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Drought adaptations in chickpea: A review of tolerance mechanisms and breeding progress

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Abstract

Chickpea (*Cicer arietinum* L.) is one of the most important pulse crops cultivated largely under rainfed environments, making it highly vulnerable to drought stress. The ongoing changes in global climate, particularly rising temperatures and erratic rainfall patterns, are expected to intensify moisture deficits in major chickpea-growing regions. Drought, especially terminal drought, remains the most important abiotic constraint limiting chickpea productivity. Developing drought-resilient cultivars has therefore become a central objective of chickpea improvement programs worldwide. This review synthesizes current knowledge on the impact of climate change on chickpea production, the physiological and morphological basis of drought tolerance, and advances in conventional and molecular breeding strategies. Recent developments in genomics, high-throughput phenotyping, genomic selection, and genome editing are also discussed. A holistic integration of physiology, phenomics, and genomics is essential for accelerating the development of climate-resilient chickpea cultivars capable of sustaining yield under water-limited conditions.

Keywords: Chickpea, climate change, drought tolerance, genomics, phenotyping

1. Introduction

Chickpea is the second most widely cultivated grain legume globally and serves as a major source of dietary protein, carbohydrates, minerals, and vitamins for millions of people, particularly in South Asia, West Asia, North Africa, and parts of Sub-Saharan Africa. The crop plays a pivotal role in sustainable agriculture due to its ability to fix atmospheric nitrogen and improve soil fertility. Despite its importance, chickpea productivity remains relatively low compared with its genetic potential, largely because the crop is grown under rainfed conditions prone to moisture stress (Gaur *et al.*, 2012; Varshney *et al.*, 2013) ^[19, 73].

Drought stress is widely recognized as the most important abiotic constraint limiting chickpea yield stability. Turner *et al.* (2007) ^[49] estimated that more than half of the global chickpea area experiences moderate to severe water deficit during the cropping season. In South Asia, terminal drought is particularly prevalent because chickpea is typically sown on residual soil moisture following the monsoon. Progressive soil drying during the reproductive phase severely affects pod set and seed filling. Climate change is expected to exacerbate these challenges. Rising temperatures, increased evaporative demand, and altered rainfall distribution are projected to intensify moisture deficits in semi-arid regions. Modeling studies suggest that chickpea yields may decline significantly in the absence of adaptive breeding and management interventions. Therefore, enhancing drought tolerance while maintaining productivity has become a central focus of chickpea improvement programs worldwide. Breeding for drought tolerance is inherently complex because the trait is controlled by multiple genes with strong environmental interactions (Blum, 2011) ^[8]. However, advances in plant physiology, genomics, and phenotyping technologies have created new opportunities to accelerate genetic gain. This review provides a comprehensive synthesis of breeding approaches for improving chickpea productivity under drought stress.

2. Drought Stress Scenario in Chickpea Production

2.1 Types and timing of drought

The severity of drought impact in chickpea is strongly governed by the stage of crop development at which water deficit occurs, along with its duration and intensity. Chickpea is predominantly cultivated under rainfed conditions in semi-arid regions, making it highly vulnerable to intermittent and terminal moisture stress. Early-season drought mainly affects seed germination, seedling emergence, and crop establishment. Poor soil moisture during this phase often results in reduced plant population and weak early vigor. Studies by Leport *et al.* (2006) ^[36] demonstrated that insufficient moisture during establishment leads to uneven stand density and delayed canopy development, ultimately lowering yield potential. Similar observations have been reported in recent reviews indicating that early drought restricts root elongation and nodulation, thereby compromising subsequent plant growth.

Mid-season drought occurring during the vegetative phase primarily limits canopy expansion, leaf area development, and biomass accumulation. Reduced leaf area index under moisture deficit decreases radiation interception and photosynthetic capacity, leading to lower dry matter production. Physiological studies have shown significant reductions in relative water content, membrane stability, and chlorophyll concentration during vegetative drought stress. For instance, recent experimental evidence indicated that most physiological traits in chickpea decline significantly under moisture stress, confirming the sensitivity of vegetative growth processes to water deficit. Although plants may partially recover if rainfall resumes, prolonged mid-season drought can predispose the crop to severe yield penalties later in the season.

Among the different drought scenarios, terminal drought occurring during flowering, pod formation, and seed filling is widely recognized as the most destructive for chickpea productivity. Kumar and Abbo (2001) ^[35] emphasized that reproductive-stage stress directly affects pod set, seed filling, and harvest index. Under terminal drought, accelerated senescence, pollen sterility, and increased flower drop are common, resulting in substantial yield losses. Field experiments across South Asia and Australia have documented yield reductions of 30-50% under severe terminal moisture stress (Kashiwagi *et al.*, 2006) ^[31]. More recent studies suggest that in extreme tropical environments, terminal drought can cause yield losses of up to 90%, highlighting the magnitude of the problem.

The high susceptibility of chickpea to terminal drought is closely associated with its growth habit and water-use pattern. Many traditional cultivars exhibit indeterminate growth and shallow to moderate rooting depth, which restricts their capacity to utilize deep soil moisture during the grain-filling phase. Reviews on root biology have emphasized that subsoil water extraction is a key determinant of drought adaptation in chickpea production systems. Deep and dense root systems enable plants to access moisture from lower soil horizons, thereby sustaining reproductive development under receding soil moisture conditions. Studies have also shown that drought conditions often increase root length density below 30 cm soil depth and enhance root-to-shoot ratio, indicating an adaptive shift toward water foraging.

Globally, drought remains one of the most serious abiotic constraints in chickpea cultivation. Estimates indicate that

abiotic stresses, particularly drought, can reduce chickpea yield by approximately 40-60% on average. The magnitude of loss varies with genotype, environment, and stress timing, but terminal drought in rainfed systems continues to be the principal yield-limiting factor in South Asia, West Asia, and parts of Africa. In recent years, climate variability has increased the frequency of late-season dry spells, further intensifying terminal drought risk in chickpea-growing regions. Consequently, breeding programs are increasingly prioritizing traits such as early maturity, deeper rooting, improved water-use efficiency, and enhanced assimilate remobilization. A comprehensive understanding of drought timing and its physiological consequences is therefore essential for designing effective breeding and management strategies aimed at stabilizing chickpea productivity under water-limited environments.

3. Detrimental effects of drought stress and plant adaptive responses

Water deficit triggers a series of physiological responses beginning with reduced leaf water potential and stomatal closure. Decreased stomatal conductance restricts CO₂ uptake and reduces photosynthetic rate (Serraj *et al.*, 2004) ^[57]. Prolonged stress leads to chlorophyll degradation, impaired photochemistry, and reduced Rubisco activity (Mafakheri *et al.*, 2010) ^[37]. At the reproductive stage, drought disrupts pollen viability, fertilization, and embryo development. Studies by Fang *et al.* (2011) showed that drought during flowering significantly increases flower abortion and reduces pod set in chickpea. These combined effects ultimately result in lower seed number and reduced seed weight.

Drought primarily limits plant productivity by restricting water availability, which directly affects photosynthesis and metabolic processes. One of the earliest responses is stomatal closure, which reduces CO₂ entry into leaves. This leads to limited carboxylation and reduced photosynthetic rate, ultimately lowering biomass accumulation.

Water deficit also decreases leaf water potential and relative water content, impairing cell expansion and growth. Under prolonged stress, plants experience oxidative damage to chloroplasts and plasma membranes due to excessive production of reactive oxygen species (ROS). This oxidative stress disrupts ATP synthesis and metabolic homeostasis, increasing susceptibility to diseases and reducing yield (Mittler, 2002; Gill and Tuteja, 2010) ^[20]. Another important consequence is the reduced uptake of nutrients. Limited soil moisture restricts mass flow and diffusion of nutrients toward roots, thereby affecting overall plant nutrition and quality.

4. Morphological Determinants of Drought Adaptation

4.1 Root system architecture

Root traits have received major attention in chickpea drought research. Deep and prolific root systems enable plants to access subsoil moisture and sustain transpiration during terminal stress. Kashiwagi *et al.* (2005) ^[32] demonstrated that root length density at deeper soil layers was positively correlated with grain yield under water-limited conditions. Among chickpea germplasm, ICC 4958 has emerged as a benchmark donor for drought-adaptive root traits. Serraj *et al.* (2004) ^[57] documented that ICC 4958 possesses greater root biomass, deeper rooting depth, and superior soil water extraction compared with many elite

cultivars. This genotype also shows higher transpiration efficiency and improved partitioning under stress. Subsequent work by Krishnamurthy *et al.* (2010) [34] confirmed that ICC 4958-derived lines could extract significantly more water from deeper soil layers, thereby sustaining photosynthesis during late-season drought.

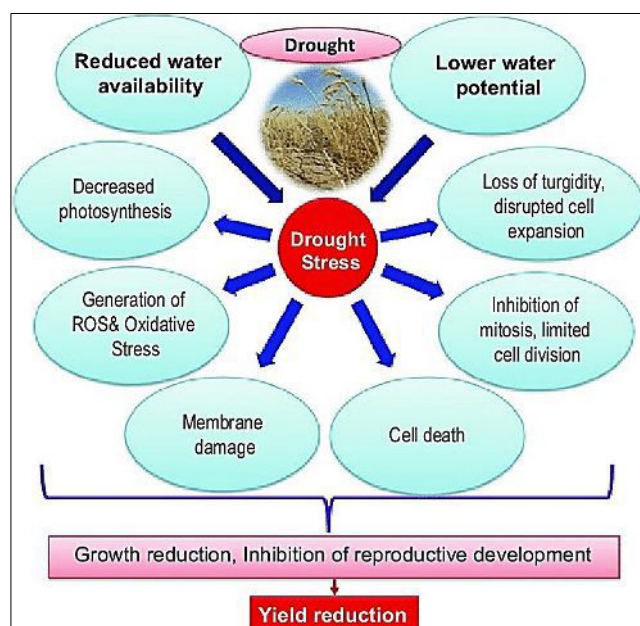


Fig 1: Detrimental effects of drought stress

The genetic basis of root traits in chickpea has been progressively elucidated. A major quantitative trait locus (QTL) cluster for root traits, often referred to as the “QTL-hotspot,” was identified from ICC 4958. Marker-assisted backcrossing (MABC) has successfully introgressed this region into several elite cultivars. Varshney *et al.* (2014) [52] demonstrated that lines carrying the introgressed root QTL showed enhanced root length density, improved drought tolerance, and yield advantage under rainfed conditions. More recently, Varshney *et al.* (2021) [51] reported the release and multilocation validation of genomics-assisted chickpea lines with improved performance under water-limited environments, underscoring the practical breeding value of RSA traits. Despite its importance, routine phenotyping of root traits remains a major bottleneck in chickpea improvement. Root measurements in field conditions are destructive, time-consuming, and highly environment-dependent. Traditional methods such as soil coring and trench profiling require extensive labor and often show high variability (Gregory *et al.*, 2009) [66]. To address this, controlled-environment platforms like PVC pipe systems, rhizotrons, and shovelomics approaches have been developed to enable higher-throughput screening (Trachsel *et al.*, 2011; Purushothaman *et al.*, 2017) [40]. Advances in imaging and phenomics are expected to further accelerate RSA-based breeding.

5. Drought survival strategies

5.1 Drought Tolerance

Drought tolerance refers to the plant's ability to withstand low tissue water potential while maintaining cellular integrity and metabolic activity. This mechanism operates largely through biochemical and molecular protection systems. One prominent feature is delayed senescence (stay-

green trait), which helps sustain photosynthesis during water deficit (Thomas and Howarth, 2000) [58].

At the molecular level, drought stress induces several transcription factors and protective proteins. Members of the DREB (Dehydration-Responsive Element Binding) family regulate expression of many downstream stress-responsive genes and are central to ABA-independent drought signaling (Agarwal *et al.*, 2006) [1]. Similarly, LEA (Late Embryogenesis Abundant) proteins stabilize membranes and proteins under cellular dehydration (Tunnacliffe and Wise, 2007) [60]. Transcription factor families such as MYB and NAC (NAM, ATAF, and CUC) modulate stress-responsive gene networks and contribute to improved drought endurance (Nakashima *et al.*, 2012) [59]. The enzyme NCED (nine-cis-epoxycarotenoid dioxygenase 3) plays a key regulatory role in abscisic acid (ABA) biosynthesis and is strongly induced under drought, thereby enhancing stomatal regulation and stress signaling (Iuchi *et al.*, 2001) [61]. Hormonal cross-talk involving ABA, brassinosteroids (BR), and auxin further fine-tunes plant responses by coordinating growth inhibition with stress protection (Cutler *et al.*, 2010; Nolan *et al.*, 2020) [62, 63]. Biochemically, drought-tolerant plants accumulate osmoprotectants such as proline, soluble sugars, and glycine betaine that maintain osmotic balance and protect macromolecules (Szabados and Saviouré, 2010) [64]. Concurrently, activation of antioxidant defense systems including superoxide dismutase, catalase, and peroxidases limits oxidative damage caused by reactive oxygen species (Mittler, 2002; Gill and Tuteja, 2010) [20]. Structural adjustments such as increased cuticular thickness also reduce non-stomatal water loss and contribute to tolerance.

5.2 Drought Avoidance

Drought avoidance enables plants to maintain relatively high tissue water status despite soil moisture deficit. This strategy primarily relies on morphological and physiological traits that improve water uptake or reduce water loss. A key avoidance trait is the development of deep and extensive root systems, which allow access to subsoil moisture and sustain transpiration during terminal drought (Kashiwagi *et al.*, 2006; Purushothaman *et al.*, 2017) [31, 40]. Above ground, plants reduce transpirational demand through stomatal closure, reduced stomatal density, and lower stomatal conductance. These responses are largely mediated by ABA signaling (Hetherington and Woodward, 2003) [65]. Additional avoidance features include reduced leaf area, altered leaf orientation, and partial inhibition of canopy expansion, all of which decrease evaporative surface area. In some cases, late flowering may help synchronize reproductive stages with periods of relatively better moisture availability in environments where early-season drought is more severe (Turner *et al.*, 2001) [49].

5.3 Drought Escape

Drought escape is a distinct adaptive strategy in which plants complete their life cycle before the onset of severe moisture stress. This mechanism is especially important in regions characterized by predictable terminal drought. It involves early flowering, rapid pod development, and accelerated grain filling, allowing the crop to avoid exposure of sensitive reproductive stages to water deficit (Kumar and Abbo, 2001) [35]. In chickpea and other grain legumes, early-maturing cultivars often show yield stability in short-season environments; however, excessively early

genotypes may sacrifice yield potential under favorable conditions due to reduced biomass accumulation (Gaur *et al.*, 2008) ^[18]. Therefore, breeding programs increasingly emphasize optimal phenology matched to target environments rather than extreme earliness.

Early flowering and maturity allow chickpea plants to avoid severe late-season moisture stress. Kumar and Abbo (2001)

^[35] emphasized the importance of phenological adjustment in Mediterranean environments. Nevertheless, excessively early genotypes may suffer yield penalties under favorable seasons. Gaur *et al.* (2008) ^[18] suggested that optimal phenology rather than extreme earliness is desirable for stable productivity.

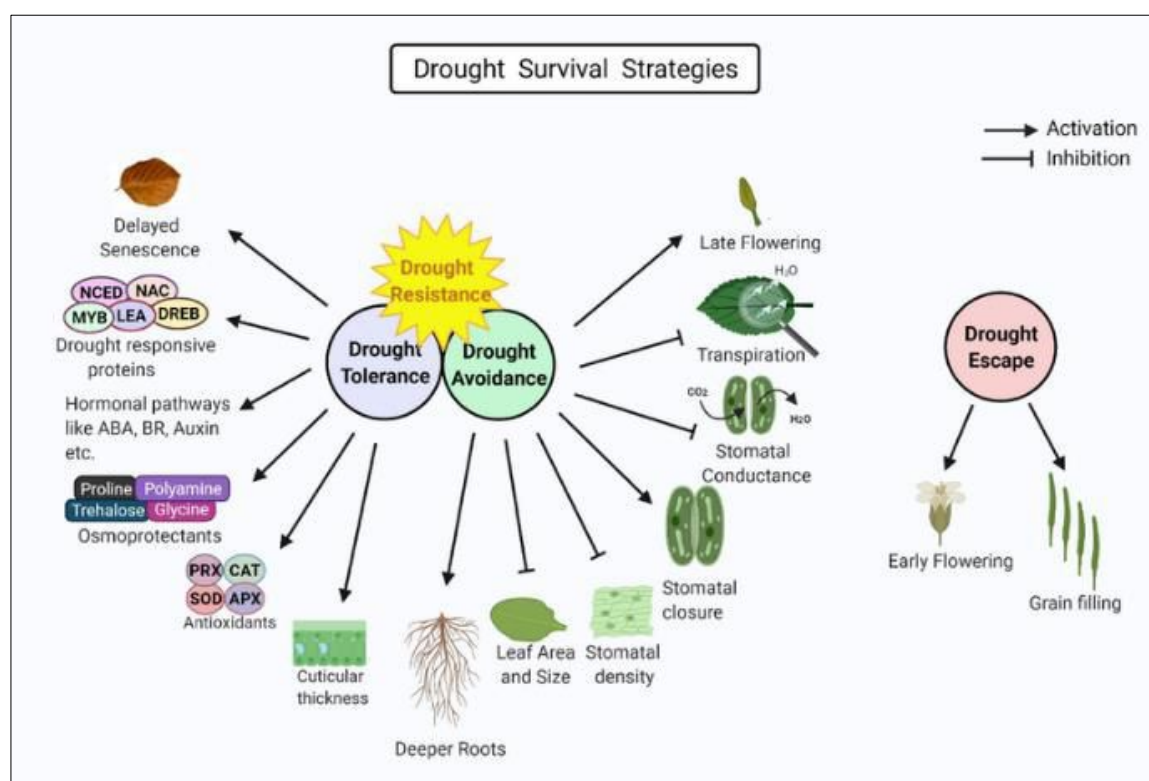


Fig 2: Drought survival strategies

6. Physiological and Biochemical Mechanisms

6.1 Relative water content and water relations

Relative water content (RWC) is widely recognized as a reliable physiological indicator of plant water status and drought tolerance in chickpea. Several studies have demonstrated that genotypic differences in RWC reflect the capacity of plants to maintain tissue hydration under moisture stress. Krouma *et al.* (2015) ^[67] reported that among the genotypes Amdoun, Kesseb, and Chetoui, Amdoun maintained the highest RWC under both control and drought conditions, showing only a 7% decline under stress, which indicated strong water retention ability. Similarly, Salma *et al.* (2016) ^[42] observed that genotypes BGD 72 and Pusa 1103 sustained significantly higher RWC under water-limited environments, suggesting effective osmotic adjustment and improved cellular water balance. Physiological evaluations by Rao *et al.* (2018) further confirmed the importance of RWC, where NBeG 47 exhibited the highest RWC along with superior seed yield and yield attributes under receding soil moisture, followed by NBeG 49 and NBeG 399, while NBeG 119 was more susceptible. Supporting these findings, studies integrating chlorophyll and water relations have shown that genotypes capable of maintaining higher RWC often also sustain better photosynthetic performance under drought (Kashiwagi *et al.*, 2015; Win *et al.*, 2017) ^[32]. More recently, Ucak and Arslan (2023) ^[68] reported a significant reduction in RWC and SPAD readings under moderate and severe deficit irrigation compared to full irrigation, reinforcing that

drought stress adversely affects plant water status. Collectively, these studies highlight that maintenance of higher RWC is a key adaptive trait associated with drought tolerance in chickpea and serves as an important selection criterion in breeding programs aimed at improving resilience under water-limited conditions.

6.2 Osmotic adjustment

Accumulation of compatible solutes such as proline and soluble sugars helps maintain cell turgor under dehydration. Mafakheri *et al.* (2010) ^[37] observed higher proline accumulation in tolerant chickpea cultivars exposed to drought. However, Blum (2011) ^[8] cautioned that osmotic adjustment alone does not guarantee yield stability and must be considered alongside whole-plant water use. Keerthi *et al.* (2023) ^[33] conducted a comprehensive study to assess the response of two chickpea varieties, ICC 4958 and HC-6, grown under varying levels of water availability represented by three different field capacities (FC): 100% FC (well-watered), 50% FC (moderate drought stress), and 25% FC (severe drought stress). Samples from both varieties were collected at three critical growth stages; 15, 30, and 45 days after sowing (DAS) to capture the dynamic physiological and biochemical changes under drought stress. Results from biochemical analyses demonstrated a marked decrease in cell membrane stability (CMS) by 29.6%. Proline content rose substantially by 54.75%, highlighting its role as an osmoprotectant that helps maintain cellular osmotic balance. Sugar levels increased by 15.2%, likely contributing to

osmotic adjustment and energy supply. Antioxidant enzyme activities also surged in response to drought stress, with catalase (CAT) by 50.5%, ascorbate peroxidase (APX) by 44.9%, and glutathione reductase (GR) by 49%. These enzymes collectively mitigate oxidative damage by scavenging reactive oxygen species (ROS), which accumulate under drought conditions.

6.3 Antioxidant defense

Antioxidant defense mechanisms play a crucial role in chickpea drought tolerance by protecting cellular components from oxidative damage caused by reactive oxygen species (ROS). Multiple studies have consistently shown that water deficit triggers the accumulation of osmolytes such as proline along with the activation of antioxidant enzymes. Durga and Jyothi (2009) [69] reported substantial increases in leaf proline content in drought-exposed chickpea genotypes, with genotypes 706 and 707 showing particularly high accumulation at flowering and pod filling stages, indicating strong osmotic adjustment capacity. Similarly, Sohrabi *et al.* (2012) [70] observed that drought stress reduced plant biomass and chlorophyll content but significantly increased proline concentration and the activities of guaiacol peroxidase (POD), catalase (CAT), and ascorbate peroxidase (APX), especially when plants were associated with *Glomus* species. Ghiabi *et al.* (2013) further confirmed that proline content was markedly higher under rainfed conditions, with genotype Flip2005-1C recording the maximum level, while Gunes *et al.* (2015) [23] noted that drought-tolerant cultivars maintained higher proline and relative water content along with lower membrane permeability compared to sensitive ones. Evidence from Dalvi *et al.* (2017) [12] demonstrated sharp increases in proline at both pre- and post-flowering stages, particularly in the wilt-resistant genotype JG 24, reinforcing its protective role. Jan *et al.* (2020) highlighted genotypic variability in antioxidant enzyme response, with GGP-1260 exhibiting the highest POD activity under drought. Likewise, Singh *et al.* (2021) [44] showed greater proline accumulation in the tolerant genotype Pusa 362 than in the sensitive SBB 377, indicating superior osmotic regulation. Recent work by Keerthi *et al.* (2023) [33] provided comprehensive biochemical evidence, reporting substantial increases in proline (54.75%), CAT (50.5%), APX (44.9%), and glutathione reductase (49%) under moisture deficit, alongside reduced cell membrane stability. Although amendments such as vermicompost can improve physiological performance under mild stress (Hosseinzadeh *et al.*, 2018) [71], severe drought still intensifies oxidative pressure. Collectively, these findings confirm that enhanced proline accumulation and upregulation of antioxidant enzymes constitute a coordinated defense system that underpins drought tolerance in chickpea and serve as reliable biochemical markers for selecting resilient genotypes.

6.4 Assimilate Partitioning and Stem Reserve Mobilization: Terminal drought markedly reduces reproductive success in chickpea by limiting flower and pod production, leading to significant declines in pod number, seed number, and overall yield. Davies *et al.* (2000) [13] demonstrated that although both desi and kabuli chickpea types experience yield losses under water deficit, desi types maintain relatively higher yield stability, which was

attributed not to differences in photosynthetic decline but to more efficient assimilate remobilization. The importance of pre-anthesis reserve utilization has been widely documented; Yang and Zhang (2006) [55] reported that in rice (*Oryza sativa*) and wheat (*Triticum aestivum*), stem and sheath reserves accumulated before flowering contribute about 10-40% of final grain weight under normal conditions, with their role becoming more critical under stress. Under drought during grain filling, remobilization of stored assimilates becomes a key determinant of seed size and yield because current photosynthesis is severely constrained. Post-anthesis soil drying has also been shown to accelerate grain filling and improve harvest index (Zhang *et al.*, 2012) [56]. In chickpea, Khoshro *et al.* (2014) emphasized that the capacity to store water-soluble carbohydrates (WSCs) in stems and efficiently remobilize them to developing seeds is an important adaptive trait for drought tolerance, with the contribution of remobilized WSCs to grain weight rising to 30-50% under stress. Similarly, higher specific weight and mobilization efficiency in internodes have been associated with drought-tolerant wheat genotypes. Nazir *et al.* (2021) [72] further highlighted stem reserve mobilization as a physiological buffer mechanism that sustains grain development when leaf photosynthesis is impaired, thereby stabilizing yield under moisture stress. Synchrony between source availability and sink demand is equally critical; Chugh and Sharma (2022) [11] reported in Indian mustard (*Brassica juncea* L.) that mismatch between seed filling and onset of heat or drought disrupts source-sink translocation, resulting in poor assimilate accumulation, increased shriveled seeds, and yield loss, whereas higher remobilization efficiency in late-sown genotypes was positively associated with dry matter at flowering and final seed weight. More recently, Gurumurthy *et al.* (2023) [24] observed that wheat genotypes exhibiting faster and greater stem reserve mobilization under delayed sowing and combined drought stress maintained superior yield stability across stress environments. Collectively, these findings underscore that stem reserve mobilization (SRM) during grain filling is a critical physiological trait for drought resilience, particularly when post-anthesis photosynthesis is limited, and thus represents an important selection criterion for improving yield stability in chickpea and other crops under terminal drought conditions.

7. Genetic Resources and Germplasm Utilization

Genetic resources and systematic germplasm utilization form the backbone of breeding chickpea for drought tolerance. Large-scale screening programs have consistently identified valuable donor genotypes with superior adaptive traits. Varshney *et al.* (2010) [73] highlighted that the cultivated chickpea gene pool is relatively narrow and stressed the need to harness diversity from both landraces and wild relatives to enhance drought resilience. Among wild progenitors, *Cicer reticulatum* and *Cicer echinospermum* have been recognized as rich sources of traits such as deep and prolific rooting, early seedling vigor, and improved water-use efficiency, all of which contribute to better performance under terminal drought. Subsequent studies have confirmed that introgression lines derived from these wild species exhibit improved root architecture and stress adaptation, validating the value of pre-breeding efforts (Thudi *et al.*, 2014; Varshney *et al.*, 2021) [47, 51]. However, utilization of wild germplasm is often constrained by

linkage drag, undesirable agronomic traits, and partial crossability barriers, which necessitate advanced backcrossing and marker-assisted selection to recover elite backgrounds. Multi-environment evaluation has also been emphasized as essential because drought response is highly influenced by genotype $\times$ environment interactions; genotypes performing well in one environment may not maintain superiority elsewhere (Krishnamurthy *et al.*, 2013) [34]. Recent germplasm screenings have identified stable drought-tolerant donors such as ICCV 4958, JG-11, and BDG-75 using physiological, yield-based, and index-based approaches. Integration of high-throughput phenotyping, genomics-assisted breeding, and wild introgression populations is therefore accelerating the identification of robust drought-tolerant lines. Collectively, these studies demonstrate that effective exploitation of genetic resources, supported by multi-location testing and modern molecular tools, is essential for broadening the chickpea genetic base and developing climate-resilient cultivars.

8. Conventional Breeding Progress

Conventional breeding has played a significant role in improving chickpea adaptation to moisture-limited environments. Traditional methods such as pedigree selection under managed drought stress have enabled the development of several cultivars with moderate drought tolerance and improved yield stability. However, the rate of progress has been constrained because drought tolerance is a complex quantitative trait governed by many genes and is highly influenced by genotype $\times$ environment interaction (Ceccarelli, 2015) [9]. To overcome the limitations of yield-based selection, breeders have increasingly adopted trait-based approaches focusing on key adaptive traits such as deeper and prolific root systems, early phenology, and higher harvest index, which are closely associated with better performance under terminal drought (Krishnamurthy *et al.*, 2013) [34]. Recent studies have further demonstrated substantial genetic variability for morpho-physiological and biochemical traits related to drought adaptation in chickpea, indicating good scope for selection when appropriate screening strategies are used (Thudi *et al.*, 2021) [47]. Despite these advances, precise phenotyping remains a major bottleneck because measurement of root traits, canopy temperature, and water-use efficiency is labor-intensive, environment-sensitive, and often low throughput (Varshney *et al.*, 2021) [51]. Emerging high-throughput phenomics platforms and image-based screening methods are beginning to improve selection accuracy and speed in conventional breeding pipelines (Araus and Cairns, 2014) [4]. Nevertheless, the narrow genetic base of cultivated chickpea and the polygenic nature of drought tolerance continue to limit rapid genetic gains, highlighting the need to integrate conventional breeding with modern genomics and phenomics tools for accelerating development of climate-resilient chickpea cultivars.

9. Molecular Breeding and QTL Mapping

The development of molecular markers revolutionized chickpea breeding. Recent advances in molecular breeding have significantly strengthened the genetic improvement of drought tolerance in chickpea. The identification of the CaLG04 “QTL-hotspot” marked a major milestone, as this genomic region harbours multiple QTLs controlling key drought-adaptive traits and explains up to about 58% of

phenotypic variation (Varshney *et al.*, 2014) [52]. (PMC) Subsequent high-density mapping using genotyping-by-sequencing refined this hotspot and integrated numerous SNP markers, improving its utility for marker-assisted selection (Jaganathan *et al.*, 2015) [30]. (Digital Library Adelaide) Marker-assisted backcrossing (MABC) programs have successfully introgressed the QTL-hotspot into elite cultivars, resulting in up to 16% higher seed yield under drought and improvements in root architecture and water-use traits (Roorkiwal *et al.*, 2020; Bharadwaj *et al.*, 2021) [6, 41]. (PMC) More recently, physiological characterization of QTL-introgression lines revealed that the hotspot influences seed weight, phenology, canopy growth, and transpiration efficiency, clarifying its role in drought adaptation (Nguyen *et al.*, 2021) [39]. (OUP Academic) In parallel, genome-wide association studies (GWAS) using high-density SNP platforms have enabled finer resolution of loci governing drought-responsive traits and facilitated the discovery of novel marker-trait associations (Thudi *et al.*, 2016; Varshney *et al.*, 2019) [47]. (ARCC Journals) Collectively, these recent genomic and molecular approaches have accelerated precision breeding in chickpea, although further validation across diverse environments and integration with high-throughput phenotyping remain important for fully exploiting drought tolerance genetics.

10. Genomics and Functional Approaches

Whole-genome sequencing of chickpea has facilitated candidate gene discovery (Varshney *et al.*, 2013). Transcriptomic analyses have revealed differential expression of genes involved in ABA signaling, DREB transcription factors, NAC proteins, and aquaporins under drought. Proteomic and metabolomic studies have provided additional insights into stress adaptation mechanisms. Integration of multi-omics datasets is increasingly being used to identify key regulatory networks controlling drought tolerance. Genomic selection is emerging as a promising approach for complex traits. Early studies indicate that genomic prediction can enhance selection efficiency for drought-related traits in chickpea breeding populations.

11. High-Throughput Phenotyping Advances

Phenotyping remains the limiting factor in drought breeding. Recent advances in remote sensing, UAV-based imaging, and automated lysimeters have improved the capacity to measure complex traits at scale (Araus and Cairns, 2014) [4]. Thermal imaging enables rapid assessment of canopy temperature, while multispectral sensors estimate biomass and vegetation indices. Integration of phenomics with genomics and machine learning is expected to transform chickpea improvement programs in the near future.

12. Climate-Smart Agronomy and Management

Genetic improvement must be complemented by improved crop management. Conservation agriculture practices enhance soil moisture retention. Optimal sowing windows help avoid peak stress periods. Balanced nutrient management improves root development and water-use efficiency. Supplemental irrigation at flowering has been shown to significantly stabilize yields (Fang and Turner, 2017) [49].

13. Future Perspectives and Research Priorities: Future chickpea breeding must adopt integrative strategies

combining physiology, genomics, and climate modeling. Speed breeding platforms can accelerate generation turnover. Gene editing technologies offer potential for precise modification of drought-responsive genes, although further validation is required.

Breeding for combined stress tolerance, particularly drought plus heat, is becoming increasingly important under climate change scenarios. Greater emphasis on farmer-preferred traits and seed system strengthening will enhance adoption of improved varieties.

14. Conclusions

Enhancing chickpea productivity under drought stress continues to be one of the foremost challenges for sustaining global pulse production, particularly in rainfed agro-ecosystems where terminal moisture stress is frequent. Over the past decades, substantial progress has been achieved in elucidating the physiological, morphological, and genetic mechanisms underlying drought tolerance, including traits related to root architecture, water-use efficiency, phenology, and assimilate remobilization. Simultaneously, advances in high-throughput phenotyping and precision physiology have improved the reliability of selection under managed stress environments. Despite these gains, drought tolerance remains a highly complex, polygenic trait strongly influenced by genotype × environment interactions, which continues to limit rapid genetic progress. Therefore, future breeding strategies must integrate conventional selection, molecular breeding, genomic prediction, and phenomics to capture both major and minor effect loci. Strengthening pre-breeding efforts using wild relatives and diverse germplasm will further broaden the genetic base of chickpea. Investment in multi-environment testing platforms and decision-support tools will enhance selection accuracy under variable climates.

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