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Genetic improvement of drought tolerance in cowpea (*Vigna unguiculata*): Integrating physiology, genomics, and breeding

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Abstract

Cowpea (*Vigna unguiculata* (L.) Walp.) is a critical grain legume for dryland agriculture, yet drought remains the major constraint to stable productivity. This review synthesizes recent progress in deciphering drought adaptation in cowpea, integrating advances in physiological trait dissection, managed stress screening, breeding strategies, and genomics-enabled improvement. We highlight how high-quality reference and pan-genomes, QTL mapping, genome-wide association studies, and genomic selection have revealed the highly polygenic and stage-dependent nature of drought tolerance, with key roles for phenology, root architecture, stomatal regulation, photosynthetic resilience, and yield stability. Emerging multi-omics and functional validation studies are uncovering regulatory networks centered on ABA signaling, redox control, and osmotic adjustment, providing candidate genes and biomarkers for precision breeding. We discuss current limitations and outline future directions to translate molecular insights into climate-resilient, farmer-preferred cowpea cultivars.

Keywords: Cowpea, drought tolerance, genomic resources, genome-wide association studies (GWAS), quantitative trait loci (QTL), genomic selection, root architecture, multi-omics integration

1. Introduction

Cowpea (*Vigna unguiculata* (L.) Walp.) is a major grain legume of the tropics and subtropics, particularly in sub-Saharan Africa and South Asia, where it supports food, nutritional, and income security of millions of smallholder farmers. Cowpea grains contain 20-25% protein along with essential amino acids, vitamins, and minerals, while crop residues serve as valuable livestock fodder, making the crop integral to mixed farming systems. In addition, cowpea improves soil fertility through biological nitrogen fixation and performs well in low-input systems with limited fertilizer access (Namatsheve *et al.*, 2020) [34].

Cowpea is mainly cultivated under rainfed conditions in semi-arid and dry sub-humid regions characterized by erratic rainfall, high temperatures, and poor soils, making production highly vulnerable to climate variability (de Melo *et al.*, 2022) [88]. Although relatively drought-resilient, cowpea yield remains unstable under water-limited environments, particularly when stress coincides with flowering and pod filling (Ezin *et al.*, 2021) [13]. Increasing drought frequency and intensity have led to severe yield losses, with reproductive-stage drought often reducing yields from >1000 kg ha⁻¹ to 300-400 kg ha⁻¹ or less (Ezin *et al.*, 2021; Santos *et al.*, 2020) [13, 41]. Early-stage drought limits canopy development and yield potential, whereas reproductive-stage stress impairs pod set, seed development, and harvest index, sometimes causing near-complete crop failure (Ezin *et al.*, 2021; Poudel *et al.*, 2025) [13, 37]. Rising temperatures further intensify drought effects by accelerating soil moisture depletion and crop water use (Nkomo *et al.*, 2021) [41].

Drought tolerance in cowpea is a complex quantitative trait with strong genotype × environment interactions, resulting in unstable performance across environments and limiting the efficiency of yield-based selection alone (Agbicodo *et al.*, 2009) [58].

Genetic gains have therefore been modest, particularly under terminal and reproductive-stage drought, and are further constrained by interacting stresses such as heat, pests, and diseases (Carvalho *et al.*, 2017) ^[7].

Although cowpea possesses adaptive traits such as deep rooting and early maturity, current breeding progress is insufficient to counter climate-driven yield instability. Consequently, recent studies emphasize integrating multi-environment testing, trait-based phenotyping, and molecular and genomic approaches including QTL mapping, GWAS, genomic selection, and marker-assisted breeding to elucidate the genetic basis of drought tolerance and develop high-yielding, climate-resilient cowpea cultivars for drought-prone agro-ecologies (Agbicodo *et al.*, 2009) ^[7].

1.1 Types of droughts in cowpea production systems

Drought occurs at different growth stages in cowpea, and its timing strongly determines physiological responses and yield loss; therefore, early-season, mid-season, and terminal drought are now distinguished for targeted phenotyping and breeding (Deffo *et al.*, 2024; Ezin *et al.*, 2021; Hall, 2012) ^[11, 13, 18].

1.1.1 Early-season drought

Early-season drought limits crop establishment, canopy expansion, and root and nodule development, reducing stomatal conductance, biomass accumulation, and nitrogen fixation, and thereby lowering yield potential even after stress relief (Olorunwa *et al.*, 2021; Melo *et al.*, 2025; Poudel *et al.*, 2025) ^[33, 26, 37]. Screening at this stage targets rooting vigor, root:shoot ratio, stem greenness, and maintenance of gas exchange (Santos *et al.*, 2020; Olorunwa *et al.*, 2021) ^[41, 33].

1.1.2 Mid-season drought

Mid-season drought, often caused by rainfall breaks, reduces leaf area, photosynthesis, and assimilate supply to developing reproductive organs. Although partial acclimation and improved water-use efficiency may occur, flower production and pod set are commonly reduced, lowering yield (Hall, 2012; Carvalho *et al.*, 2019; Olorunwa *et al.*, 2021) ^[18, 33, 6]. Key traits include delayed senescence, water-use efficiency, and deeper rooting (Carvalho *et al.*, 2019) ^[8].

1.1.3 Terminal drought

Terminal drought, from flowering to pod filling, is the most damaging, causing declines in plant water status, chlorophyll, and photochemical efficiency, leading to flower and pod abortion, reduced seed size, and low harvest index (Deffo *et al.*, 2024; Ezin *et al.*, 2021; Nunes *et al.*, 2022) ^[11, 13, 32]. Even small genotypic differences in stomatal control and stay-green behavior can result in large yield differences under terminal stress (Moreira *et al.*, 2023) ^[29]. Phenological escape, reproductive-stage tolerance, and stress priming are therefore major breeding targets (Hall, 2012; Tankari *et al.*, 2021) ^[18, 49]. Across stages, drought effects are stage-dependent: early stress reshapes root and nodule development, mid-season stress limits assimilate supply, and terminal stress directly restricts pod set and grain filling, causing the greatest yield losses. Multi-stage screening is thus essential to identify genotypes combining early resilience, reproductive-stage tolerance, and stable yield under variable rainfall (Deffo *et al.*, 2024; Ezin *et al.*, 2021; Hall, 2012) ^[11, 13, 18].

1.2 Sensitive growth stages of cowpea to drought stress

1.2.1 Germination and seedling stage

Germination and early seedling growth are highly drought-sensitive, with reduced imbibition, germination percentage, and seedling vigor, leading to poor crop establishment (Carvalho *et al.*, 2017; Esan *et al.*, 2021; Tanasale *et al.*, 2025) ^[7, 12, 48]. PEG-induced stress consistently reduces germination, radicle and

plumule length, and seedling biomass across cowpea genotypes (Carvalho *et al.*, 2017; Tanasale *et al.*, 2025) ^[7, 48]. Early drought strongly restricts root and shoot growth, leaf area, and nodulation, thereby lowering early source capacity and later yield potential (Nkomo *et al.*, 2022; Poudel *et al.*, 2025; Ritte *et al.*, 2025) ^[31, 37, 40]. Physiologically, stress rapidly decreases stomatal conductance, increases canopy temperature, and suppresses photosynthesis and chlorophyll fluorescence, and although partial recovery after rewatering may occur, early stress often leaves persistent reductions in canopy size and yield (Nkomo *et al.*, 2022; Olorunwa *et al.*, 2021) ^[31, 33].

1.2.2 Flowering stage

Flowering is consistently identified as the most drought-sensitive stage in cowpea (Deffo *et al.*, 2024; Ezin *et al.*, 2021; Tankari *et al.*, 2021) ^[11, 13, 49]. Water deficit at flowering causes greater yield penalties than vegetative stress by reducing plant water status, chlorophyll content, and photochemical efficiency and by inducing extensive flower and pod abortion (Gnankambary *et al.*, 2020; Nunes *et al.*, 2022) ^[15, 32]. Elevated canopy temperature and vapor pressure deficit further impair pollen function and fertilization, sharply reducing pod number the primary determinant of grain yield (Carvalho, Castro, *et al.*, 2019; Ezin *et al.*, 2021; Deffo *et al.*, 2024) ^[6, 8, 13, 11].

1.2.3 Pod filling stage

Terminal drought during pod filling shortens the grain-filling period, accelerates senescence, and restricts assimilate and nitrogen remobilization, resulting in smaller seeds, reduced 100-seed weight, and lower harvest index (Ezin *et al.*, 2021; Muhammed *et al.*, 2024; Tankari *et al.*, 2021) ^[13, 30, 49]. Stress imposed at early seed filling markedly reduces pod weight, seed number, and total grain yield, and under severe terminal drought, premature pod abortion and incomplete seed development can lead to drastic yield losses or near crop failure (Ezin *et al.*, 2021; Muhammed *et al.*, 2024) ^[13, 30].

1.3 Impact of drought on cowpea growth and yield

1.3.1 Germination and establishment

Low water potential reduces imbibition and delays or suppresses germination, causing poor and nonuniform emergence (Carvalho *et al.*, 2019; Esan *et al.*, 2021; Tanasale *et al.*, 2025) ^[6, 8, 12, 48]. PEG-induced stress consistently lowers germination percentage, radicle growth, and seedling vigor, although tolerant genotypes maintain relatively higher establishment (Carvalho *et al.*, 2019) ^[19]. Poor establishment reduces stand density, early biomass, nodulation, and radiation interception, constraining nitrogen fixation and season-long yield potential (Esan *et al.*, 2021; Olorunwa *et al.*, 2021) ^[12, 33].

1.3.2 Vegetative growth

Vegetative-stage drought reduces leaf area, plant height, and shoot biomass (often by >50%) and alters biomass partitioning, increasing root:shoot ratio under moderate stress (Olorunwa *et al.*, 2021; Poudel *et al.*, 2025; Santos *et al.*, 2020) ^[33, 37, 41]. Declines in stomatal conductance, transpiration, and photosynthesis, coupled with elevated canopy temperature and oxidative stress, reduce chlorophyll content and photochemical efficiency (Carvalho, Castro, *et al.*, 2019; Nunes *et al.*, 2022; Olorunwa *et al.*, 2021) ^[6, 8, 32, 33]. Severe or prolonged stress restricts both lateral and deep root development, impairing water and nutrient uptake and limiting source capacity for reproductive growth (Poudel *et al.*, 2025; Santos *et al.*, 2020) ^[37, 41].

1.3.3 Flower drop, pod abortion, and seed filling

Reproductive stages are the most drought-sensitive. Water deficit at flowering or early pod set sharply increases flower and pod abortion, reduces pod number, seeds per pod, and seed weight, and can decrease yield by 50-90% (Deffo *et al.*, 2024; Ezin *et al.*, 2021; Muhammed *et al.*, 2024; Tankari *et al.*, 2021)

[11, 13, 30, 49]. Terminal drought shortens the grain-filling period, accelerates senescence, and restricts assimilate and nitrogen remobilization, producing small, shriveled, low-quality seeds and a reduced harvest index (Ezin *et al.*, 2021; Muhammed *et al.*, 2024) [13, 30].

1.3.4 Effects on yield components

Across environments, drought consistently reduces pods per plant, grains per plant, seed size, biomass, and harvest index, with pod number emerging as the most sensitive and yield-determining component under reproductive-stage stress (Deffo *et al.*, 2024; Ezin *et al.*, 2021) [11, 13].

2. Physiological and morphological traits associated with drought tolerance

2.1 Root-based traits in cowpea

Drought-tolerant cowpea genotypes typically develop deeper root systems and redistribute root length density to deeper soil layers, enabling improved subsoil water extraction and sustained biomass under stress (Matsui *et al.*, 2003; Santos *et al.*, 2020; Kou *et al.*, 2022) [25, 41, 23]. Early-stage screening shows that tolerant lines combine greater total root length, surface area, and fine-root proliferation with better shoot performance, reflecting efficient soil exploration rather than increased root mass alone (Poudel *et al.*, 2025) [37]. Drought commonly increases root:shoot ratio and induces architectural plasticity, with genotypes maintaining shoot growth also showing stronger root investment (Santos *et al.*, 2020) [41]. Highly resilient accessions further exhibit anatomical plasticity that supports efficient water uptake across contrasting moisture regimes (Iseki & Olaleye, 2025a) [19].

2.2 Shoot-based physiological traits associated with drought tolerance

Shoot traits provide integrative, relatively high-throughput indicators of drought tolerance and often show strong associations with yield-based indices. Drought-tolerant cowpea genotypes consistently maintain higher relative water content (RWC), reflecting superior water uptake, osmotic adjustment, and membrane stability, and this trait is repeatedly linked to improved recovery and yield under stress (Shardendu *et al.*, 2011) [24]. Canopy temperature serves as a robust proxy for stomatal conductance and root function, with tolerant lines maintaining cooler canopies and thermal imaging platforms showing strong correlations with biomass and yield under drought (Kim *et al.*, 2020; Nunes *et al.*, 2022) [22, 37].

Variation in stomatal sensitivity to soil drying underpins contrasting drought strategies in cowpea; optimized regulation rather than extreme closure supports carbon assimilation while conserving water, and high-throughput phenotyping combined with GWAS has identified genomic regions controlling stomatal dynamics (Shardendu *et al.*, 2011) [38]. Maintenance of chlorophyll content and stay-green behavior reflects protection of the photosynthetic apparatus and delayed senescence, with tolerant genotypes showing smaller SPAD declines, sustained photosynthesis, and improved pod and grain set under terminal drought.

Drought-tolerant lines also retain higher photosynthetic efficiency (Fv/Fm, ETR), improved intrinsic water-use efficiency, and stronger post-stress recovery of gas exchange and fluorescence traits, indicating reduced irreversible damage and greater physiological resilience (Nunes *et al.*, 2022; Lima *et al.*, 2025b) [32, 37].

2.3 Biochemical and metabolic bases of cowpea drought tolerance

Drought tolerance in cowpea involves strong osmotic adjustment, driven by accumulation of proline, soluble sugars, galactinol, organic acids, phenylpropanoids, and inorganic ions, many of which correlate positively with yield under stress (Goufo *et al.*, 2017; Ozturk *et al.*, 2021) [16, 35].

Tolerant genotypes display more efficient antioxidant systems, with higher activities of SOD, CAT, APX, and GR and lower H₂O₂ and MDA, conferring improved membrane stability and recovery (Miri *et al.*, 2022; Ribeiro *et al.*, 2023) [27, 39]. Proteomic studies consistently identify oxidoreductases as central components of drought adaptation (Ribeiro *et al.*, 2023) [39].

At the regulatory level, rapid ABA biosynthesis and signaling drive early stomatal control and maintenance of plant water status, while drought-responsive miRNAs and hormone cross-talk (ABA, JA, SA, ethylene, cytokinins, brassinosteroids) coordinate osmolyte accumulation, antioxidant capacity, and stress-responsive growth modulation (Mishra *et al.*, 2021; Tochiara-Tanaka *et al.*, 2025; Sharma *et al.*, 2019; Singh *et al.*, 2023) [28, 50, 43, 45].

3. Breeding approaches for genetic improvement of drought tolerance in cowpea

3.1 Major germplasm sources and their roles

3.1.1 Global collections and genebanks

Cowpea drought improvement is fundamentally supported by the extensive diversity conserved in global genebanks, particularly at IITA, which maintains >15,000 cultivated accessions and >1,500 wild *Vigna* accessions capturing wide variation in phenology, architecture, root traits, and abiotic stress adaptation (Boukar *et al.*, 2020; C. Fatokun *et al.*, 2018; C. A. Fatokun *et al.*, 2012) [59, 60, 61]. Large diversity panels (~99 to >1,288 accessions) evaluated under managed drought have enabled the identification of stay-green, early-maturing, and drought-tolerant donors now widely used in climate-resilient breeding (Boukar *et al.*, 2020) [19].

3.1.2 Landraces and wild relatives

Landraces from Southern Africa, Mozambique, and the Sahel harbor high adaptive diversity and frequently outperform modern cultivars under terminal and intermittent drought (Gomes *et al.*, 2021; Macharia *et al.*, 2025) [62, 63]. Wild *Vigna* relatives provide additional drought-adaptive alleles, particularly for root plasticity (stele proportion, aerenchyma, fine-root proliferation) and dual tolerance to water deficit and excess moisture (Boukar *et al.*, 2020) [19], and are increasingly targeted for pre-breeding and introgression.

3.2 Mini-core collections and MAGIC resources

3.2.1 Mini-core panels

IITA mini-core collections (~300 accessions) capture most global SNP diversity and are central to drought phenotyping and GWAS (C. Fatokun *et al.*, 2018) [19]. These panels have facilitated the discovery of loci controlling flowering time, stay-green behavior, root traits, and yield stability, thereby accelerating parental selection and gene discovery.

3.2.2 MAGIC populations

The eight-parent cowpea MAGIC population (~305 F₈ RILs) integrates diverse drought-tolerance, disease-resistance, and agronomic alleles into highly recombined, breeding-ready backgrounds (B. L. Huynh *et al.*, 2018; B.-L. Huynh *et al.*, 2017, 2019; Ravelombola *et al.*, 2021) [64, 65, 66]. GWAS within this population has resolved SNPs for drought indices, phenology, seed weight, and grain yield, positioning MAGIC lines as dual-purpose resources for high-resolution mapping and rapid breeding deployment (Ravelombola *et al.*, 2021) [66].

3.3 Managed stress screening strategies

3.3.1 Field-based managed drought

Reproducible field stress environments are central to cowpea drought breeding due to strong G×E and stage-specific sensitivity (Alidu *et al.*, 2019; Carvalho, Castro, *et al.*, 2019; Deffo *et al.*, 2024; Ezin *et al.*, 2021) [6, 8, 11, 13]. Terminal drought

imposed from flowering to pod filling, combined with rainout shelters, off-season nurseries, and multi-environment trials, enables robust estimation of drought indices (STI, GMP, MP, YI, HM) and identification of elite, stable lines (Alidu *et al.*, 2019; Carvalho, Castro, *et al.*, 2019; Deffo *et al.*, 2024; Ezin *et al.*, 2021; Gnankambary *et al.*, 2020) [6, 8, 11, 13, 15].

3.3.2 Stage-specific and multi-environment screening.

Vegetative-stage screening targets seedling vigor, nodulation, and root development, while reproductive-stage screening emphasizes flower retention, pod set, and harvest index (Alidu *et al.*, 2019; Ezin *et al.*, 2021) [13, 37]. Sequential filtering across growth stages and locations improves selection efficiency and retention of broadly resilient genotypes (Alidu *et al.*, 2019) [11].

3.3.3 Semi-controlled and controlled platforms

Screenhouse, pot, lysimeter, rhizotron, and PEG-based systems enable precise moisture control and detailed measurement of physiological and root traits, including transpiration efficiency, rooting depth, and post-stress recovery (Nkomo *et al.* 2022; Olorunwa *et al.*, 2021; Poudel *et al.*, 2025) [31, 33, 37].

3.3.4 High-throughput phenotyping integration

Infrared thermography, multispectral indices (NDVI, PRI), and chlorophyll fluorescence provide rapid, non-destructive indicators of canopy temperature, photosynthetic performance, and stress progression, strongly associated with drought tolerance and root traits (Carvalho, Castro, *et al.*, 2019; Olorunwa *et al.*, c; Poudel *et al.*, 2025) [6, 33, 37]. These phenomic traits are increasingly integrated with GWAS and genomic selection to enable predictive drought breeding pipelines (Nkomo *et al.*, 2022; Poudel *et al.*, 2025) [31, 37].

3.4 Drought tolerance indices and selection metrics in cowpea

3.4.1 Behavior, heritability, and G×E of yield-based indices

Under managed drought and non-stress environments, most yield-based drought indices in cowpea show significant genetic variation and strong genotype, environment, and G×E effects, closely paralleling grain yield responses and confirming their biological relevance (Singini *et al.*, 2024) [67]. Across studies, STI, GMP, MP, HM, YI, YSI, DRI, and modified indices (MST1, MST2) consistently emerge as the most reliable for identifying genotypes combining high yield and drought tolerance (Ajayi, 2024) [11]. These indices generally exhibit moderate to high broad-sense heritability (≈30-60% or higher) and substantial genetic advance, supporting their use for indirect selection (Ajayi, 2020, 2024) [2]. MP, GMP, HM, YI, and STI are repeatedly reported as highly correlated with yield under both stressed and non-stressed conditions, making them particularly suitable for selecting broadly adapted, high-yielding genotypes (Singini *et al.*, 2024) [67]. Comparable trends across legumes and cereals further validate STI-, GMP-, HM-, MP-, YSI-, YI-, and DRI-based selection frameworks (Sánchez-Reinoso *et al.*, 2020) [42].

By contrast, TOL, SSI, YR, and DSI mainly quantify yield loss and, while useful for identifying susceptible genotypes, show weaker associations with stressed yield and may misclassify high-yielding but drought-sensitive lines when used alone (Ajayi, 2020; Sánchez-Reinoso *et al.*, 2020) [2, 42].

3.4.2 Functional grouping and rank-based selection

Multivariate grouping approaches (Fernandez grouping, PCA, clustering, and rank-sum methods) are widely used to translate multiple indices into breeding decisions. Greenhouse and field studies consistently place STI, GMP, MP, HM, YI, and REI on the primary productivity-tolerance axis, efficiently distinguishing high-yielding tolerant genotypes (Group A), while SSI and TOL reliably flag unstable, drought-susceptible

materials (Deffo *et al.*, 2024) [11]. Rank-sum selection across MP, GMP, HM, YI, and STI has repeatedly identified a small, elite subset of drought-tolerant parents for arid and semi-arid environments (Singini *et al.*, 2024) [67]. Multi-trait base indices and biplots further partition genotypes into functional classes (high-yielding/tolerant, high-yielding/susceptible, low-yielding/tolerant, low-yielding/susceptible), facilitating early-generation advancement.

3.4.3 Multivariate and stability analyses

Across cowpea panels, PCA typically explains ~70-80% of total variation within the first two components, with PC1 dominated by STI, GMP, MP, HM, YI, YSI, DRI, and stressed yield, defining a composite axis of productivity, drought tolerance, and stability (Ajayi, 2020, 2024; Deffo *et al.*, 2024) [2, 11]. Cluster analysis and GT/GYT biplots simplify simultaneous selection across indices (Deffo *et al.*, 2024) [11]. For multi-environment performance, AMMI and GGE biplots effectively discriminate unstable high-yielding genotypes from those combining yield and wide adaptation, supporting targeted cultivar recommendation (Mekonnen *et al.*, 2022) [68].

3.4.4 Physiology-integrated and multiple-indicator frameworks

Integration of physiological traits strengthens index-based selection. Canopy temperature, stomatal conductance, chlorophyll-based indices (*e.g.*, PRI), and root system traits are strongly associated with drought response and biomass production, highlighting vigorous rooting as a key donor trait (Poudel *et al.*, 2025) [37]. Photosynthetic rate, transpiration, water-use efficiency, chlorophyll fluorescence, and staygreen behavior consistently differentiate tolerant and susceptible genotypes (Nunes *et al.*, 2022) [33]. Composite frameworks integrating yield indices with physiological and root traits have successfully identified accessions with dual tolerance to drought and excess moisture (Isek & Olaleye, 2025a), consistent with evidence from other legumes supporting multi-indicator selection for climate resilience (Abderemane *et al.*, 2025) [1].

3.4.5 Genomic integration of drought indices

Drought indices are increasingly used as quantitative phenotypes for genetic analysis. GWAS in a 305-line cowpea MAGIC population detected numerous SNPs and interaction networks associated with yield-based drought indices (Ravelombola *et al.*, 2021) [66]. Although prediction accuracies are generally low to moderate, they support marker-assisted and genomic selection directly targeting integrated drought response phenotypes rather than stressed yield alone (Ravelombola *et al.*, 2021) [66].

3.5 Trait-Based Selection in Cowpea for Drought Tolerance

Trait-based selection targets heritable component traits underpinning drought avoidance, tolerance, and recovery. These traits now function not only as phenotypic selection criteria but also as quantitative targets in QTL mapping, GWAS, and genomic selection, enabling their systematic integration into modern breeding pipelines (Agbicodo *et al.*, 2009; Jalal *et al.*, 2023) [51, 56].

3.5.1 Phenology and development

Early flowering and maturity consistently confer advantage under terminal drought, though excessively early genotypes may compromise yield potential, necessitating multi-environment evaluation (Agbicodo *et al.*, 2009) [13]. Significant genetic variation and moderate-to-high heritability for flowering and maturity enable reliable classification for environment specific breeding (Ezin *et al.*, 2021) [13]. Drought indices for phenology and associated SNPs identified in

MAGIC populations further validate phenology as a priority genomic target (Ravelombola *et al.*, 2021) ^[66].

3.5.2 Root system architecture and water acquisition

Drought-tolerant genotypes typically express greater root biomass, higher root:shoot ratios, and deeper, denser root systems, which are associated with improved shoot growth and yield stability (Poudel *et al.*, 2025; Santos *et al.*, 2020) ^[37, 41]. Early root vigor, surface area, and tap-root diameter correlate strongly with biomass and are increasingly dissected through GWAS, with major loci identified particularly on chromosome 5 supporting marker-assisted selection for root-mediated drought adaptation (Poudel *et al.*, 2025; Zaffar *et al.*, 2024) ^[37, 77].

3.5.3 Physiological traits and plant water relations

Tolerant genotypes maintain higher relative water content, lower canopy temperature, and superior photosynthetic performance (Φ PSII, ETR), coupled with sensitive stomatal regulation under soil drying (Poudel *et al.*, 2025; Ravelombola *et al.*, 2020) ^[37, 56]. High-throughput phenotyping of transpiration dynamics (θ cri, K) reveals substantial genetic variation and SNPs governing stomata responsiveness (Wu *et al.*, 2021a) ^[56]. Chlorophyll fluorescence, SPAD, PRI, and NDVI are strongly associated with drought injury and grain yield, establishing them as powerful non-destructive screening and GWAS tools (Poudel *et al.*, 2025) ^[37]. Biochemical markers, including osmolytes, antioxidant capacity, and membrane stability, further differentiate tolerant cultivars (Jalal *et al.*, 2023; Ritte *et al.*, 2025) ^[51, 40].

3.5.4 Reproductive resilience and yield components

Under drought, tolerant landraces and improved lines maintain higher pod number, seed weight, harvest index, and yield despite reduced biomass (Ezin *et al.*, 2021) ^[13]. Photosynthetic stability traits correlate with grain yield and map to genes involved in photoprotection and stress signaling, linking physiology with reproductive success (Sansa *et al.*, 2024) ^[69]. Seedling greenness, chlorosis tolerance, and post-stress recovery reliably predict survival and later field performance, supporting their use as early-generation filters (Ravelombola *et al.*, 2020, 2025a; Ritte *et al.*, 2025) ^[38, 40].

3.5.5 Integration with modern breeding strategies

Drought-related traits including phenology, root architecture, stomatal behavior, canopy temperature, greenness, and photosynthetic parameters are now routinely integrated into GWAS and MAGIC analyses, yielding numerous SNPs associated with drought indices and adaptive traits (Poudel *et al.*, 2025; Ravelombola *et al.*, 2021) ^[37, 56]. Although genomic prediction accuracies are generally low to moderate, they support genomic selection when combined with robust phenotypic indices (Li *et al.*, 2018; Ravelombola *et al.*, 2021) ^[70, 66].

Modern cowpea drought-breeding pipelines increasingly

Screen early generations under controlled stress for seedling survival, greenness, root vigor, transpiration dynamics, and canopy temperature (Li *et al.*, 2018; Poudel *et al.*, 2025; Ravelombola *et al.*, 2020, 2025a; Santos *et al.*, 2020; Wu *et al.*, 2021a) ^[38, 37, 41, 56]; advance selected lines to managed-stress field trials integrating drought indices with phenology, physiology, and reproductive traits (Ezin *et al.*, 2021; Sansa *et al.*, 2025) ^[13, 69]; and apply GWAS and genomic selection to pyramid complementary alleles for phenology, root systems, stomatal control, photosynthesis, and reproductive resilience into elite backgrounds (Ravelombola *et al.*, 2021; Sansa *et al.*, 2024; Wu *et al.*, 2021a; Zaffar *et al.*, 2024) ^[38, 51, 56, 77].

3.6 Conventional vs. modern breeding strategies for drought tolerance in cowpea

Cowpea drought breeding is shifting from purely phenotypic, field-based selection toward integrated pipelines combining managed stress screening, trait-based phenotyping, and molecular tools. Because drought tolerance is complex and polygenic, no single strategy is sufficient; genetic gain increasingly depends on the strategic integration of conventional and modern approaches.

3.6.1 Conventional selection and pedigree breeding

Early cowpea improvement relied on mass and pedigree selection for yield and survival under drought, sometimes supported by seedling screening systems (e.g., wooden box methods) that showed correspondence with adult-stage tolerance (Agbicodo *et al.*, 2009; Mofokeng & Mashingaidze, 2019; Nkomo *et al.*, 2020) ^[58, 71, 72]. While this approach delivered adapted cultivars, progress has been slow due to low heritability, strong environmental effects, and large G×E interactions (Agbicodo *et al.*, 2009; Mofokeng & Mashingaidze, 2019) ^[58, 71]. Consequently, multi-environment testing with AMMI and GGE biplots is now routine to identify stable, high-yielding parents and advanced lines for drought-prone regions (Sansa *et al.*, 2025; Singini *et al.*, 2024) ^[67, 69].

3.6.2 Marker-assisted selection and QTL introgression

Early cowpea improvement relied on mass and pedigree selection for yield and survival under drought, sometimes supported by seedling screening systems (e.g., wooden box methods) that showed correspondence with adult-stage tolerance (Agbicodo *et al.*, 2009; Mofokeng & Mashingaidze, 2019; Nkomo *et al.*, 2020) ^[58, 71, 72]. While this approach delivered adapted cultivars, progress has been slow due to low heritability, strong environmental effects, and large G×E interactions (Agbicodo *et al.*, 2009; Mofokeng & Mashingaidze, 2019) ^[58, 71]. Consequently, multi-environment testing with AMMI and GGE biplots is now routine to identify stable, high-yielding parents and advanced lines for drought-prone regions (Sansa *et al.*, 2025; Singini *et al.*, 2024) ^[69, 67].

3.6.3 GWAS-enabled breeding

GWAS using GBS, resequencing, and MAGIC populations has greatly expanded marker density and mapping resolution, identifying loci controlling chlorosis tolerance, greenness, yield components, phenology, and drought indices, with strong signals on chromosomes 1, 3, 5, and 11 and sets of diagnostic SNPs suitable for marker development (Ravelombola *et al.*, 2021, 2025b) ^[38]. These resources provide a foundation for candidate gene discovery, marker pyramiding, and low-cost diagnostic panels.

3.6.4 Genomic selection for drought tolerance

Genomic prediction for phenology, yield traits, and drought indices in cowpea shows low-to-moderate accuracy, with higher performance for simpler traits (Ravelombola *et al.*, 2021; Rosero *et al.*, 2020) ^[66, 73]. Despite this, both empirical and simulation studies indicate that genomic selection can significantly increase genetic gain per unit time when combined with phenotypic selection, making it a promising complement for improving complex, polygenic drought tolerance.

3.6.5 Speed breeding and rapid-cycling pipelines

Although formal speed-breeding systems are less developed in cowpea, accelerated generation advance through off-season nurseries, controlled environments, and early-generation phenotypic and molecular screening is increasingly emphasized (Mofokeng & Mashingaidze, 2019; Nkomo *et al.*, 2021) ^[71]. Seedling drought screening combined with marker filtering

enables rapid elimination of inferior lines before resource-intensive field testing (Nkomo *et al.*, 2020; Ravelombola *et al.*, 2020) [72, 74].

3.6.6 Integrated synthesis

Evidence across Sections 4.3-4.6 demonstrates that effective cowpea drought improvement now depends on integrated, multi-stage pipelines aligning managed stress environments, drought indices, and mechanistic traits with GWAS, MAS, and genomic selection. Managed screening increases selection accuracy, indices stabilize genotype ranking across environments, and physiological traits anchor selection in biological function. The convergence of high-throughput phenotyping, MAGIC populations, and genomic tools is enabling earlier, faster, and more predictive selection, shifting cowpea breeding from yield-only approaches toward physiology-guided, genomics-assisted frameworks.

4. Genomic and molecular approaches for drought tolerance in cowpea

4.1 Genomic resources and reference genomes

The development of high-quality reference genomes and pan-genomes has transformed cowpea into a genomics-enabled crop for drought research. A chromosome-scale reference genome of IT97K-499-35 resolved the 11 chromosomes, revealed extensive synteny with common bean, and provided a foundation for QTL discovery and candidate gene identification (Muñoz-Amatriáin *et al.*, 2018; Lonardi *et al.*, 2017) [64, 65]. Recent pan-genome analyses across cultivated accessions identified ~35,000 pan-genes, including ~5,000 non-core genes enriched for stress- and defense-related functions, highlighting presence/absence and structural variation as major reservoirs of drought-adaptive diversity (Liang *et al.*, 2024) [84]. High-density SNP resources now support population-scale drought genomics, including the 51K iSelect array, GBS and DArTseq platforms, whole-genome resequencing panels, and breeder-friendly KASP markers (Boukar *et al.*, 2016; Muñoz-Amatriáin *et al.*, 2017) [75, 64]. Global diversity panels and a cowpea MAGIC population provide structured germplasm for high-resolution GWAS and drought trait dissection (Ravelombola *et al.*, 2021; Sansa *et al.*, 2024) [66, 69].

These resources have enabled precise mapping of loci controlling drought injury, photosynthetic resilience, stomatal behavior, and yield stability, consistently identifying hotspots on Vu01, Vu03, Vu05, and Vu11 and linking genome variation to ABA signaling, ROS detoxification, and photoprotection pathways.

4.2 QTL mapping for drought and adaptive traits in cowpea

Early biparental QTL studies established drought tolerance in cowpea as a polygenic and environment-sensitive trait. Mapping in RIL populations identified multiple loci for premature senescence, biomass recovery, stay-green phenotype, and yield under drought, with pleiotropic QTL linking delayed senescence to post-flowering drought tolerance (Muchero *et al.*, 2009, 2013) [76]. Candidate-gene anchored QTL further implicated stress-responsive genes associated with photosynthesis and membrane protection.

Although these studies provided foundational drought-linked regions and markers, their resolution and allelic diversity were limited. The expansion of genomic resources has shifted cowpea drought research toward GWAS-based, population-scale dissection of complex drought responses.

4.3 Genome-wide association studies (GWAS) for drought and adaptive traits in cowpea

GWAS using resequencing, GBS, DArTseq, and SNP arrays across diversity panels and MAGIC populations has revealed drought adaptation as highly polygenic, with loci distributed

across all chromosomes (Ravelombola *et al.*, 2021, 2025b; Sansa *et al.*, 2024) [56, 69]. Seedling-stage GWAS identified major loci for leaf chlorosis and greenness linked to ABA signaling, ROS detoxification, and chloroplast maintenance (Ravelombola *et al.*, 2025b) [38]. Gravimetric GWAS uncovered loci controlling stomatal closure dynamics and water-use strategies (Wu *et al.*, 2021b) [56].

Field GWAS connected chlorophyll fluorescence parameters and yield stability with photoprotective and redox-related genes (Sansa *et al.*, 2024) [69]. Root-focused GWAS further identified loci for root biomass and architecture, particularly on Vu05, highlighting belowground adaptation mechanisms (Zaffar *et al.*, 2024) [77].

Collectively, cowpea GWAS converge on recurrent genomic hotspots and core processes involving ABA signaling, stomatal regulation, photosynthetic resilience, and root system plasticity, delivering validated markers and candidate genes for genomics-assisted breeding.

4.4 Multi-omics dissection of drought tolerance in cowpea

Transcriptomic, proteomic, and metabolomic studies demonstrate that cowpea drought tolerance is governed by coordinated regulatory networks integrating ABA signaling, transcription factor cascades, ROS detoxification, and osmotic adjustment (Goufo *et al.*, 2017; Ribeiro *et al.*, 2023b) [16, 39]. ABA biosynthesis and signaling genes (*e.g.*, VuNACD), WRKY, NAC, bZIP, and DREB transcription factors, aquaporins, and trehalose metabolism genes consistently emerge as central regulatory hubs (Fang *et al.*, 2023; Matos *et al.*, 2022) [55, 78].

Proteomics shows that tolerant genotypes maintain photosynthetic and protective proteins while redirecting metabolism toward stress defense (Ribeiro *et al.*, 2023b) [39]. Metabolomics highlights accumulation of osmoprotectants, amino acids, and flavonoids particularly in roots supporting a central role for root metabolic plasticity in drought sensing and signaling (Goufo *et al.*, 2017) [16].

These convergent omics datasets provide functional bridges between GWAS/QTL signals and drought-responsive biological pathways.

4.5 Functional validation and candidate gene confirmation

Functional genomics has confirmed several cowpea drought regulators. Overexpression of VuNAC1/2 improved growth, yield components, and drought tolerance through enhanced photosynthesis, antioxidant activity, and water-use efficiency (Srivastava *et al.*, 2022) [79]. miR408 was validated as a drought-regulatory hub controlling lignin remodeling, chlorophyll retention, and stomatal behavior (Mishra *et al.*, 2021b) [28]. Heterologous studies further support roles for VuDREB and NAC factors in dehydration tolerance.

CRISPR/Cas9 editing in hairy roots, cowpea protoplast systems, and agroinfiltration platforms now enable direct functional testing of candidate genes and promoters (Ji *et al.*, 2019; Bridgeland *et al.*, 2023) [80, 81]. Integration of GWAS, omics, and *in planta* validation increasingly prioritizes regulatory network nodes controlling stomatal sensitivity, photosynthetic protection, and carbon remobilization.

Functionally validated genes and biomarkers now support marker-assisted selection, biologically informed genomic selection, and emerging genome-editing strategies, positioning functional genomics as a critical bridge between association mapping and precision breeding of drought-resilient cowpea.

5. Future perspectives and research gaps

Despite major advances in genomics and functional studies, translating drought biology into climate-resilient cowpea cultivars remains constrained by environmental complexity,

limited root integration, and slow breeding uptake. Future progress requires shifting from reductionist drought assays to integrative, climate-relevant, and breeder-oriented research frameworks.

Climate-realistic phenotyping: Most studies rely on simplified drought screens that poorly represent farmer field conditions. There is a critical need for multi-season, multi-stress managed platforms with precise envirotyping to capture drought timing, intensity, recovery, and heat interactions, thereby improving the relevance of GWAS, genomic selection, and trait discovery.

Root-centered drought biology: Cowpea drought research remains largely shoot-focused, despite the central role of root architecture, hydraulics, and rhizosphere interactions in drought avoidance. Field-scalable root phenotyping, genetic dissection of deep and plastic root systems, and integration of microbiome and symbiosis studies must become priority frontiers.

- **From loci to systems:** Most drought-associated SNPs show small, environment-dependent effects. Future efforts should move toward systems-level drought genomics by integrating GWAS with regulatory networks, eQTL/pQTL mapping, pan-genomes, and machine-learning approaches to identify pathway hubs rather than isolated markers.
- **Closing the translational gap:** Although many drought-responsive genes have been identified, very few have been functionally validated or deployed. Priorities include scalable transformation and editing systems, validation of natural alleles, CRISPR-based allele mining, and early incorporation of functional markers into breeding pipelines.
- **Predictive and farmer-centered breeding:** Next-generation cowpea improvement should integrate high-throughput phenomics, omics predictors, envirotyping, and crop modeling into AI-supported breeding pipelines. Equally important is aligning molecular drought tolerance with farmer-preferred traits through participatory breeding and on-farm evaluation to ensure adoption and impact.

6. Conclusion

Cowpea drought research is rapidly advancing through the integration of conventional breeding, physiological trait analysis, and genomics tools such as reference genomes, GWAS, MAGIC populations, and genomic selection. These efforts have clarified the complex, polygenic architecture of drought adaptation, highlighting key traits including root plasticity, stomatal regulation, and stay-green-mediated photosynthetic resilience. However, translation into farmer-preferred, climate-resilient cultivars remains limited, particularly under multi-stress field conditions. Critical gaps include underexplored root biology, limited functional validation of candidate genes, and weak integration of multi-omics with predictive breeding. Future research should prioritize climate-realistic managed stress platforms, systems-level genomics, and participatory breeding approaches to accelerate early-generation selection and environment-specific cultivar design. Such convergence offers a practical pathway to develop drought-resilient cowpea cultivars that sustain productivity, stabilize livelihoods, and enhance food security in drought-prone regions.

References

1. Abderemane BA, Fakiri M, Zeroual A, Mitache M, Houasli C. Selection of chickpea (*Cicer arietinum* L.) genotypes through a combining of tolerance indices and root architecture: an efficient approach for the identification of drought-tolerant genotypes. *Plant Breeding*. 2025.
2. Ajayi AT. Relationships among drought tolerance indices and yield characters of cowpea (*Vigna unguiculata* L. Walp.). *International Journal of Scientific Research in Biological Sciences*. 2020;7(5).
3. Baby J, Minimol JS, Santhoshkumar AV, Joseph J, Abd-ElGawad AM, Ullah F. Identification and development of drought-tolerant cocoa hybrids: physiological insights for enhanced water use efficiency under water stress conditions. *BMC Plant Biol*. 2025;25. <https://doi.org/10.1186/s12870-025-06448-3>
4. Belko N, Cisse N, Diop NN, Zombre G, Thiaw S, Muranaka S, *et al*. Selection for postflowering drought resistance in short- and medium-duration cowpeas using stress tolerance indices. *Crop Science*. 2014;54(1):25-33.
5. Blum A. Osmotic adjustment is a prime drought stress adaptive engine in support of plant production. *Plant Cell Environ*. 2017. <https://doi.org/10.1111/pce.12800>
6. Carvalho M, Castro I, Moutinho-Pereira J, Correia C, Egea-Cortines M, Matos M, *et al*. Evaluating stress responses in cowpea under drought stress. *J Plant Physiol*. 2019;241. <https://doi.org/10.1016/j.jplph.2019.153001>
7. Carvalho M, Lino-Neto T, Rosa E, Carnide V. Cowpea: a legume crop for a challenging environment. 2017.
8. Carvalho M, Matos M, Castro I, Monteiro E, Rosa E, Lino-Neto T, *et al*. Screening of worldwide cowpea collection to drought tolerant at a germination stage. *Sci Hortic*. 2019;247:107-115. <https://doi.org/10.1016/j.scienta.2018.11.082>
9. Chamarthi SK, Belko N, Togola A, Fatokun CA, Boukar O. Genomics-assisted breeding for drought tolerance in cowpea. In: *Genomics Assisted Breeding of Crops for Abiotic Stress Tolerance*. Vol II. Cham: Springer International Publishing; 2019. p. 187-209.
10. Diallo S, Badiane FA, Diédhiou I, Diouf M, Ngom M, Diouf D. Development of cowpea (*Vigna unguiculata*) mutant lines for dissecting resilience to drought through physiological and molecular crosstalk analysis. *Plant Mol Biol Reporter*. 2025;43(2):428-446.
11. Deffo TN, Kouam EB, Mandou MS, Bara RAT, Chotangui AH, Souleymanou A, *et al*. Identifying critical growth stage and resilient genotypes in cowpea under drought stress contributes to enhancing crop tolerance for improvement and adaptation in Cameroon. *PLoS One*. 2024;19. <https://doi.org/10.1371/journal.pone.0304674>
12. Esan VI, Omilan OO, Osuntuyinbo YO, Olutayo GT, Sangoyomi TE. Assessment of Harmattan weather on cowpea (*Vigna unguiculata* (L.) Walp.) production under drought stress. *Aust J Crop Sci*. 2021;15:1298-1306. <https://doi.org/10.21475/ajcs.21.15.10.p3221>
13. Ezin V, Tosse AGC, Chabi IB, Ahanchede A. Adaptation of cowpea (*Vigna unguiculata* (L.) Walp.) to water deficit during vegetative and reproductive phases using physiological and agronomic characters. *Int J Agronomy*. 2021. <https://doi.org/10.1155/2021/9665312>
14. Farooq M, Romdhane L, Rehman A, Al-Alawi AK, Al-Busaidi WM, Asad SA, *et al*. Integration of seed priming and biochar application improves drought tolerance in cowpea. *J Plant Growth Regulat*. 2021;40(5):1972-1980.
15. Gnankambary K, Sawadogo N, Diéni Z, Batiéno TBJ, Tignegré JBDS, Sawadogo M, *et al*. Assessment of cowpea (*Vigna unguiculata* (L.) Walp.) mutant lines for drought tolerance. *Int J Agronomy*. 2020. <https://doi.org/10.1155/2020/8823498>
16. Goufo P, Moutinho-Pereira JM, Jorge TF, Correia CM, Oliveira MR, Rosa EAS, *et al*. Cowpea (*Vigna unguiculata* L. Walp.) metabolomics: osmoprotection as a physiological strategy for drought stress resistance and improved yield. *Front Plant Sci*. 2017;8:586. <https://doi.org/10.3389/fpls.2017.00586>

17. Guo C, Bao X, Sun H, Zhu L, Zhang Y, Zhang K, *et al.* Optimizing root system architecture to improve cotton drought tolerance and minimize yield loss during mild drought stress. *Field Crops Res.* 2024;308:109305.
18. Hall AE. Phenotyping cowpeas for adaptation to drought. *Front Physiol.* 2012;3. <https://doi.org/10.3389/fphys.2012.00155>
19. Iseki K, Olaleye O. Dual tolerance to soil drought and excess moisture stresses in cowpea genetic resources assessed using multiple indicators. *Front Plant Sci.* 2025;16. <https://doi.org/10.3389/fpls.2025.1573313>
20. Javornik T, Carović-Stanko K, Gunjača J, Šatović Z, Vidak M, Safner T, *et al.* Phenotyping common bean under drought stress: high-throughput approaches for enhanced drought tolerance. *Agronomy.* 2025. <https://doi.org/10.3390/agronomy15061344>
21. Khatri ISHA, Ali HE, Yaish MW. Melatonin improves drought tolerance in cowpea through growth modulation, antioxidant response, and ionic homeostasis, supporting sustainable agriculture. *Environ Res Commun.* 2025;7. <https://doi.org/10.1088/2515-7620/add85f>
22. Kim SL, Kim N, Lee H, Lee E, Cheon KS, Kim M, *et al.* High-throughput phenotyping platform for analyzing drought tolerance in rice. *Planta.* 2020;252. <https://doi.org/10.1007/s00425-020-03436-9>
23. Kou X, Han W, Kang J. Responses of root system architecture to water stress at multiple levels: a meta-analysis of trials under controlled conditions. *Front Plant Sci.* 2022. <https://doi.org/10.3389/fpls.2022.1085409>
24. Lima EN, Magalhães CHC de, Mesquita RO, Pessoa AM dos S, Coutinho IB de L. Physiological and biochemical characterization of contrasting cowpea genotypes for drought tolerance. *Rev Agrar Acad.* 2025;8:1-12. <https://doi.org/10.32406/v8n1/2025/1-12/agrariacad>
25. Matsui T, Singh BB. Root characteristics in cowpea related to drought tolerance at the seedling stage. *Experimenta Agriculture.* 2003;39(1):29-38.
26. Melo AAR, Araujo MA, Mendes NAC, Reis AR. Drought stress disrupts biological nitrogen fixation and starch accumulation compromising growth and yield of cowpea plants. *Plant Physiol Biochem.* 2025;224:109931.
27. Miri MR, Ghoshchi F, Tohidi Moghadam HR, Larijani HR, Kasraie P. Cowpea seeds from plants subjected to restricted- and full-irrigation regimes show differential phytochemical activity. *Bot Stud.* 2022;63.
28. Mishra S, Sahu G, Shaw BP. Integrative small RNA and transcriptome analysis provides insight into key role of miR408 towards drought tolerance response in cowpea. 2021. <https://doi.org/10.21203/rs.3.rs-462359/v1>
29. Moreira R, Nunes C, Pais P, Nobre Semedo J, Moreira J, Sofia Bagulho A, *et al.* Are Portuguese cowpea genotypes adapted to drought? Phenological development and grain quality evaluation. *Biology (Basel).* 2023;12. <https://doi.org/10.3390/biology12040507>
30. Muhammed HM, Stephen DY, Gabi UA, Rabe AM, Saratu ML. Effect of drought at different reproductive stages on yield and yield components of some cowpea (*Vigna unguiculata* L. Walp) varieties in Lapai, Niger State, Nigeria. *Science World J.* 2024;18:674-677. <https://doi.org/10.4314/swj.v18i4.21>
31. Nkomo GV, Sedibe MM, Mofokeng MA. Phenotyping cowpea accessions at the seedling stage for drought tolerance in controlled environments. *Open Agric.* 2022;7:433-444. <https://doi.org/10.1515/opag-2022-009>
32. Nunes C, Moreira R, Pais I, Semedo J, Simões F, Veloso MM, *et al.* Cowpea physiological responses to terminal drought: comparison between four landraces and a commercial variety. *Plants.* 2022;11. <https://doi.org/10.3390/plants11050593>
33. Olorunwa OJ, Shi A, Barickman TC. Varying drought stress induces morpho-physiological changes in cowpea (*Vigna unguiculata* (L.)) genotypes inoculated with *Bradyrhizobium japonicum*. *Plant Stress.* 2021;2. <https://doi.org/10.1016/j.stress.2021.100033>
34. Omomowo OI, Babalola OO. Constraints and prospects of improving cowpea productivity to ensure food, nutritional security and environmental sustainability. *Front Plant Sci.* 2021. <https://doi.org/10.3389/fpls.2021.751731>
35. Ozturk M, Turkyilmaz Unal B, García-Caparrós P, Khursheed A, Gul A, Hasanuzzaman M. Osmoregulation and its actions during the drought stress in plants. *Physiol Plant.* 2021;172:1321-1335. <https://doi.org/10.1111/ppl.13297>
36. Pappula-Reddy SP, Kumar S, Pang J, Chellapilla B, Pal M, Millar AH, *et al.* High-throughput phenotyping for terminal drought stress in chickpea (*Cicer arietinum* L.). *Plant Stress.* 2024;11. <https://doi.org/10.1016/j.stress.2024.100386>
37. Poudel S, Valsala Sankarapillai L, Sivarathri BS, Hosahalli V, Harkess RL, Bheemanahalli R. Characterization of cowpea genotypes for traits related to early-season drought tolerance. *Agriculture (Switzerland).* 2025;15. <https://doi.org/10.3390/agriculture15101075>
38. Ravelombola W, Xiong H, Bhattarai G, Manley A, Cason J, Pham H, *et al.* Genome-wide association study for drought tolerance in cowpea (*Vigna unguiculata* (L.) Walp.) at seedling stage using a whole genome resequencing approach. *Int J Mol Sci.* 2025;26. <https://doi.org/10.3390/ijms26125478>
39. Ribeiro DG, Bezerra ACM, Santos IR, Grynberg P, Fontes W, de Souza Castro M, *et al.* Proteomic insights of cowpea response to combined biotic and abiotic stresses. *Plants.* 2023;12. <https://doi.org/10.3390/plants12091900>
40. Ritte IP, Egnin M, Bernard GC, Mortley D, Idehen O, Okoma MP, *et al.* Morpho-physiological and molecular responses to seedling-stage drought stress in different cowpea cultivars. *Int J Plant Biol.* 2025;16. <https://doi.org/10.3390/ijpb16010025>
41. Santos R, Carvalho M, Rosa E, Carnide V, Castro I. Root and agro-morphological traits performance in cowpea under drought stress. *Agronomy.* 2020;10. <https://doi.org/10.3390/agronomy10101604>
42. Satharaj D, Sabesan T. Evaluation of drought tolerant indices for screening of some elite rice genotypes under normal and drought stress condition. *Ecology Environment and Conservation.* 2025;31.
43. Sharma A, Shahzad B, Kumar V, Kohli SK, Sidhu GPS, Bali AS, *et al.* Phytohormones regulate accumulation of osmolytes under abiotic stress. *Biomolecules.* 2019. <https://doi.org/10.3390/biom9070285>
44. Shoaib M, Banerjee BP, Hayden M, Kant S. Roots' drought adaptive traits in crop improvement. *Plants.* 2022. <https://doi.org/10.3390/plants11172256>
45. Singh A, Roychoudhury A. Absciscic acid in plants under abiotic stress: crosstalk with major phytohormones. *Plant Cell Rep.* 2023;42(6):961-974.
46. Singh SK, Reddy KR. Regulation of photosynthesis, fluorescence, stomatal conductance and water-use efficiency of cowpea (*Vigna unguiculata* [L.] Walp.) under drought. *Journal of Photochemistry and Photobiology B: Biology.* 2011;105(1):40-50.
47. Srivastava R, Kobayashi Y, Koyama H, Sahoo L. Cowpea NAC1/NAC2 transcription factors improve growth and tolerance to drought and heat in transgenic cowpea through combined activation of photosynthetic and antioxidant

- mechanisms. *Journal of Integrative Plant Biology*. 2023;65(1):25-44.
48. Tanasale MTN, Karuwal RL, Sangur K. Morphological response of local cowpea varieties of Southwest Maluku to drought stress with PEG 6000 induction in the germination phase. *BIOPENDIX: Jurnal Biologi, Pendidikan dan Terapan*. 2025;12:70-76. <https://doi.org/10.30598/biopendixvol12issue1page70-76>
 49. Tankari M, Wang C, Ma H, Li X, Li L, Soothar RK, *et al.* Drought priming improved water status, photosynthesis and water productivity of cowpea during post-anthesis drought stress. *Agric Water Manage*. 2021;245. <https://doi.org/10.1016/j.agwat.2020.106565>
 50. Tochihara-Tanaka M, Kai S, Murakami N, Murakami S, Miura N, Komai R, *et al.* Drought tolerance of cowpea is associated with rapid abscisic acid biosynthesis via VuWRKY57 in root. *AoB Plants*. 2025;17. <https://doi.org/10.1093/aobpla/plaf038>
 51. V T, Dey S, G BG, Pujar DM, K DH. Legumes: breeding strategies and adaptive traits for drought tolerance. *International Journal of Environment and Climate Change*. 2025;15:278-298. <https://doi.org/10.9734/ijecc/2025/v15i74929>
 52. Wahab A, Abdi G, Saleem MH, Ali B, Ullah S, Shah W, *et al.* Plants physio-biochemical and phyto-hormonal responses to alleviate the adverse effects of drought stress: a comprehensive review. *Plants*. 2022. <https://doi.org/10.3390/plants11131620>
 53. Waltram R, Ainong S, Chen S, Haizheng X, Yang Y, Qirui C, *et al.* Evaluation of cowpea for drought tolerance at seedling stage. *Euphytica*. 2020;216(8).
 54. Wang S, Zhu L, Zhang P, Wang X, Sun H, Zhang K, *et al.* Synergistic optimisation of root hydraulic architecture enhances drought tolerance in cotton. *Plant, Cell and Environment*. 2025.
 55. Wasaya A, Zhang X, Fang Q, Yan Z. Root phenotyping for drought tolerance: a review. *Agronomy*. 2018;8. <https://doi.org/10.3390/agronomy8110241>
 56. Wu X, Sun T, Xu W, Sun Y, Wang B, Wang Y, *et al.* Unraveling the genetic architecture of two complex, stomata-related drought-responsive traits by high-throughput physiological phenotyping and GWAS in cowpea (*Vigna unguiculata* L. Walp). *Front Genet*. 2021;12. <https://doi.org/10.3389/fgene.2021.743758>
 57. Yu L, Sussman H, Khmelnitsky O, Ishka MR, Srinivasan A, Nelson ADL, *et al.* Development of a mobile, high-throughput, and low-cost image-based plant growth phenotyping system. 2023. <https://doi.org/10.1101/2023.07.18.549560>
 58. Agbicodo EM, Fatokun CA, Muranaka S, Visser RGF, Linden van der CG. Breeding drought tolerant cowpea: constraints, accomplishments, and future prospects. *Euphytica*. 2009;167(3):353-370. <https://doi.org/10.1007/s10681-009-9893-8>
 59. Boukar O, Abberton M, Oyatomi O, Togola A, Tripathi L, Fatokun C. Introgression breeding in cowpea [*Vigna unguiculata* (L.) Walp.]. *Frontiers in Plant Science*. 2020;11. <https://doi.org/10.3389/fpls.2020.567425>
 60. Fatokun C, Girma G, Abberton M, Gedil M, Unachukwu N, Oyatomi O, *et al.* Genetic diversity and population structure of a mini-core subset from the world cowpea (*Vigna unguiculata* (L.) Walp.) germplasm collection. *Scientific Reports*. 2018;8(1). <https://doi.org/10.1038/s41598-018-34555-9>
 61. Fatokun CA, Boukar O, Muranaka S. Evaluation of cowpea (*Vigna unguiculata* (L.) Walp.) germplasm lines for tolerance to drought. *Plant Genetic Resources*. 2012;10(3):171-176. <https://doi.org/10.1017/s1479262112000214>
 62. Gomes AMF, Draper D, Nhantumbo N, Massinga R, Ramalho JC, Marques I, *et al.* Diversity of cowpea [*Vigna unguiculata* (L.) Walp] landraces in Mozambique: new opportunities for crop improvement and future breeding programs. *Agronomy*. 2021;11(5):991. <https://doi.org/10.3390/agronomy11050991>
 63. Macharia MW, Caproni L, Solemanegy M, Takele R, Chiulele RM, Munisse P, *et al.* Cowpea (*Vigna unguiculata* L. Walp.) landraces in Mozambique and neighbouring Southern African countries harbour genetic loci with potential for climate adaptation. *Communications Biology*. 2025;8(1). <https://doi.org/10.1038/s42003-025-08227-0>
 64. Huynh B, Ehlers JD, Huang BE, Muñoz-Amatriain M, Lonardi S, Santos JRP, *et al.* A multi-parent advanced generation inter-cross (MAGIC) population for genetic analysis and improvement of cowpea (*Vigna unguiculata* L. Walp.). *The Plant Journal*. 2018;93(6):1129-1142. <https://doi.org/10.1111/tjp.13827>
 65. Huynh B, Ehlers JD, Munoz-Amatriain M, Lonardi S, Santos JRP, Ndeve A, *et al.* A multi-parent advanced generation inter-cross population for genetic analysis of multiple traits in cowpea (*Vigna unguiculata* L. Walp.). 2017. <https://doi.org/10.1101/149476>
 66. Ravelombola W, Shi A, Huynh B. Loci discovery, network-guided approach, and genomic prediction for drought tolerance index in a multi-parent advanced generation intercross (MAGIC) cowpea population. *Horticulture Research*. 2021;8(1). <https://doi.org/10.1038/s41438-021-00462-w>
 67. Singini M, Chipeta MM, Njira K, Fiwa L. Dissecting cowpea genetic variability under moisture stress conditions and implications for drought tolerance breeding. *International Journal of Agronomy*. 2024;2024(1). <https://doi.org/10.1155/2024/5358207>
 68. Mekonnen TW, Mekbib F, Amsalu B, Gedil M, Labuschagne M. Genotype by environment interaction and grain yield stability of drought tolerant cowpea landraces in Ethiopia. *Euphytica*. 2022;218(5). <https://doi.org/10.1007/s10681-022-03011-1>
 69. Sansa O, Abberton MT, Ariyo J, Paliwal R, Ige A, Dieng I, *et al.* Genome-wide association studies of photosynthetic and agronomic traits in cowpea collection. *G3: Genes, Genomes, Genetics*. 2024. <https://doi.org/10.1093/g3journal/jkae233>
 70. Li H, Zhang Y, Li X, Xue R, Zhao H. Identification of wheat d-cysteine desulfhydrase (TaD-CDes) required for abscisic acid regulation of seed germination, root growth, and stomatal closure in *Arabidopsis*. *Journal of Plant Growth Regulation*. 2018;37(4):1175-1184. <https://doi.org/10.1007/s00344-018-9817-8>
 71. Mofokeng MA, Mashigaidze K. Breeding and genetic management of drought in cowpea: progress and technologies. *Australian Journal of Crop Science*. 2019;13(12):1920-1926. <https://doi.org/10.21475/ajcs.19.13.12.p1289>
 72. Nkomo GV, Sedibe MM, Mofokeng MA. Phenotyping cowpea accessions at the seedling stage for drought tolerance using the pot method. 2020. <https://doi.org/10.1101/2020.07.10.196915>
 73. Rosero A, Granda L, Berdugo-Cely JA, Šamajová O, Šamaj J, Cerkal R. A dual strategy of breeding for drought tolerance and introducing drought-tolerant, underutilized crops into production systems to enhance their resilience to water deficiency. *Plants*. 2020;9(10):1263. <https://doi.org/10.3390/plants9101263>

74. Ravelombola WS, Qin J, Shi A, Nice L, Bao Y, Lorenz A, *et al.* Genome-wide association study and genomic selection for tolerance of soybean biomass to soybean cyst nematode infestation. PLOS ONE. 2020;15(7):e0235089. <https://doi.org/10.1371/journal.pone.0235089>
75. Boukar O, Fatokun CA, Huynh B, Roberts PA, Close TJ. Genomic tools in cowpea breeding programs: status and perspectives. Frontiers in Plant Science. 2016;7. <https://doi.org/10.3389/fpls.2016.00757>
76. Muchero W, Ehlers JD, Roberts PA. Restriction site polymorphism-based candidate gene mapping for seedling drought tolerance in cowpea [*Vigna unguiculata* (L.) Walp.]. Theoretical and Applied Genetics. 2009;120(3):509-518. <https://doi.org/10.1007/s00122-009-1171-6>
77. Zaffar A, Paliwal R, Abberton M, Akhtar S, Mengnoo RA, Sheikh AN, *et al.* Elucidating the genomic regions through genome-wide association study (GWAS) for root traits in cowpea (*Vigna unguiculata* (L.) Walp) mini-core collection. Plant Stress. 2024;12:100440. <https://doi.org/10.1016/j.stress.2024.100440>
78. Matos MKdS, Benko-Iseppon AM, Bezerra-Neto JP, Ferreira-Neto JRC, Wang Y, Liu H, *et al.* The WRKY transcription factor family in cowpea: genomic characterization and transcriptomic profiling under root dehydration. Gene. 2022;823:146377. <https://doi.org/10.1016/j.gene.2022.146377>
79. Srivastava R, Kobayashi Y, Koyama H, Sahoo L. Cowpea NAC1/NAC2 transcription factors improve growth and tolerance to drought and heat in transgenic cowpea through combined activation of photosynthetic and antioxidant mechanisms. Journal of Integrative Plant Biology. 2022;65(1):25-44. <https://doi.org/10.1111/jipb.13365>
80. Ji J, Zhang C, Sun Z, Wang L, Duanmu D, Fan Q. Genome editing in cowpea *Vigna unguiculata* using CRISPR-Cas9. International Journal of Molecular Sciences. 2019;20(10):2471. <https://doi.org/10.3390/ijms20102471>
81. Bridgeland A, Biswas S, Tsakirpaloglou N, Thomson MJ, Septiningsih EM. Optimization of gene editing in cowpea through protoplast transformation and agroinfiltration by targeting the phytoene desaturase gene. PLOS ONE. 2023;18(4):e0283837. <https://doi.org/10.1371/journal.pone.0283837>
82. De Melo CM, Torralba A, Guibas L, DiCarlo J, Chellappa R, Hodgins J. Next-generation deep learning based on simulators and synthetic data. Trends in Cognitive Sciences. 2022;26(2):174-187.
83. Cooper M, Messina CD. Breeding crops for drought-affected environments and improved climate resilience. The Plant Cell. 2023;35(1):162-186.
84. Liang Q, Herniter IA, Muñoz-Amatriaín M, Lo S, Muñoz N, Close TJ, *et al.* A view of the pan-genome of domesticated cowpea (*Vigna unguiculata* [L.] Walp.). The Plant Genome. 2024;17(1):e20319.