of Food Legumes. 21(2): 77-85.

Vadez, V., Soltani, A. and Sinclair, T. R. 2012. Modelling possible benefits of root related traits to enhance terminal drought adaptation of chickpea. Field Crops Research. 137: 108-115.

Varshney, R. K., Nayak, S. N., May, G. D. and Jackson, S. A. 2009. Next-generation sequencing technologies and their implications for crop genetics and breeding. Trends in biotechnology. 27(9): 522-530.

Varshney, R. K., Tuberosa, R. and Tardieu, F. 2018. Progress in understanding drought tolerance: From alleles to cropping systems. Journal of Experimental Botany. 69: 3175–3179.

Wang, L. S., Chen, Q. S., Xin, D. W., Qi, Z. M., Zhang, C., Li, S. N. and Wu, X. X. 2018. Overexpression of GmBIN2, a soybean glycogen synthase kinase 3 gene, enhances tolerance to salt and drought in transgenic Arabidopsis and soybean hairy roots. Journal of integrative agriculture. 17(9):1959-1971.

Wang, L., Zhu, J., Li, X., Wang, S. and Wu, J. 2018. Salt and drought stress and ABA responses related to bZIP genes from *V. radiata* and *V. angularis*. Gene. 651:152-160.

Yagoob, H. and Yagoob, M. 2014. The effects of water deficit stress on protein yield of mung bean genotypes. Peak Journal of Agricultural Sciences. 2:30-35.

Yamamoto, E., Karakaya, H. C. and Knap, H. T. 2000. Molecular characterization of two soybean homologs of Arabidopsis thaliana CLAVATA1 from the wild type and fasciation mutant. Biochimica et Biophysica Acta (BBA)-Gene Structure and Expression. 1491(1-3): 333-340.

Yang, S., Pang, W., Ash, G., Harper, J., Carling, J., Wenzl, P. and Kilian, A. 2006. Low level of genetic diversity in cultivated pigeon pea compared to its wild relatives is revealed by diversity arrays technology. Theoretical and applied genetics. 113: 585-595.

Ye, H., Roorkiwal, M., Valliyodan, B., Zhou, L., Chen, P., Varshney, R. K. and Nguyen, H. T. 2018. Genetic diversity of root system architecture in response to drought stress in grain legumes. Journal of Experimental Botany. 69(13): 3267-3277.

Yoo, J. H., Park, C. Y., Kim, J. C., Do Heo, W., Cheong, M. S., Park, H. C. and Cho, M. J. 2005. Direct interaction of a divergent CaM iso form and the transcription factor, MYB2, enhances salt tolerance in Arabidopsis. Journal of Biological Chemistry. 280(5): 3697-3706.

Zaman-Allah, M., Jenkinson, D. M. and Vadez, V. 2011. Chickpea genotypes contrasting for seed yield under terminal drought stress in the field differ for traits related to the control of water use. Functional Plant Biology. 38(4): 270-281.