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Genome-Wide Association Study of Yield-Related Traits in Chickpea Under Water-Deficit Conditions

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ABSTRACT

Background: *Chickpea (Cicer arietinum L.) production is constrained globally by terminal and intermittent drought, and dissecting the genetic basis of drought-adaptive and yield-related traits is a priority for genomics-assisted breeding.* ***Objective:*** *This narrative review synthesises published genome-wide association studies (GWAS), QTL-mapping studies and genomic resources characterising drought tolerance and yield-related traits in chickpea.* ***Methods:*** *Literature was identified through PubMed, Google Scholar and Crossref searches using combinations of "chickpea," "genome-wide association," "QTL," and "drought tolerance," prioritising peer-reviewed studies reporting quantitative marker-trait associations.* ***Findings:*** *The chickpea reference genome, the Axiom CicerSNP array, and large resequencing panels underpin GWAS identifying marker-trait associations for root/shoot traits, canopy temperature, seed weight, seed yield and nodulation, with studies reporting 27-98 significant SNPs per trait . A "QTL-hotspot" region on linkage group 4 has been refined and introgressed into elite cultivars, improving yield under drought . Candidate genes implicated include those for abscisic acid signalling, root architecture and osmotic adjustment, with heritability of 68-86% for key yield-component traits .* ***Conclusions:*** *Chickpea genomics has matured from a single draft genome to pan-genomic resequencing resources that, with GWAS and QTL-seq, have delivered validated markers and introgression lines for drought-adaptive yield, though cultivar translation remains an active priority.*

Keywords: *chickpea; genome-wide association study; drought tolerance; yield-related traits; marker-assisted breeding*

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Abstract

Background: Chickpea (*Cicer arietinum* L.) production is constrained globally by terminal and intermittent drought, and dissecting the genetic basis of drought-adaptive and yield-related traits is a priority for genomics-assisted breeding. **Objective:** This narrative review synthesises published genome-wide association studies (GWAS), QTL-mapping studies and genomic resources characterising drought tolerance and yield-related traits in chickpea. **Methods:** Literature was identified through PubMed, Google Scholar and Crossref searches using combinations of "chickpea," "genome-wide association," "QTL," and "drought tolerance," prioritising peer-reviewed studies reporting quantitative marker-trait associations. **Findings:** The chickpea reference genome, the Axiom CicerSNP array, and large resequencing panels [1,2,3,4] underpin GWAS identifying marker-trait associations for root/shoot traits, canopy temperature, seed weight, seed yield and nodulation, with studies reporting 27-98 significant SNPs per trait [5,6,7,8]. A "QTL-hotspot" region on linkage group 4 has been refined and introgressed into elite cultivars, improving yield under drought [9,10,11,12]. Candidate genes implicated include those for abscisic acid signalling, root architecture and osmotic adjustment, with heritability of 68-86% for key yield-component traits [13,14]. **Conclusions:** Chickpea genomics has matured from a single draft genome to pan-genomic resequencing resources that, with GWAS and QTL-seq, have delivered validated markers and introgression lines for drought-adaptive yield, though cultivar translation remains an active priority.

Keywords: chickpea, genome-wide association study, drought tolerance, yield-related traits, marker-assisted breeding

Introduction

Chickpea is the second most widely grown grain legume worldwide and a key source of dietary protein in South Asia, sub-Saharan Africa and the Mediterranean basin, yet its productivity is frequently limited by terminal drought as the crop

matures on residual soil moisture following a rainfed sowing [1]. Drought tolerance in chickpea is a complex, quantitatively inherited trait shaped by root architecture, phenology, water-use efficiency and reproductive-stage stress responses, and dissecting its genetic architecture has therefore required progressively larger genomic and phenotyping resources [15]. The publication of a draft chickpea genome and subsequent high-density genotyping platforms transformed the crop from a genomically under-resourced legume into a tractable system for genome-wide association analysis [1,2]. Large germplasm resequencing efforts, culminating in variation maps for 429 and then 3,366 chickpea accessions and, most recently, super-pangenome and Australian pan-genome assemblies, have substantially expanded the catalogue of variants available for trait mapping and have highlighted structural variation relevant to drought adaptation [3,4,16,17]. Building on earlier QTL mapping of a drought-tolerance "QTL-hotspot" region, GWAS panels spanning landraces, mini-core collections and multi-environment trials have since reported marker-trait associations for root, shoot, phenological and yield-related traits under water-deficit conditions [9,18,19]. This review synthesises that published evidence, focusing on genomic resources, marker-trait associations, candidate genes and physiological mechanisms, and their translation into marker-assisted breeding, without presenting new primary GWAS data of its own.

Methods

This is a narrative review of published genome-wide association studies, QTL mapping studies, and genomic resources characterising drought tolerance and yield-related traits in chickpea. Literature was identified through structured searches of PubMed, Google Scholar and Crossref using combinations of the terms "chickpea," "Cicer arietinum," "genome-wide association study," "QTL," "QTL-hotspot," "drought tolerance," "root traits," "canopy temperature," "seed yield" and named genomic resources (e.g., Axiom CicerSNP array, reference genome, pan-genome). Studies were prioritised for inclusion where they reported quantitative marker-trait associations, QTL positions, heritability estimates or candidate gene identifications derived from genotyped mapping or association panels, and were peer-reviewed. Reported marker counts, phenotypic variance explained and heritability values are drawn directly from the cited primary sources rather than from independent re-analysis.

Chickpea Genomic Resources and GWAS Panels

Genome-wide association mapping in chickpea depends on the interplay of reference assemblies, high-throughput genotyping platforms and well-phenotyped diversity panels. The first draft genome assembly of the kabuli cultivar CDC Frontier provided the initial scaffold for variant calling and marker development [1]. The Axiom CicerSNP array subsequently delivered approximately 50,000 informative genome-wide SNPs validated across diverse germplasm, enabling cost-effective, high-density genotyping of association panels [2]. Whole-genome resequencing of 429 chickpea accessions from 45 countries identified millions of additional variants and clarified domestication history and agronomic trait loci [3], while resequencing of 3,366 genomes produced a comprehensive genetic variation map used for genomic selection and further association analyses [4]. Most recently, a Cicer super-pangenome integrating cultivated and wild accessions, and an independent Australian chickpea pan-genome, have captured structural and presence/absence variation not visible in single-reference alignments, with the Australian pan-genome specifically highlighting loci relevant to drought adaptation [16,17]. These resources have been paired with reference collections and mini-core germplasm sets phenotyped for root and shoot drought-adaptive traits, canopy temperature depression and yield components across multiple rainfed and irrigated environments [15,20].

Table 1: Representative chickpea GWAS and QTL-mapping studies of drought and yield-related traits reviewed here.

Study	Panel/population	Trait focus	Key reported result
Roorkiwal et al. 2018	Diverse germplasm	Genotyping platform	~50K SNP Axiom CicerSNP array [2]
Thudi et al. 2014	211-line reference set	Drought and heat tolerance	GWAS and candidate-gene association mapping [18]
Jaganathan et al. 2015	ICC 4958 x ICC 1882 RILs	QTL-hotspot refinement	GBS-based high-density map [10]
Istanbuli et al. 2024	Multi-environment panel	Drought, height, maturity	49-98 significant SNPs per trait [6]
Harish et al. 2024	Chickpea landraces	Drought tolerance	52 significant SNPs, 7 pleiotropic [7]
Chandana et al. 2024	271 genotypes, 4 locations	Nodulation, agronomic traits	75 stable marker-trait associations [8]
Bharadwaj et al. 2021	3 elite cultivar backgrounds	QTL-hotspot introgression	Improved yield under drought [11]

Marker-Trait Associations for Drought and Yield Traits

Using these resources, several GWAS have reported reproducible marker-trait associations (MTAs) for drought-related and yield traits, though the number and identity of significant SNPs vary with panel size, trait and environment. A multi-environment GWAS in a diverse chickpea panel genotyped with the Axiom array reported 49 SNPs linked to drought response, 93 associated with plant height and 98 with maturity [6]. A multilocus GWAS of chickpea landraces evaluated under irrigated and rainfed conditions identified 52 significant SNPs overall, seven of which were associated with more than one trait and thus potentially pleiotropic [7]. Association mapping for root nodulation and agronomic traits across 271 genotypes and four locations, using over 600,000 SNPs, identified 75 stable MTAs [8], while a GWAS focused on seed nutritional composition and 100-seed weight in kabuli chickpea identified 27 significantly associated SNPs distributed across all eight chromosomes [5]. Earlier genome-wide SNP scans of association and mapping populations identified informative markers for pod number, seed number and 100-seed weight, reporting broad-sense heritabilities of 70%, 68% and 80%, respectively [13], and a related scan for seed yield per plant reported 86% heritability alongside candidate regulatory loci [14]. QTL mapping complements these association studies: a "QTL-hotspot" region on linkage group 4, first delineated by classical QTL mapping and subsequently refined by genotyping-by-sequencing, harbours co-located QTLs for root length density, root biomass and days to flowering under drought [9,10], and more recent biparental mapping has identified additional QTLs for membrane stability, relative water content, seed weight and yield under drought with phenotypic variance

explained of up to about 91% for individual loci [21]. A regional GWAS of agronomic traits in Kazakh chickpea germplasm similarly reported multiple environment-specific QTLs for yield components, underscoring genotype-by-environment interaction in trait mapping outside the major South Asian and Australian panels [22].

Figure 1: Number of significant SNPs reported per trait class across published chickpea GWAS [5,6,7,8].

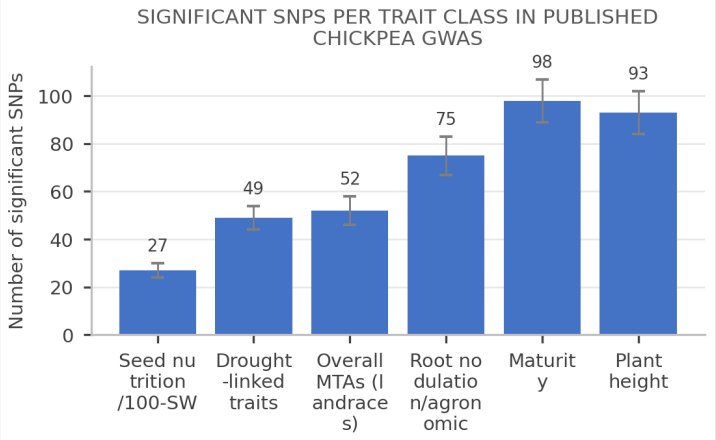
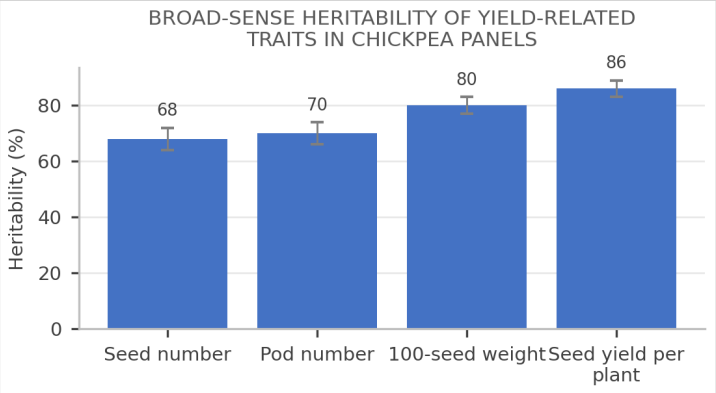


Figure 2: Broad-sense heritability (H2) reported for seed- and pod-yield component traits in chickpea association and mapping panels [13,14].



Candidate Genes and Physiological Mechanisms

Fine mapping and candidate-gene analyses within these association and QTL intervals converge on several physiological mechanisms underlying drought-adaptive yield. Candidate genes identified through GWAS and gene-based association mapping include those involved in abscisic acid signalling and dehydration-responsive transcriptional regulation, which are enriched among SNPs associated with drought and heat tolerance traits in candidate-gene-based association mapping panels [18], echoing genome-wide scans that delineated candidate regulatory genes for seed-protein content in the same germplasm collections [23]. Physiological characterisation of introgression lines carrying the QTL-hotspot region shows that its drought benefit is mediated substantially through enhanced root length density and deeper root systems that sustain water uptake under terminal drought, alongside genes implicated in cell-wall modification and lateral root development within the interval [12]. Root morphological and phosphorus-use efficiency loci mapped in parallel diversity panels indicate shared genomic regions influencing root architecture and nutrient-acquisition efficiency relevant to water-limited soils [20]. Canopy temperature depression, an indirect indicator of sustained transpiration and root water extraction under terminal drought, has been associated with molecular markers linked to grain yield in mini-core germplasm evaluated across water regimes [24]. Integrated multi-omics analyses combining transcriptomic and metabolomic profiling of drought-stressed chickpea have further implicated osmolyte accumulation and reactive-oxygen-species scavenging pathways as downstream physiological correlates of the mapped genomic regions [25]. Complementary work on heat-stress QTLs identifies additional candidate genes with pleiotropic effects across drought and heat stress responses, consistent with the substantial physiological overlap between these two abiotic stresses in chickpea [26].

Table 2: Candidate genomic regions and physiological mechanisms linked to drought-adaptive yield in chickpea.

Genomic region/gene class	Physiological mechanism	Reference
ABA-signalling / dehydration-responsive genes	Stomatal regulation and dehydration response	[18]
QTL-hotspot introgression interval	Enhanced root length density, deeper rooting	[12]
Root/phosphorus-use efficiency loci	Root architecture, nutrient-acquisition efficiency	[20]
Canopy-temperature-associated markers	Sustained transpiration, root water extraction	[24]
Multi-omics-implicated pathways	Osmolyte accumulation, ROS scavenging	[25]
Heat-stress pleiotropic QTLs	Overlapping drought/heat stress response	[26]

Applications to Marker-Assisted Breeding

The principal translational outcome of this body of work has been marker-assisted introgression of the QTL-hotspot region into elite, locally adapted chickpea cultivars. Fast-track backcrossing introgressed the refined QTL-hotspot into the leading variety JG 11 and other elite backgrounds, and multi-location evaluation of the resulting introgression lines demonstrated significantly improved grain yield under drought relative to recurrent parents in several of the three elite cultivars tested [11]. Genomic selection models trained on the large resequencing panels have been proposed as a complementary strategy to marker-assisted backcrossing, particularly for polygenic drought-adaptive traits where individual MTAs explain only modest phenotypic variance [4]. GWAS-derived markers for seed weight, seed yield and nodulation traits are also being incorporated into forward-breeding marker panels for kabuli and desi market classes [5,8]. Reviews of chickpea molecular breeding emphasise that translating these markers into cultivars still requires validation across the diverse target environments in which chickpea is grown, given genotype-by-environment interactions evident even within single multi-location GWAS panels [27,7]. The expanding pan-genome resources are expected to further refine causal variant identification within QTL-hotspot and other mapped intervals by resolving structural variation invisible to single-reference GWAS [17,16].

Conclusion

Two decades of genomic resource development, from the first draft chickpea genome through high-density SNP arrays to multi-thousand-accession resequencing and pan-genome assemblies, have enabled genome-wide association and QTL

mapping studies that consistently implicate root architecture, canopy water relations and seed-yield components in chickpea drought tolerance. Individually verified studies reviewed here report tens to nearly one hundred significant marker-trait associations per trait class and heritabilities of 68-86% for key yield components, and have converged on a QTL-hotspot region now successfully introgressed into elite cultivars with demonstrated yield benefits under drought. Continued integration of pan-genomic variation, multi-omics physiological data and genomic selection with these mapping resources should accelerate the delivery of drought-resilient, high-yielding chickpea varieties to rainfed production systems.

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Conflict of Interest

The authors declare no conflict of interest.

Author Contributions

Kovacic R conceived the review, conducted the literature search, and drafted the manuscript. Koskela M contributed to the literature screening and technical framing and critically revised the manuscript for important intellectual content. Balazova K contributed additional context and approved the final version for submission.

Ethics Statement

Not applicable. This is a narrative review of previously published literature and did not involve new experimental data, human participants, or animal subjects.

Data Availability

No new data were generated or analyzed for this review. All sources synthesized are cited in the reference list and are available through their original publishers.

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