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REVIEW

Chickpea (*Cicer arietinum* L.) battling against heat stress: plant breeding and genomics advances

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Abstract

Global climate change, particularly the increasing frequency and intensity of heat stress, poses a significant threat to crop productivity. Chickpea (*Cicer arietinum* L.) employs various physiological, biochemical, and molecular mechanisms to cope with elevated temperatures, including maintaining leaf chlorophyll content to preserve the functional integrity of photosystem II (PSII) and enhancing canopy temperature depression to reduce overheating. These traits are crucial for sustaining photosynthetic efficiency, plant health, and yield stability under heat stress. Recent advances in multi-omics approaches—including genomics, transcriptomics, proteomics, and metabolomics—have enhanced our understanding of the genetic basis of heat stress tolerance in chickpea. These tools have facilitated the identification of key genes and molecular pathways involved in heat stress responses. Functional characterization of these genes has provided insights into their roles within the complex metabolic and signaling networks that underpin heat resilience. This review explores integrating conventional and modern breeding technologies with high-throughput phenotyping (HTP) platforms to accelerate genetic gains in chickpea under heat stress. HTP tools enable rapid, precise screening of heat-resilient traits, facilitating early selection of superior genotypes. We also highlight recent genomic advancements, including genome-wide association studies, whole-genome resequencing, and pangenome assemblies, which have uncovered novel structural variants, candidate genes, and haplotypes associated with heat tolerance. Leveraging these resources in conjunction with functional analyses offers new opportunities for breeding climate-resilient chickpea cultivars capable of delivering stable yields and quality under adverse conditions. These developments are crucial for safeguarding chickpea productivity and ensuring global food and nutrition security amid climate change.

Key message

Increasing intensity of heat stress poses a major threat to chickpea productivity. Integrating multi-omics approaches with modern plant breeding, physiological and biochemical insights, and advanced phenotyping tools offers promising avenues for improving genetic gains in chickpea under heat stress.

Keywords Heat stress · Chickpea · Genomics · QTL · Genetic variability

Introduction

Chickpea (*Cicer arietinum* L.) is a key grain legume that significantly contributes to global food and nutritional security (Gaur et al. 2012). As an affordable source of protein and essential micronutrients, it plays a vital role in combating malnutrition, especially in developing regions (Jha et al. 2024). However, the increasing frequency of heat stress, exacerbated by global climate change, threatens chickpea yields.

With global ambient temperatures projected to rise by 1–6 °C by the end of the twenty-first century (De Costa 2011), extreme heat events are expected to become more frequent and intense, posing a serious threat to crop yields and global food security (Callahan and Mankin 2022). In chickpea, heat stress adversely affects all key developmental stages (Fig. 1), significantly reducing yield (Rani et al. 2020; Devi et al. 2022; Arslan 2023). For example, exposure to high temperatures during flower initiation can lead to flower drop, pollen sterility, disrupted pollen tube growth, impaired

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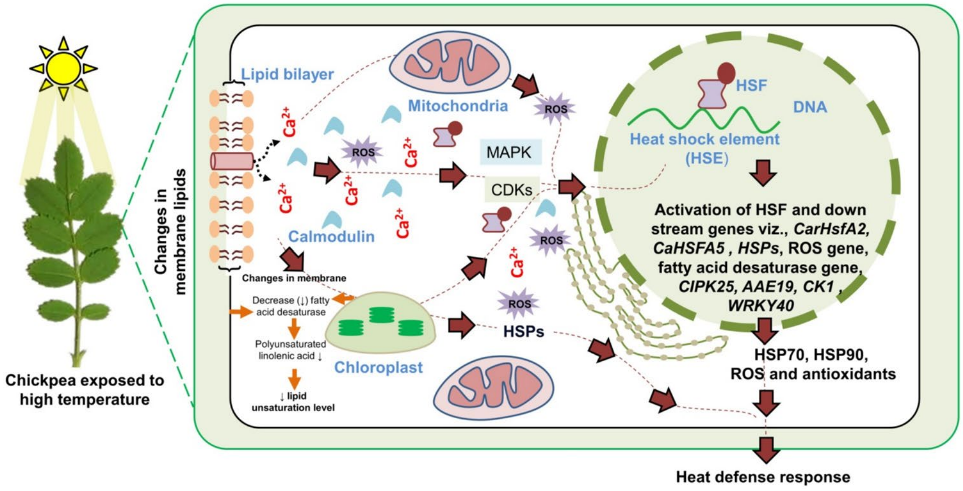


Fig. 1 Schematic representation of heat stress perception and response mechanisms in plants. Heat stress alters cell membrane fluidity by modifying membrane lipids (Zhao et al. 2023), triggering signal transduction through ion channels, which activates cellular calmodulins and cytosolic Ca^{2+} ions (Kan and Lin 2021), transmitting heat stress signals to the nucleus via MAP kinase and CDK pathways (Liu et al. 2006). In the nucleus, heat shock elements (HSEs) in DNA are activated, upregulating transcription factors such as *HSF*s and *WRKY*s, these, in turn, activating the expression of heat shock proteins (HSPs) and reactive oxygen species-related genes (Agarwal et al. 2016; Chidambaranathan et al. 2018; Kohli et al. 2018; Mohanty et al. 2024a). This cascade produces various HSPs and antioxidants, enhancing heat tolerance (Agarwal et al. 2016; Chidambaram et al. 2018; Mohanty et al. 2024a). Lipid remodeling further supports thermotolerance by decreasing polyunsaturated fatty acids (e.g., C18:3) in phospholipids like phosphatidylcholine (PC), phosphatidylethanolamine (PE), phosphatidylserine (PS), and phosphatidylinositol (PI) (Narayanan et al. 2020), while increasing saturated fatty acids (e.g., C32:0 PC/PI and C34:1 PI/PC). Reduced fatty acid desaturase activity limits the conversion of 18:2 to 18:3 lipids in extraplastidic membranes, helping maintain membrane stability during heat stress (Narayanan et al. 2020)

stigma receptivity, pod malformation, and reduced grain filling, ultimately resulting in lower seed yields (Devasirvatham et al. 2013; Bhandari et al. 2020; Devi et al. 2022). Temperatures exceeding 35 °C during the reproductive stage—particularly during seed set—have been associated with yield losses of up to 39% (Devasirvatham et al. 2015).

Plant breeding offers a practical and sustainable approach to mitigating the impacts of heat stress. Significant progress has been made in harnessing genetic variation for heat tolerance within chickpea germplasm sourced from diverse genepools (Krishnamurthy et al. 2011; Kushwah et al. 2021; Jha et al. 2023a). Classical genetic studies have shown that heat tolerance in chickpea is a quantitatively inherited trait with strong genotype × environment (G × E) interactions (Upadhyaya et al. 2011; Jha et al. 2019a).

Modern genomic tools—such as single-nucleotide polymorphism (SNP) markers—have enabled the identification of quantitative trait loci (QTLs), genes, and genomic regions associated with heat tolerance through biparental mapping and genome-wide association studies (GWAS) (Jha et al. 2021b,c; Mohanty et al. 2024a). The availability of a high-quality chickpea reference genome, along with advancements in whole-genome resequencing (WGRS) and pangenome assembly, has further facilitated the discovery of structural variations, copy number variations, and haplotypes linked to heat stress tolerance.

Functional genomics approaches, including RNA sequencing (RNA-seq), have identified candidate genes and non-coding RNAs involved in chickpea's heat stress response, offering insights into their regulatory roles. In parallel, proteomics and metabolomics studies have revealed key proteins and metabolites that contribute to stress adaptation, shedding light on the complex regulatory networks underpinning heat tolerance.

Recent technological advances—including robotics, unmanned aerial vehicles (UAVs), and machine learning algorithms—have greatly enhanced our capacity to monitor and assess plant responses to heat stress with increased precision and scale. These tools facilitate large-scale phenotyping of chickpea germplasm in both field and controlled environments, enabling the early identification and selection of heat-tolerant genotypes.

Furthermore, emerging genome-editing technologies present promising opportunities to develop chickpea cultivars with enhanced heat resilience. By integrating genomics, phenomics, and advanced breeding strategies, researchers can accelerate the development of climate-resilient chickpea varieties capable of maintaining yield stability under increasing heat stress. This review synthesizes recent advances, identifies key challenges, and outlines future directions for mitigating the impacts of heat stress and ensuring sustainable chickpea production in the face of climate change.

Physiological response and anomalies of chickpea under heat stress

As a cool-season legume, chickpea is particularly sensitive to elevated temperatures, especially during critical developmental stages such as flowering and seed filling (Devi et al. 2023a). Heat stress disrupts key physiological including photosynthesis, transpiration, processes, respiration, and nitrogen metabolism. It also induces oxidative stress, reducing plant growth and yield (Allakhverdiev et al. 2008; Jha et al. 2021a; Makyona et al. 2021; Devi et al. 2022; Arslan 2023; Devi et al. 2023a). In addition to impairing these primary functions, heat stress adversely affects several physiological traits essential for plant function and productivity, including compromised cell membrane stability (Ibrahim 2011), reduced chlorophyll fluorescence (Kumar et al. 2020), inhibited stomatal conductance (Bindra et al. 2021), diminished chlorophyll content, accelerated leaf senescence (Abdelrahman et al. 2017; Djanaguiraman et al. 2023), increased canopy temperature depression (Kumar et al. 2017), and disrupted carbohydrate and sucrose metabolism (Awasthi et al. 2014, 2017) (see Fig. 2).

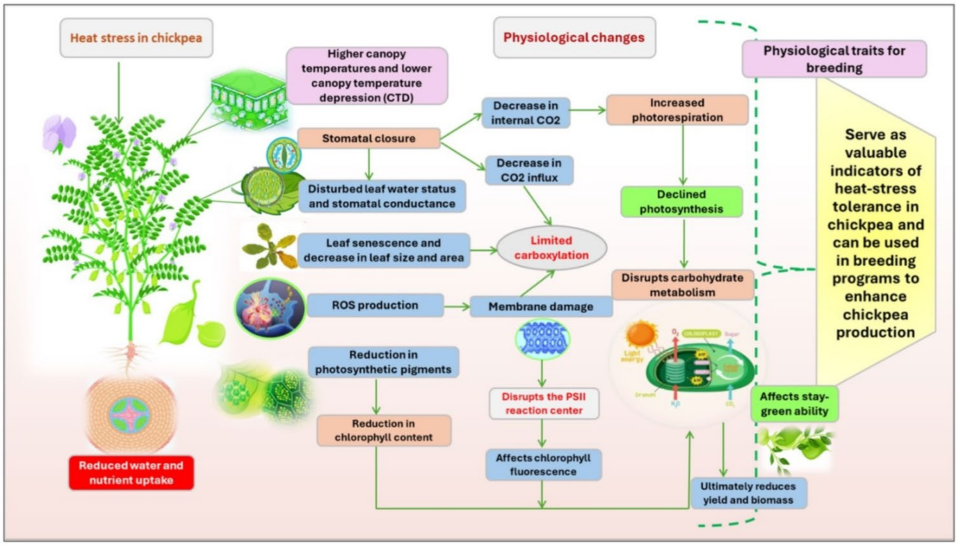
The reproductive stage is particularly sensitive to high temperatures, often leading to excessive flower drop, reduced pollen viability, impaired stigma receptivity, and ultimately, decreased fertilization success (Devasirvatham et al. 2012b, 2013). Temperatures exceeding 35 °C during seed formation can result in yield losses of up to 39% (Devasirvatham et al. 2015). Thus, heat stress poses major challenges across all critical stages of chickpea growth, significantly undermining yield potential.

Membrane thermostability

Membrane thermostability is a key physiological indicator of heat tolerance in plants, as it reflects the ability to maintain cellular integrity under stress (Jain 2014). Chickpea exhibits greater sensitivity to high temperatures in terms of cell membrane stability compared to other legumes (Devasirvatham et al. 2012a, b), making this trait especially important for successful cultivation in dry and semi-arid regions (Ibrahim 2011). Significant genotypic variation in membrane thermostability has been observed in chickpea, making it a valuable selection trait in breeding programs (Ibrahim 2011; Kaushal et al. 2013; Kumar et al. 2013). For example, Dua (2001) identified heat-tolerant genotypes ICCV88, ICC512, and ICC513 based on their membrane stability. In a field study of 115 chickpea genotypes exposed to 36.5 °C, genotype GNG 663 was identified as heat tolerant (23% electrolyte leakage), whereas Pusa 244 was heat sensitive (50% leakage) (Kumar et al. 2012).

Further studies have shown that reproductive-stage temperatures exceeding 32/20 °C cause significant membrane damage in heat-sensitive genotypes such as ICC10685 (28.3%) and ICC5912 (26.3%), while heat-tolerant genotypes like ICC15614 (17.3%) and ICCV 92944 (19.6%) exhibited comparatively lower levels of damage (Kaushal et al. 2013). A gradual increase to 42/25 °C over eight days during flowering caused 20–25% more electrolyte leakage (EL) in the sensitive chickpea genotype ICC16374 than in the tolerant ICCV92944 (Parankusam et al. 2017). Similarly, exposure to 37/27 °C increased EL by 16–25%, with ICC1205 showing strong heat resistance (13–14% EL) (Pareek et al. 2019). These findings underscore the substantial genetic diversity in membrane thermostability among

Fig. 2 Physiological responses and impacts of heat stress in chickpea



chickpea genotypes, representing a valuable resource for breeding heat-tolerant varieties (Gaur et al. 2013; Paul et al. 2018a; Mohanty et al. 2024a).

Canopy temperature depression

Canopy temperature depression (CTD) is another critical physiological trait that reflects a plant's ability to maintain lower canopy temperatures under heat stress (de Souza et al. 2012). CTD is closely linked to plant water status and the effectiveness of transpiration, which cools the canopy using soil moisture (Kumar et al. 2017). In many crops, higher CTD values are positively associated with seed yield and are used as a selection trait for heat tolerance. However, in chickpea, CTD negatively correlates with water potential, osmotic pressure, relative leaf water content, and seed yield (Sharma et al. 2015). This inverse relationship limits its effectiveness as a heat tolerance marker, especially in high-humidity environments where evaporative cooling is negligible and canopy temperature differences become less distinct (de Souza et al. 2012).

Despite this, studies have shown that CTD remains a valuable trait for identifying heat-tolerant genotypes. For instance, Kumar et al. (2017) reported that chickpea genotypes with higher CTD values also exhibited improved photosynthetic performance and more stable yields under heat stress. Heat-tolerant chickpea genotypes such as ICCVs 95,311, 98,902, 07109, and 92,944 recorded higher CTD values than their sensitive counterparts ICCVs 07116, 07117, and 14,592 (Devasirvatham et al. 2015). Moreover, Saeed et al. (2023) found that CTD values between 4.2 and 5.5 °C were associated with significantly improved seed yield (16.3–20.2 g) and biological yield (59.5–70.4 g) under heat stress conditions. These studies highlight the considerable genetic variation in CTD among chickpea genotypes (Kumar et al. 2017), suggesting its potential utility in breeding programs to enhance heat stress resilience. Selecting genotypes with superior CTD could play a critical role in improving chickpea productivity in heat-prone environments (Kumar et al. 2017).

Chlorophyll fluorescence

In chickpea, heat stress significantly disrupts chlorophyll fluorescence (ChlF), leading to reduced photosynthetic efficiency and overall plant health (Srinivasan et al. 1996). Studies have shown that heat stress decreases the quantum yield of photosystem II (PSII), a key indicator of plant stress (Herzog et al. 2012). The magnitude of this decline varies among chickpea genotypes, highlighting the importance of genetic factors in heat tolerance (Devi et al. 2023b). For example, heat stress reduces the Fv/Fm ratio—an essential indicator of PSII efficiency—signaling potential damage to the photosynthetic system (Kumar et al. 2020). Field evaluations conducted over two winter seasons revealed contrasting responses among chickpea genotypes. Based on ChlF, two genotypes (Acc#RR-3, Acc#7) exhibited heat tolerance, maintaining Fv/Fm values between 0.83 and 0.85, whereas two others (Acc#2, Acc#8) showed sensitivity, with lower Fv/Fm values of 0.78–0.80. In another field study, heat-tolerant genotypes (ICC1356, ICC15614) maintained higher chlorophyll fluorescence (Fv/Fm ~ 0.60) under heat stress (> 32/20 °C) than sensitive ones (ICC4567, ICC5912), which exhibited lower values (Fv/Fm ~ 0.50) (Awasthi et al. 2017). Similarly, Devi et al. (2023b) reported a more substantial decline in the Fv/Fm ratio in heat-sensitive genotypes (44–56%) than in heat-tolerant ones (19.7–25.3%) under heat stress, relative to controls.

Incorporating ChlF measurements into breeding strategies offers an effective tool for selecting heat-tolerant chickpea genotypes—a critical step toward maintaining yield stability under changing climatic conditions (Djanaguiraman et al. 2023).

Photosynthetic efficiency and sucrose metabolism

Enhancing the function of key photosynthetic components is a strategic approach to improving photosynthetic efficiency and seed yield in chickpea, particularly under heat stress conditions (Chandel and Sharma 2023). Heat stress reduces the net photosynthetic rate, chlorophyll content, and photosystem efficiency, ultimately disrupting carbohydrate metabolism (Awasthi et al. 2014; Yadav et al. 2022; Devi et al. 2023b). Maintaining photosynthetic activity under heat stress is crucial for sustaining productivity (Gaur et al. 2013), especially during the reproductive phase, when a decline in photosynthesis can significantly impact yield (Kaushal et al. 2013). Consequently, numerous studies have focused on the physiological traits and mechanisms that contribute to heat tolerance in chickpea (Kaushal et al. 2013; Awasthi et al. 2014; Yadav et al. 2022; Devi et al. 2023b). Key photosynthetic indicators—such as the stay-green trait, chlorophyll concentration, and chlorophyll fluorescence—are closely linked to RuBisCo activation and overall photosynthetic performance (Salvucci and Crafts-Brandner 2004; Sharkey 2005). These traits are potential selection criteria for heat-tolerant chickpea breeding programs.

Field studies consistently report that heat stress reduces photosynthetic efficiency and carbohydrate levels, particularly in heat-sensitive chickpea cultivars (Makonya et al. 2019). In contrast, heat-tolerant genotypes such as Acc#7 and Acc#RR-3 maintain stable physiological responses during flowering and preserve grain yield across field and controlled laboratory environments (Makonya et al. 2019). Heat stress in chickpea also impairs electron transport efficiency and quantum yield, while increasing ion leakage and levels of oxidative stress markers such as malondialdehyde (MDA) and hydrogen peroxide (H_2O_2) (Arslan 2023). Moreover, heat stress disrupts sucrose metabolism, adversely affecting reproductive success and seed quality (Awasthi et al. 2014; Agrawal 2016). Heat stress significantly reduces the activity of key enzymes involved in carbon fixation (RuBisCo) and sucrose synthesis, including sucrose phosphate synthase (SPS) and sucrose synthase (SS), leading to lower sucrose content in leaves (Kaushal et al. 2013). This decline is notably more severe in heat-sensitive genotypes (Kaushal et al. 2013). More recently, Devi et al. (2023b) reported that heat stress significantly restricts leaf sucrose production, negatively affecting seed composition and nutritional quality. Chandel and Sharma (2023) further showed that heat-induced disruptions in sucrose and starch metabolism stem from the downregulation of genes involved in carbohydrate metabolism. By integrating insights of photosynthetic efficiency and carbohydrate metabolism, chickpea breeding programs can more effectively develop heat-resilient cultivars suited to a warming climate.

Stomatal conductance

Stomatal conductance, which regulates gas exchange and water loss, plays a vital role in maintaining plant homeostasis under stress conditions (Diao et al. 2024). Enhancing this trait can significantly improve chickpea resilience to heat stress, thereby contributing to more stable crop yields (Gaur et al. 2013). Effective regulation of stomatal conductance is essential for minimizing water loss while maximizing carbon dioxide uptake—both vital processes for sustaining plant growth under high temperatures (Kumari et al. 2020; Bindra et al. 2021). Genotypes that demonstrate superior stomatal control tend to show enhanced heat tolerance, likely due to their ability to retain higher leaf water content and mitigate heat-induced damage (Bindra et al. 2021). Heat stress induces significant physiological changes in chickpea, particularly affecting stomatal function. This disruption influences water and nutrient balance and reduces photosynthesis, ultimately leading to declines in both seed yield and quality (Devi et al. 2023a; Fig. 1). High temperatures reduce stomatal conductance, which limits CO_2 uptake and photosynthetic efficiency (Kaushal et al. 2013; Devi et al. 2023a, b). Sensitive genotypes experience a more pronounced reduction in stomatal conductance than tolerant ones, resulting in more severe yield losses (Kaushal et al. 2013; Devi et al. 2023b).

Wild chickpea genotypes exhibit greater variation in stomatal conductance under heat stress, indicating their potential utility in breeding programs (Başdemir and Yildirim 2020). Jain (2014) reported that elevated temperatures reduced stomatal conductance by 44.25% compared to normal conditions. Similarly, Bhandari et al. (2020) observed high stomatal conductance (gs) in chickpea genotypes at 40/30 °C (413.4–435.8 mmol m^{-2} s^{-1}), followed by a decline at 42/32 °C (387.6–410.6 units), with genotype-specific variation. Zhou et al. (2020) further demonstrated that rising temperatures lowered intracellular CO_2 concentration (Ci), stomatal conductance (gs), and transpiration rate (E) in genotypes Acc#3 and Acc#8 compared to their respective controls.

Genetic resources for heat tolerance

As heat stress continues to pose a growing challenge to chickpea production, exploring the genetic diversity within its gene pool presents a promising strategy for sustaining yields (Krishnamurthy et al. 2011). Chickpea has evolved several adaptive mechanisms to cope with elevated temperatures, broadly categorized into three strategies: (1) heat escape, which involves phenological shifts such as early flowering and maturity, allowing the crop to complete its life cycle before peak temperatures occur (Kumar and Rao 1996; Kumar and Abbo 2001); (2) heat avoidance, which includes morphological traits like waxy leaf cuticles, increased leaf area, and deeper root systems that reduce water loss and enable access to moisture and nutrients from deeper soil layers (Rani et al. 2020); and (3) heat tolerance, which encompasses physiological and biochemical mechanisms such as heat shock protein accumulation, osmotic adjustment, and enhanced antioxidant activity, all of which help maintain metabolic function during heat stress (Rani et al. 2020).

Extensive screening of chickpea genotypes exposed under field and controlled environments has revealed significant genetic variation in phenological, physiological, and yield-related traits (Fig. 3) (Devi et al. 2022; Jha et al. 2023a, b). Institutions such as the Indian Institute of Pulses Research (Kanpur) and the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) have reported substantial genetic variability in chickpea germplasm for heat-related traits, including stomatal conductance, chlorophyll content, and canopy temperature depression (Krishnamurthy et al. 2011; Upadhyaya et al. 2011; Bhandari et al. 2020; Devi et al. 2022; Jha et al. 2023a). The development of mapping populations such as DCP92-3 × ICCV92944 and ICC15614 × ICC4567 has been pivotal in identifying genes associated with heat resilience (Paul et al. 2018a; Jha et al. 2021a). Several heat-escape genotypes—such as ICC96030 and ICC96029 (Kumar and Rao 1996), ACC316 and

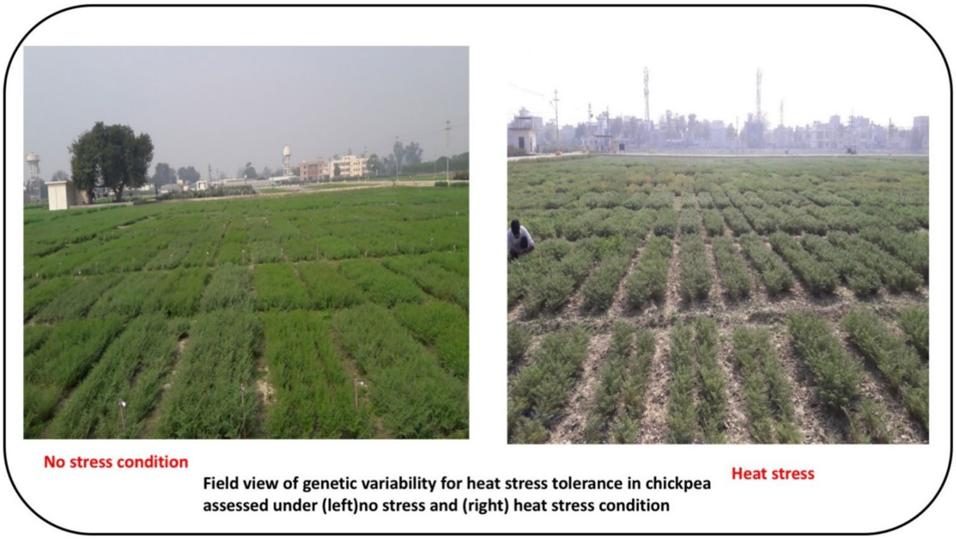


Fig. 3 Field-based screening of chickpea genotypes under non-stress and heat stress conditions

ACC317 (Canci and Toker 2009), ICC14346 (Upadhyaya et al. 2011), and ICCV92944 (Gaur et al. 2012)—exhibit early flowering and improved yield performance under heat stress and have been incorporated into breeding programs to develop early-maturing, heat-resilient cultivars.

Reproductive success is also a key component of heat tolerance, as traits like pollen viability, stigma receptivity, and successful fertilization underpin yield under heat stress (Bhandari et al. 2020). Genotypes such as ICC1205, ICCV92944, and ICC15614 have demonstrated improved reproductive success under heat stress (Devasirvatham et al. 2012a, 2013; Gaur et al. 2012; Bhandari et al. 2020; Fig. 4; Table 1).

Beyond reproductive traits, genotypes have been evaluated for yield-related performance under heat stress, including pod set and seed yield per plant. For instance, genotypes with improved pod set (Canci and Toker 2009; Devi et al. 2022) and higher seed yield (Jumrani and Bhatia 2014; Kumar et al. 2017; Jha et al. 2023a, b) are considered heat-tolerant (Table 1).Various heat tolerance indices have been developed to assist with the selection of such genotypes (Krishnamurthy et al. 2011; Jha et al. 2018b). Promising heat-tolerant lines screened under field conditions include JG130, RVG203, JAKI9218, ICCV07118, ICC1356, GNG1958, ICC15955, and ICC15925 (Jha et al. 2015, 2018b, 2023a, b).

Some landraces and breeding lines also exhibit notable phenotypic plasticity, making them valuable sources of adaptive traits. For example, landraces such as ICC14778 and ICC15618 have shown useful adaptations and are considered important genetic resources for enhancing heat tolerance through breeding (Varshney et al. 2021). Jha et al. (2021d) developed a "*multi-parent advanced generation inter-cross* (MAGIC)" population using eight parental lines

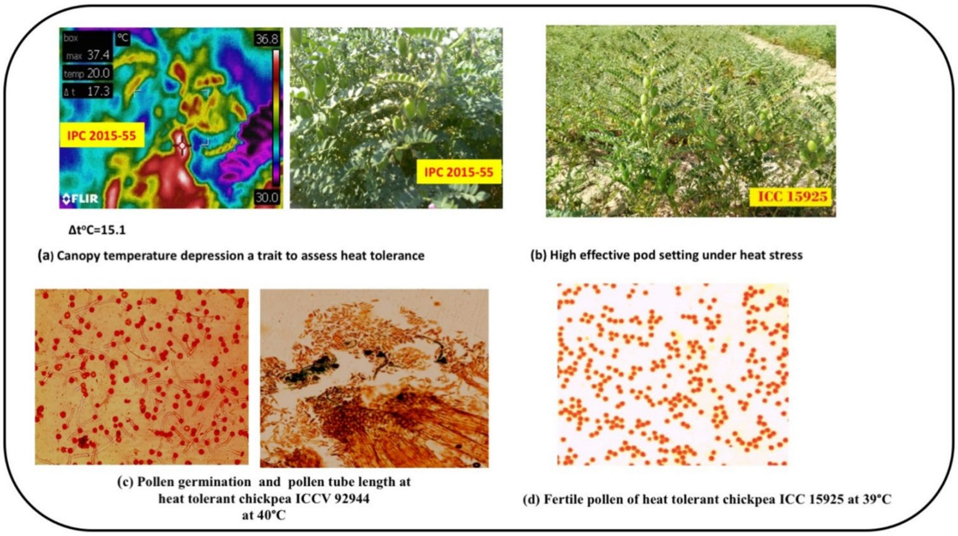


Fig. 4 Screening of heat-tolerant chickpea genotypes based on several physiological traits under heat stress: **a** canopy temperature depression, **b** pollen viability, and (**c**) pod set percentage

Table 1 Potential heat tolerant chickpea genotypes identified in controlled growth chamber and field experiments

Genotype name and their status	Testing environment	Reported from	Basis of tolerance	Reference
ILC 482, Annegiri (released cultivar), ICCV 10 (released cultivar)	Growth chamber; high temperatures (40 and 45 °C)	–	Physiological traits cell membrane stability	Srinivasan et al. (1996)
ACC 316 and ACC 317		Antalya region, Turkey	Early phenology	Canci and Toker (2009)
ICC 1205 (landrace)	Field condition (late sown)	ICRISAT, Hyderabad, India	Reproductive function	Devasirvatham et al. (2010)
ICC 4958, ICC 14778, ICC 1205, ICC 456 (landrace)	Field condition (late sown)	ICRISAT, Hyderabad and Indian Institute of Pulses Research, Kanpur India	Yield trait	Krishnamurthy et al.(2011)
ICC 1205 and ICC 15614 (landrace)	Field condition (late sown)	ICRISAT, Hyderabad, India	Reproductive function	Devasirvatham et al. (2012b, 2013); Gaur et al. (2012);
BG 256 (released cultivar)	Growth chamber (34/20 and 38/22 °C)	Indore, India	Yield traits	Jumrani and Bhatia(2014)
ICC 4958, ICC 92944 (released cultivar), ICC 1205	Field condition (late sown)	Indian Institute of Pulses Research, Kanpur, India	Yield traits	Jha et al.(2015)
RVG 203, RSG 888, JAKI 9218, GNG 469, IPC 06–11 (advanced breeding line)	Field condition (late sown)	Indian Institute of Pulses Research, Kanpur, India	Stress susceptibility index	Jha et al.(2018b)
JAKI 9218 (released cultivar)	Field condition (late sown)	Indian Institute of Pulses Research, Kanpur, India	Yield trait	Jha et al.(2019b)
ICC 14778, ICC 15618 (landrace)	Field condition (late sown)	ICRISAT, Hyderabad, India		Varshney et al.(2019)
ICCVO7110,and ICCV92944 (released cultivar)	Growth chamber (35/25, 38/28, 40/30, and 42/32 °C; day/night)	Panjab University, Chandigarh, India	Physiological, yield, and reproductive function traits	Bhandari et al.(2020)
DZ-Cr-0034	Field condition(late sown)	ICRISAT, Hyderabad, India and Debre Zeit, Ethiopia	Phenological and yield traits	Getahun et al.(2021)
GNG2171, GNG1969, GNG1488, PantG186, CSJ515, RSG888, RSG945, RVG202, and GNG469 (released cultivar)	Growth chamber (> 32/20 °C)	Panjab University, Chandigarh, India	Physiological and yield trait	Devi et al.(2022)
JG74, JAKI9218, Pusa 547, GNG1958, RVG202, RSG11, RSG931, RSG10, GG2, and Pusa240 (released cultivar)	Field condition (late sown)	Indian Institute of Pulses Research, Kanpur, India	Yield trait	Jha et al.(2023a)
ICC15925	Field condition (late sown)	Indian Institute of Pulses Research, Kanpur, India	Yield trait	Jha et al.(2023b)
ICC 9590, ICC 1194, ICC 1205, ICC 1915, ICC 2629, ICC 6537	Field condition (late sown)	Indian Institute of Pulses Research, Kanpur India	Yield traits	Mohanty et al.(2024b)

Modified and updated Jha et al.(2022)

to broaden the genetic base and recover novel drought and heat tolerance alleles. These efforts deepen our understanding of heat tolerance's physiological and genetic bases and provide a strong foundation for developing heat-resilient, high-yielding chickpea varieties.

Chickpea crop wild relatives (CWRs) represent an underutilized reservoir of genetic diversity, offering novel genes and quantitative trait loci (QTLs) associated with abiotic stress resilience, including heat tolerance (Mohanty et al. 2022). Having evolved under harsh environmental conditions, these wild relatives possess unique adaptations that can be harnessed and introduced into cultivated chickpea through targeted breeding programs. For example, *Cicer reticulatum* (ILWC 292) has been integrated into breeding programs targeting heat tolerance, with mapping populations demonstrating significant genetic variation in phenology and yield under stress (Kushwah et al. 2021). Similarly, *Cicer turcicum* exhibits valuable traits such as an improved pod-to-plant ratio under heat stress (Toker et al. 2021). These findings underscore the potential of CWRs to contribute valuable traits to cultivated lines. Harnessing the genetic variability in chickpea gene and genes associated with heat stress tolerance banks could help identify novel alleles, thereby accelerating the development of climate-resilient chickpea varieties and promoting sustainable agricultural production.

Genetics and genomics for heat stress tolerance in chickpea

Heat stress tolerance in chickpea is a complex trait governed by multiple genes and strongly influenced by genotype × environment interactions. A classical breeding study involving a diallel analysis of six parental lines highlighted both additive and non-additive genetic variances, underscoring the intricate genetic architecture of this trait (Jha et al. 2019a). These findings suggest that both gene actions play an important role in the inheritance of heat stress tolerance, offering valuable insights for guiding breeding programs.

Due to the polygenic nature of heat tolerance and the considerable influence of environmental interactions, several biparental mapping populations have been developed to dissect its genetic basis (Paul et al. 2018a; Jha et al. 2021b; Kushwah et al. 2021). These populations have been phenotyped for physiological and yield-related traits under heat stress and genotyped using molecular markers, such as simple sequence repeats (SSRs) (Jha et al. 2018a, 2021a). For instance, genotyping the F_2 mapping population derived from the DCP92-3 × ICCV92944 cross with 78 SSR markers revealed a major QTL for chlorophyll content (CHL) on linkage group 6 (LG6), accounting for 17.2% of the phenotypic variation (PV) (Jha et al. 2021b).

The advent of high-throughput SNP markers has identified additional QTLs for traits such as days to first flower, podding, and maturity, chlorophyll content, NDVI, and cell membrane stability (Jha et al. 2021c). Moreover, QTLs associated with yield-related traits—including pods per plant, seed yield, 100-seed weight, and total biomass—have also been mapped (Paul et al. 2018b; Jha et al. 2021c; Kushwah et al. 2021) (see Table 2).

Phenotyping RILs from the ICC4567 × ICC15614 cross under heat stress identified four major yield-related QTLs on CaLG5 (*qfpod02_5, qts02_5, qgy02_5*, and *q%podset06_5*) and three QTLs on CaLG6 (*qfpod03_6, qgy03_6*, and *q%podset08_6*), explaining 3.92–16.56% of the PV (Paul et al. 2018b) (Table 2). These regions contained 25 candidate genes. A comprehensive phenotyping study of the DCP92-3 × ICCV92944 population across two seasons identified 37 major and 40 minor QTLs (Jha et al. 2021c). Notably, a major QTL for days to podding explained 30% of the PV, while other significant regions associated with 100-seed weight and nitrogen balance index explained over 10% each on CaLG07 (Jha et al. 2021c). These identified QTLs harboured 32 candidate genes, many encoding heat shock proteins and transcription factors integral to heat tolerance mechanisms (Jha et al. 2021c). Given the quantitative nature of heat tolerance and its strong dependence on environmental factors, multi-location evaluations are essential to identify stable QTL(s). For instance, phenotyping the GPF2 × ILWC292 population using ddRAD-Seq-based SNP markers revealed 28 QTLs in Ludhiana and 23 in Faridkot (Punjab, India) for traits such as germination, flowering time, membrane permeability, and yield (Kushwah et al. 2021). Thirteen of these QTLs were consistent across both locations, confirming their relevance to heat tolerance.

GWAS approach provides insights into genomic regions associated with heat tolerance

To overcome the limitations of biparental QTL mapping, advances in next-generation sequencing (NGS) and high-density SNP genotyping have made GWAS a powerful approach for identifying novel alleles, genes, and QTLs linked to complex agronomic traits in large germplasm collections (Huang and Han 2014). GWAS identifies associations between genomic variants and target phenotype using statistical models. Jha et al. (2021a) performed a GWAS on 182 chickpea genotypes, identifying 17 marker-trait associations (MTAs) for phenological and physiological traits and 34 MTAs for yield traits under heat stress over 2 years. Using SNPs derived from WGRS of chickpea facilitated the identification of MTAs distributed across the entire genome, including those linked to heat tolerance. More recently, Mohanty et al. (2024a) combined QTL-seq and GWAS on 217 chickpea accessions, pinpointing a major 156.8 kb genomic region harbouring *CaHSFA5* and reactive oxygen species (ROS)-related candidate genes associated with heat stress tolerance. In a follow-up study, Mohanty et al. (2024b) employed 97,454 high-quality SNPs to detect five significant MTAs for harvest index and one each for seed number per plant, 100-seed weight, pod number per plant, and NDVI. These MTAs explained 7.5–20% of the PV, and key candidate genes identified included *RAD23b*, *CIPK25*, *AAE19, CK1*, and *WRKY40*.

Table 2 List of QTLs/ gene(s) contributing to heat tolerance in chickpea

Trait	Mapping Population	Type of population	Population size	Genes/QTLs	Linked marker	LG	Phenotypic variation %	References
Filled pods per plot	ICC 4567	Bi-parental, RIL	292	*qfpod02_5, qts02_5, qgy02_5,*	*Ca5_44667768* and	CaLG05 and	4–16	Paul et al. (2018a)
total number of	×ICC 15614			*and q%podset06_5*	*Ca5_46955940*	CaLG06		
seeds per plot				*qvs05_6, qfpod03_6,*	*Ca6_7846335-Ca6_14353624*			
grain yield per plot				*qgy03_6, q%podset08_6*				
pod setting percentage								
Days to germination, days to	GPF 2			13 consensus QTLs		CaLG1,2,4,6	5.7–11.3	Kushwah et al.(2021)
flower initiation, days to	×ILWC292	Bi-parental, RIL	187	*qdg-02,qdg-03,qdfi-01,*	(CNC_021165.1.18056125,	and 7		
				qdfi-02,qdff-01,qdff-03, *qdff-04,qdhf-01,* *qdhf-03,qdhf-04,* *qph-01,qyld-01,qmpi-01,*	CNC_021165.1.513774), (CNC_021166.1.28474588, CNC_021166.1.8118822), (CNC_021160.1.35885685, CNC_021160.1.8023246), (CNC_021163.1.11351378, CNC_021163.1.11351447), (CNC_021160.1.35885685, CNC_021160.1.8023246), (CNC_021163.1.11351378, CNC_021163.1.11351447), (CNC_021165.1.18056125, CNC_021165.1.513774) (CNC_021160.1.35885685, CNC_021160.1.80232460 (CNC_021163.1.13462111, CNC_021163.1.11351378) (CNC_021163.1.48163277, CNC_021163.1.48245021) (CNC_021161.1.31430073, CNC_021161.1.9956999), (CNC_021161.1.31430073, CNC_021161.1.9956999), CNC_021161.1.3663690, CNC_021161.1.31430073), Single nucleotide polymorphism (SNP)			
Phenological, physiological		GWAS	182	17 and 34 significant marker trait associations	ICCM0297, NCPGR150,			Jha et al. (2021a)
and yield-related traits					TAA160 and NCPGR156			
Primary branch number	DCP92-3×	Bi-parental	206		-	CaLG03	2–17.2	Jha et al. (2021b)
chlorophyll content	ICCV92944					and CaLG06		
50% flowering, days to 100%	DCP92-3×	Bi-parental, RIL	184	37 major and 40 minor	(SCA1_888,SCA1_30956998),	CaLG01-	10–39.3	Jha et al. (2021c)

Table 2 (continued)

Trait	Mapping Population	Type of population	Population size	Genes/QTLs	Linked marker	LG	Phenotypic variation %	References
flowering, plant height,	ICCV92944			*CaDM_LS1.1,CaDM_LS1.3,*	(SCA1_11502160, SCA1_19572921),	CaLG08		
grain yield,				*CaCMS_NS4.1,*	(SCA4_48720031, SCA4_11271232),	except CaLG07		
membrane permeability				*CaNBI_LS8.3,CaNBI_LS8.2, CaNBI_LS7.2,*	(SCA8_11012719, SCA8_6301805),			
index				*CaNDVI_LS2.1,CaNDVI_LS2.1, CaDPI_LS7.2,*	(SCA8_6301805, SCA8_15284963),			
				CaDPF_LS8.1, Ca100SW_LS7.1, CaSYPP_LS2.1,	(SCA7_47907019, SCA7_9555338),			
				CaSYPP_LS6.1,CaBYPP_LS6.5	(SCA2_31975221, SCA2_8484804),			
					(SCA2_31975221, SCA2_8484804),			
					(SCA7_47907019, SCA7_9555338),			
					(SCA8_1742959,SCA8_3665619),			
					(SCA7_47907019, SCA7_9555338),			
					(SCA2_22704770, SCA2_35770691)			
					(SCA6_35796441, SCA6_2512179),			
					(SCA6_7929647,SCA6_7939281)			
Abiotic tolerance index,	CDC Leader ×	Bi-parental	195	19 significant MTAs	*Ca2_34600347, SNP*	CaLG3 and 4		Kalve et al. (2022)
Tolerance index	*C. reticulatum,*							
stress suceptibility index,	CDC Consul ×							
mean productivity,	*C. reticulatum,*							
and seed yield under stress								
Phenology and yield traits		GWAS		*RAD23b*, *CIPK25*,				Mohanty et al. (2024b)
				AAE19, CK1 and WRKY40				
Phenological, physiological				six Meta-QTL regions		CaLG01		Kumar et al. (2023)
and yield-related traits				*Pollen receptor-like kinase 3 (CaPRK3),*		and CaLG06		
				Flowering-promoting factor 1				
				Flowering Locus C (CaFLC),				
				Heat stress transcription factor A-5 (CaHsfsA5)				
				Pollen-specific leucine-rich repeat extensins				
				(CaLRXs)				
Cell membrane stability	DCP92-3 ×	Bi-parental	206	*CaqHT6.1, CaHSFA5*		CaLG06	15.30%	Mohanty et al. (2024a)
and pods/plant	ICCV92944	GWAS	217	*Ca_08536*				

Table 2 (continued)

Trait	Mapping Population	Type of population	Population size	Genes/QTLs	Linked marker	LG	Phenotypic variation %	References
Yield and yield related traits		GWAS	153	27 significant MTAs	Ca3:37,444,451, SNP			Danakumara et al.(2024)
				indole-3-acetic acid–amido synthetase GH3.1				
				aspartic proteinase				
Yield, seed size, time to flowering, time to maturity, and final canopy closure		GWAS	148	Fourteen QTL	Diversity Arrays Technology			Jeffery et al. (2024)

RIL = recombinant line, GWAS = genome wide association study

Similarly, Danakumara et al. (2024) conducted a GWAS on 153 chickpea genotypes across three locations over 2 years, identifying 27 MTAs for yield-related traits under heat stress (Table 2). In silico analysis revealed associations with important candidate genes, such as *indole-3-acetic acid amido synthetase GH3.1* and *pentatricopeptide repeat-containing protein* genes, implicated in heat tolerance mechanisms. Beyond yield-related traits, Jeffery et al. (2024) identified 14 QTLs related to days to flowering, days to maturity, and final canopy closure in a GWAS on 148 chickpea genotypes under heat stress over three years at two locations. However, the detected QTLs were distributed across different chromosomal regions and lacked consistency and stability across environments.

The meta-QTL approach can identify more stable, consistent, and precise QTLs (Goffinet and Gerber 2000; Soriano et al. 2021). Using this method, Kumar et al. (2023) identified meta-QTLs on CaLG01 and CaLG06 for traits such as days to flowering, podding, and maturity, leaf chlorophyll content, filled pods per plant, seed yield per plant, and plant biomass. Several key candidate genes were found within these regions, including the heat stress transcription factor *CaHsfsA5* and pollen-specific leucine-rich repeat extensins (*CaLRXs*), which play important roles in heat stress tolerance (Kumar et al. 2023).

Genes responsible for heat tolerance in chickpea

Recent advances in omics technologies—such as QTL mapping, transcriptome profiling, and genome-wide association studies (GWAS)—have greatly enhanced our understanding of the genomic regions and variants associated with heat stress tolerance in chickpea. These tools offer critical insights into the genetic mechanisms underlying the heat stress response and present promising opportunities for developing improved breeding strategies to enhance thermotolerance. Globally, there is increasing interest in identifying candidate genes and quantifying the genetic variation that contributes to heat tolerance in crop species.

Plants exhibit various responses to high temperatures, manifesting as visible symptoms and measurable changes in growth and morphology. One of the early impacts of heat stress is the alteration of membrane fluidity, which activates calcium (Ca^{2+}) channels, resulting in an influx of Ca^{2+} ions into the cytosol (Kang et al. 2023). This increase in cytosolic calcium acts as a secondary messenger and is detected by sensor molecules such as calmodulin (CaM) and calcium-dependent protein kinases (Kang et al. 2023). These sensors initiate downstream signaling cascades that activate various stress-responsive genes and physiological responses essential for plant adaptation to high-temperature conditions (Huang et al. 2022). The regulatory networks triggered by heat stress involve genes associated with protein and RNA stability, signal transduction, molecular transport, and antioxidant defense. Multi-omics studies have helped uncover several key genes within these networks. Among these, heat stress transcription factors (*Hsfs*) are key regulators of thermotolerance, operating at the terminal stage of the heat stress signaling pathway (Chidambaranathan et al. 2018). *Hsfs* play a crucial role in inducing the expression of heat-responsive genes, particularly those encoding heat shock proteins (HSPs), which act as molecular chaperones and are conserved across a wide range of plant species, including chickpea (Vierling 1991; Liu et al. 2024).

HSPs represent an ancient and evolutionarily conserved family of proteins found in all domains of life—Archaea, Bacteria, and Eukarya—underscoring their fundamental role in cellular protection (Waters 2013). Despite sequence diversity, HSPs share common structural features, typically forming oligomeric complexes with a β-sandwich architecture (Waters 2013).

In chickpea, various transcription factors are vital in modulating the heat stress response. These include members of the *HSF, bHLH, ERF, WRKY*, and *MYB* families, which regulate gene expression to support adaptive responses under elevated temperatures (Kudapa et al. 2023). Among these, the *AP2/ERF* superfamily stands out for its well-established role in mediating responses to biotic and abiotic stresses. Notably, the ethylene-responsive transcription factor *CarERF116* has been identified as a key gene contributing to abiotic stress tolerance in chickpea, playing a significant role in improving stress resilience (Deokar et al. 2015; Kudapa et al. 2023). These transcriptional regulators operate within complex, hormone-driven signaling networks involving ethylene, abscisic acid (ABA), jasmonates, salicylic acid, auxin, cytokinins, gibberellins, and brassinosteroids. These networks collectively fine-tune the plant's physiological and molecular responses to environmental stressors, including high temperatures.

Potential of the chickpea genome, pangenome, and WGRS for identifying heat-tolerant genomic regions

Advancements in NGS technologies have enabled the assembly of the chickpea genome, with the kabuli-type genome estimated at 738 Mb (Varshney et al. 2013) and the desi-type genome approximately 740 Mb (Jain et al. 2013). In addition, Gupta et al. (2017) sequenced the genome of *C. reticulatum*, the closest wild relative of chickpea. To harness the genetic diversity preserved in global gene banks—particularly for breeding-relevant traits such as heat stress tolerance—Varshney et al. (2019, 2021) conducted WGRS of 429 and later 3,366 chickpea accessions. These large-scale studies uncovered several structural variants and presence/absence variations (PAVs), including key candidate genes associated with heat stress tolerance, such as *TIC*, *REF6*, aspartic protease, *cc-NBS-LRR*, and *RGA3*.

Further building on this work, Varshney et al. (2021) and Khan et al. (2024) assembled the chickpea pangenome to capture genome variation across *Cicer* species. These comprehensive genomic resources have significantly improved our understanding of structural variants, PAVs, and copy number variations, which are crucial for identifying genomic regions associated with key agronomic traits, including thermotolerance.

Functional genomics

Advances in functional genomics, particularly RNA-sequencing (RNA-seq), have revolutionized transcriptomic analyses, enabling the identification of candidate genes involved in complex traits such as heat stress tolerance (Agarwal et al. 2016; Kudapa et al. 2023). RNA-seq studies conducted on heat-treated leaf, root, and flower tissues from heat-tolerant (ICCV 92944, ICC 1356, ICC 15614) and heat-sensitive (ICC 5912, ICC 4567, ICC 10685) chickpea genotypes identified several heat-responsive genes, including two DREB genes (*Ca_02170* and *Ca_16631*) and three HSP90 genes (*Ca_23016, Ca_09743*, and *Ca_25602*) (Agarwal et al. 2016) (Table 3).

A comprehensive transcriptome analysis of 48 samples from the same genotypes identified 14,544 differentially expressed genes associated with key processes such as photosynthesis, metabolism, calcium signaling, and cell wall remodeling (Kudapa et al. 2023). Several transcription factors, including MYB (*Ca_18699*), *WRKY, bHLH,* and *ERF* (*Ca_00326, Ca_01683*, and *Ca_15022*), also showed differential expression under heat stress. Among these, HSPs, particularly HSP90s, function as molecular chaperones that facilitate protein folding and repair during abiotic stress (Ticha et al. 2020). Quantitative real-time PCR (qRT-PCR) analyses of *kabuli* and *desi* chickpea varieties demonstrated that selected heat shock transcription factors (HSFs), HSPs, and associated miRNAs exhibit distinct expression patterns under drought and heat stress. Notably, most *CaHsf* and *CaHsp* genes showed strong differential expression in response to combined drought priming and heat stress treatments (Juneja et al. 2023). Furthermore, whole-genome transcriptomic analysis of the *HSP20* gene family identified 21 *CaHSP20* genes distributed across seven chromosomes. Promoter analysis indicated that these genes possess multiple *cis*-acting elements involved in biotic and abiotic stress responses (Liu et al. 2024).

The importance of HSPs in abiotic stress tolerance has been documented in other crops. For example, overexpression of *GmHsp90* from soybean significantly improved the detrimental impact of abiotic stress in *Arabidopsis thaliana* (Xu et al. 2013), while increased expression of *PpHSP70* in rice conferred enhanced resilience to both heat and drought stress (Kou et al. 2023).

Non-coding RNAs, including small-interfering RNAs (siRNAs), microRNAs (miRNAs), and long-non-coding RNAs (lncRNAs), also contribute toheat and cold stress tolerance by regulating chromatin structure, transcription, histones, and post-translational processes (Jha et al. 2020, 2023c). RNA-seq analysis of heat-treated tissues from tolerant (ICC 1356, ICC 15614) and sensitive (ICC

Table 3 List of candidate gene(s) with putative function elucidated through functional annotation

Genotype	Candidate gene(s)	Function	Tissue type used	Validation approach	References
ICC 15614, ICC 1356, and ICC 92944	*Ca_25811, Ca_23016,*	HSP90 proteins	Leaves and flowers	RNA-seq	Agarwal et al. (2016)
ICC 5912, ICC 4567, and ICC 10685	*Ca_09743, Ca_17680 and Ca_25602,*		Root tissues	qRT-PCR	Agarwal et al. (2016)
–	*CarHSFB2*	Controlling heat stress response	Seedlings	–	Ma et al. (2016)
ICCV92944 and ICC16374	acetyl-CoA carboxylase, pyrroline-5-carboxylate synthase (P5CS), ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO), phenylalanine ammonia-lyase (PAL) 2, ATP synthase, glycosyltransferase, sucrose synthase and late embryogenesis abundant (LEA) proteins	Expression of these proteins showed positively related to heat stress tolerance	Reproductive stage	qRT-PCR	Parankusam et al. (2017)
–	*CarHsfA2, A6, and B2; CarHsfA2, A6a, A6c, B2a*	Transcription factors controlling heat stress response	Seedling stage and pod development	Q-PCR expression	Chidambaranathan et al. (2018)
Acc#7 and Acc#8	sucrose-phosphate synthase, sucrose-phosphate phosphatase, HSP70, ribulose bisphosphate carboxylase / oxygenase activase, plastocyanin and protoporphyrinogen oxidase,	Up regulation in tolerant genotype	Flowering stage		Makonya et al. (2021)
ICC 1356, ICC 15614; one sensitive- ICC 4567	894 putative lincRNAs and 61,110 mRNAs *HsfA4A* (TCONS_00046766), *HsfA5* (TCONS_00052321), class II small HSP (sHSP, TCONS_00039852), *heavy metal* ATPase (TCONS_00052630, TCONS_00052631, and TCONS_00052633), F-box protein-encoding mRNAs (TCONS_00039602, TCONS_00039604)	–	Leaf and root tissues	qRT-PCR	Bhogireddy et al. (2023)
PBG1 and PBG5	3 *Hsfs*, 4 *sHsps*, 1 *Hsp70*, 1*Hsp90* and 1 Hsp100 targeting miR156, miR166, miR319, miR171 and miR5213	Up regulated in tolerant genotype	All growth and development stage	qPCR	Juneja et al.(2023)

Table 3 (continued)

Genotype	Candidate gene(s)	Function	Tissue type used	Validation approach	References
ICCV 92944, ICC 1356, and ICC 15614	3,811 heat stress-responsive DEGs	Encodes heat shock proteins, encoding receptor-like kinase, encodes major intrinsic (MIP) family transporter, encodes ABC transporter	Leaf and root tissues	–	Kudapa et al. (2023)
ICC 5912, ICC 4567, and ICC 10685	*Ca_13061, Ca_14916, Ca_18632, Ca_20147*	Encodes leucine-rich repeats (LRR) receptor-like kinase			
-	Twenty-one *HSP20* genes including *CaHSP20-17, CaHSP20-20, CaHSP20-7, CaHSP20-3*, and *CaHSP20-12*	Up regulation except CaHSP20-5	root, mature leaf, young leaf, flower, seed	qRT-PCR	Liu et al. (2024)
F2:3 population developed from DCP92-3 × ICCV92944	*CaHSFA5*	ROS homeostasis related to heat stress	Leaf tissues	qRT-PCR	Mohanty et al. (2024a)
–	*RAD23b, CIPK25, AAE19, CK1*, and *WRKY40*	ROS homeostasis related to heat stress	Leaf tissue	qRT-PCR	Mohanty et al. (2024b)

4567) chickpea genotypes identified 894 putative long intergenic non-coding RNAs (lincRNAs), along with 613 cis-regulated targets and 61,110 mRNAs (Bhogireddy et al. 2023) (Table 3). Co-expression analysis linked these lincRNAs to regulatory pathways involving genes encoding *HSF, bHLH, NAC, MYB, C2H2, ERF, late embryogenesis abundant (LEA)* proteins*, TPP, chloride channels,* and *erythronate-4-phosphate dehydrogenase* (Bhogireddy et al. 2023). Some lincRNAs were also associated with starch and sucrose metabolism pathways in leaves under heat stress (Bhogireddy et al. 2023).

More recently, Mohanty et al. (2024a) identified a 156.8 kb QTL region using NGS-based QTL-seq analysis, highlighting *CaHSFA5* as a key candidate gene. Expression profiling suggested that interactions between *CaHSFA5* and a ROS-scavenging gene may play a pivotal role in mediating heat stress tolerance in chickpea. Ongoing advances in functional genomics, particularly those exploring lncRNA–target gene interactions, are expected to deepen our understanding of the molecular mechanisms governing thermotolerance in chickpea.

Proteomics and metabolomics insights

Heat stress in plants leads to protein misfolding, triggering a heat shock response that prevents the aggregation of heat-sensitive proteins. This response involves the induction of various heat-responsive proteins, including HSFs, signaling proteins, metabolic enzymes, and molecular chaperones such as HSPs (Pandey et al. 2024). Plant thermotolerance is governed by transcriptional networks that offer short-term protection through chaperone activation and long-term adaptation via chromatin remodeling. Additionally, heat stress alters the fluidity of the plasma membrane, initiating heat-sensing signals and activating calcium ion channels. Proteomic analyses have been used widely to investigate changes in protein expression under heat stress, offering insights into the underlying molecular responses. For example, a proteomic study by Parankusam et al. (2017) on two contrasting genotypes, JG14 (heat-tolerant) and ICC4567 (heat-sensitive), identified 482 heat-responsive proteins. Key proteins associated with heat tolerance in JG14 included sucrose synthase, LEA protein, acetyl-CoA carboxylase, glycosyltransferase, and pyrroline-5-carboxylate synthase. Pathway analysis highlighted the role of osmoprotectants, antioxidants, amino acid biosynthesis, and hormone signaling in conferring thermotolerance (Parankusam et al. 2017). Similarly, comparative proteomic profiling of Acc#7 (heat-tolerant) and Acc#8 (heat-sensitive) revealed differential expression of proteins such as SPS, sucrose phosphate phosphatase, ribulose bisphosphate carboxylase/oxygenase activase, HSP70, plastocyanin, and protoporphyrinogen oxidase, particularly during the flowering stage (Makonya et al. 2021).

Heat stress also activates complex signaling pathways and molecular networks that produce diverse metabolites, aiding plant acclimation. Metabolomics provides a comprehensive view of these biochemical changes. For instance, Pareek et al. (2019) identified 49 heat-responsive metabolites in the tolerant genotype ICC1205, including polycarboxylic acids, sugar acids, sugar alcohols, and amino acids, contributing to thermotolerance. Similarly, Devi et al. (2023b) reported significant changes in seed nutritional content, such as carbohydrates, proteins, fats, and minerals, under heat stress. Leaf sucrose levels and sucrose synthase activity, both influenced by heat, also play key roles in the chickpea heat stress response (Chandel and Sharma 2023; Devi et al. 2023b).

Despite its promise, metabolomics remains underutilized in chickpea heat stress research. Broader and more integrated metabolomic studies are needed to unravel the complex metabolic pathways involved in heat stress resilience, offering valuable insights for improving chickpea thermotolerance.

Gene editing to understand heat stress tolerance in chickpea

Chickpea breeders have adopted various strategies to develop stress-tolerant cultivars, including conventional, mutation, and molecular breeding approaches (Gaur et al. 2018; Bharadwaj et al. 2021; Laxuman et al. 2024). Advances in functional genomics have identified key genes associated with heat stress tolerance (Jha et al. 2021c; Liu et al. 2024). For instance, integrated genomic approaches have identified candidate genes such as *CaHSFA5* and its natural alleles (Mohanty et al. 2024a) and *CaHSP20* (Liu et al. 2024), which play crucial roles in chickpea growth and adaptation to high temperatures. Several transcription factors, including *bHLH, ERF, WRKY*, and *MYB*, have also been identified as heat-regulated, exhibiting differential expression between heat-tolerant and heat-sensitive genotypes (Kudapa et al. 2023). These discoveries offer promising targets for genome editing to enhance thermotolerance (Singh et al. 2023).

Genome editing technologies have revolutionized precise gene modification in plants, particularly with the emergence of the CRISPR (clustered, regularly interspaced short palindromic repeats)/Cas system.Compared to earlier tools like zinc-finger nucleases and transcription activator-like effector nucleases (TALENs), CRISPR/Cas is simpler (Bhuyan et al. 2023), relying only on a guide RNA and the Cas9 enzyme.CRISPR has already been employed successfully in crops such as rice and tomato to enhance heat stress tolerance (Yin et al. 2018; Liu et al. 2024). However, its application in chickpea remains in the early stages. Challenges such aslow DNA uptake, poor tissue regeneration, limited in vitro rooting, low transformation efficiency, limited regeneration capacity, and weak transmission of edits to subsequent generations hinder broader adoption (Das Bhowmik et al. 2019; Nivya and Shah 2023). Despite these barriers, progress has been maded in developing a stable CRISPR/Cas9-based genome editing system for chickpea (Ganguly et al. 2020; Gupta et al. 2023). For instance, successful editing has been achieved in drought-related genes such as *4CL* and *RVE7*, with higher efficiency observed for *RVE7* (Badhan et al. 2021).

The CRISPR-Cas system, especially Cas9, has also been engineered for advanced applications beyond conventional genome editing. These include disabling nuclease activity, fusing Cas to effector domains, or altering protospacer adjacent motif (PAM) specificity to broaden targeting potential (Huang and Puchta 2021). Among recent innovations, base editing has emerged as a powerful tool, enabling precise single-nucleotide substitutions without inducing double-stranded breaks or requiring donor templates. This method offers up to 100-fold greater efficiency than traditional homology-directed repair (Biswas et al. 2022). Cytosine and adenine base editors facilitate targeted C-to-T and A-to-G substitutions, respectively, and have demonstrated high efficiency in crops like rice, wheat, and maize (Biswas et al. 2022). Prime editing, which combines Cas9 nickase, reverse transcriptase, and guide RNA, further expands the range of possible DNA modifications,with reported efficiencies of up to 17% in crops (Lin et al. 2021). However, these technologies still require optimization in legumes such as chickpea.

Integrating genome editing with other disciplines—including plant breeding, genomics, proteomics, metabolomics, phenomics, and systems biology—will be key to accelerating the development of heat-resilient chickpea cultivars. Such interdisciplinary efforts are vital for addressing the challenges of climate change and ensuring global food security (Fig. 5).

Scope and progress of high-throughput phenotyping for heat stress response in chickpea

Despite significant advances over the past two decades in assembling the chickpea genome and pangenome, phenotyping complex traits such as heat stress response remains a key bottleneck. Accurate phenotyping of heat-related traits is critical for understanding genotype × environment interactions and advancing breeding efforts to develop heat-tolerant chickpea genotypes. Recent innovations in HTP technologies using automated UAVs (Fu et al.2024), fluorescence imaging (Pineda et al. 2020), 3D laser imaging (Harandi et al. 2023), thermal infrared imaging (Wen et al. 2023),

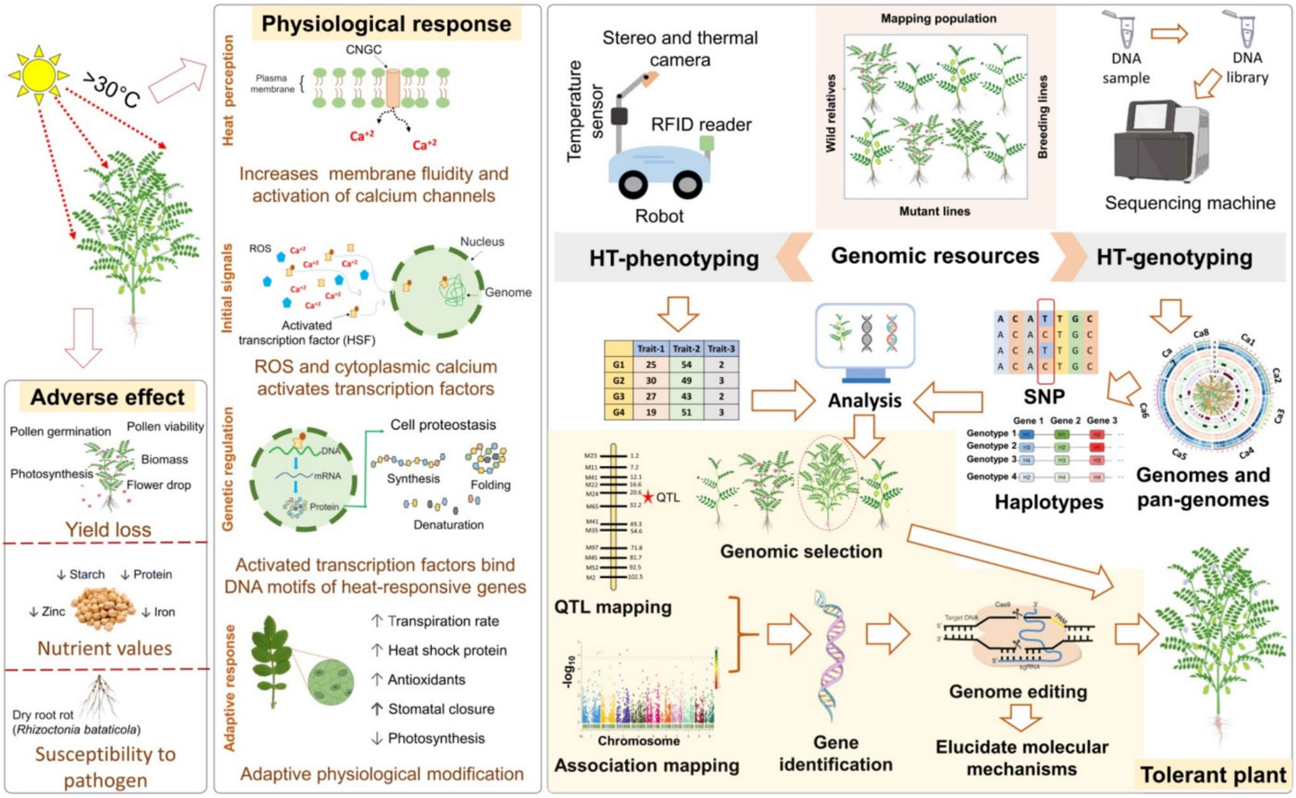


Fig. 5 Overview of heat stress responses in chickpea and integration of high-throughput phenotyping and genomics for cultivar improvement**.** Heat signals perceived at the plasma membrane trigger secondary messengers such as calcium ions (Ca^{2+}) and reactive oxygen species (ROS), activating transcription factors that regulate heat-responsive genes. High-throughput sequencing identifies genomic variants, including SNPs and haplotypes, contributing to reference and pan-genome development. Advanced phenotyping technologies—such as thermal and stereo imaging, ground-based vehicles, and RFID-based systems—provide precise trait data. These data support genomic approaches like trait mapping and genomic selection, facilitating the discovery of key genes and loci associated with heat tolerance in chickpea

magnetic resonance imaging (Blystone et al. 2024), and advanced image processing tools (Li et al. 2020) are beginning to transform the phenotyping of complex traits (Bian et al. 2022; Tanaka et al. 2024). These technologies provide high-throughput, precise, and non-destructive methods for capturing plant traits, enabling rapid and detailed measurements across large populations (Zhang et al. 2023). Moreover, the evolution of UAV and sensor technologies has resulted inincreasingly versatile, commercially available imaging platforms used in phenotyping applications.

In chickpea, UAVs equipped with integrated RGB cameras have proven effective in estimating leaf area index, biomass, and yield (Avneri et al. 2023; Pappula-Reddy et al. 2024), confirming their utility for monitoring crop growth. Specifically, UAVs equipped with multispectral sensors, integrating visible and near-infrared bands, are widely used to assess biophysical parameters in field crops, including chickpea (Zhang et al. 2025). These multispectral platforms are valuable for monitoring traits that reflect plant stress. While single optical sensors on UAVs offer general insights into crop status, using multiple sensors covering broader spectral ranges provides more detailed and accurate assessments of plant responses to biotic and abiotic stresses (Chakhvashvili et al. 2024). Combining multispectral or hyperspectral sensors with thermal infrared sensors enhances spectral coverage and allows early stress detection. For instance, monitoring canopy or leaf temperature can reveal changes in stomatal conductance within minutes or hours, offering real-time indicators of plant stress (Graf et al. 2021).

In chickpea, heat stress leads to membrane damage and decreased stomatal conductance, leaf water content, chlorophyll concentration, fluorescence, and photosynthetic efficiency (Devi et al. 2023b). These parameters are promising indicators of heat stress. Integrating visible and near-infrared data enables the analysis of pigment-related responses, such as chlorophylls, carotenoids, and anthocyanins—critical components of photosynthesis and primary productivity (Chakhvashvili et al. 2024). Combining different spectral resolutions and sensor types further improves stress detection accuracy.

Integrating machine learning and deep learning techniques with HTP platforms is gaining momentum because they can analyze complex datasets and improve post-processing of thermal images, enhancing throughput (Solimani et al. 2023). Machine learning algorithms—such as random forests, multivariate linear regression, and gradient boosting—have been used to correlate thermal data with environmental factors like temperature, solar radiation, and humidity, helping to quantify stomatal responses to heat stress (Marchin et al. 2022; Pignon et al. 2021). Deep learning models, including "convolutional neural networks", "deep neural networks", and "recurrent neural networks", are increasingly used to interpret large phenotypic datasets (Murphy et al. 2024). These AI-based models identify complex patterns and link phenotypic traits to underlying genetic factors related to heat tolerance, enabling more efficient selection of heat-resilient lines (Sheikh et al. 2024). While HTP tools are extensively applied to study heat stress in other crops, their use in chickpea remains relatively limited. Broader adoption of HTP platforms in chickpea breeding programs would enable rapid screening of diverse germplasm and early-stage identification of heat-tolerant genotypes, expediting the development of climate-resilient chickpea cultivars.

Challenges and gaps

The limited availability of heat-tolerant chickpea genotypes continues to constrain the development of cultivars suited to high-temperature environments. There is an urgent need to broaden the genetic base of chickpea by systematically exploiting underutilized global germplasm for large-scale screening under heat stress conditions to identify heat-tolerant genotypes. In particular, chickpea wild relatives and landraces, which harbor novel alleles and genetic variants associated with adaptive traits, offer promising sources of heat tolerance. Incorporating these genetic resources into breeding programs could facilitate the development of climate-resilient, heat-adapted, and sustainable chickpea cultivars.

Recent progress in chickpea genomics—including the availability of reference genomes, pangenomes, super-pangenome assemblies, and WGRS data—provides valuable tools for identifying genomic regions associated with heat stress tolerance. However, structural variations such as PAVs, copy number variations, and candidate gene(s) linked to heat tolerance require functional validation to unravel the molecular pathways governing these traits. Leveraging these genomic resources in genomics-assisted breeding can accelerate the development of chickpea genotypes with improved resilience to heat stress.

Beyond genomic variation, emerging evidence highlights the role of heritable epigenetic modifications in regulating phenotypic variation. Nonetheless, the extent to which these epigenetic modifications, such as DNA methylation, contribute to chickpea's heat stress response remains unclear (Daware et al.2024). Genome-wide epigenetic profiling may provide deeper insights into the regulation of heat stress responses and help identify stable epigenetic markers for use in breeding programs.

Chickpea pan-transcriptome

Advances in transcriptomics and emerging single-cell omics technologies have enabled detailed characterization of gene expression patterns at the cellular, tissue, and organ levels, opening opportunities for constructing a comprehensive pan-transcriptome for cultivated and wild chickpea accessions. Integrating pangenome and pan-transcriptome would enhance our understanding of the transcriptional control of complex traits, including heat stress tolerance, across diverse genetic backgrounds.

Chickpea pan-proteome and pan-metabolome

Recent innovations in mass spectrometry have enabled the large-scale profiling of proteins and metabolites in response to abiotic stress, including heat. These advances facilitate the development of pan-proteomes and pan-metabolomes (Tian et al. 2025), which could uncover novel molecules and pathways involved in heat stress responses. However, such approaches have not been explored thoroughly in chickpea. Establishing a chickpea pan-proteome and pan-metabolome holds promise for enhancing our understanding of molecular and biochemical plant responses under heat stress.

Furthermore, emerging genome editing technologies have the potential to elucidate the function of genes associated with heat stress responses. However, the lack of efficient transformation protocols has hampered progress in chickpea genome editing. Therefore, developing and optimizing reliable transformation systems are essential to advance functional genomics and genome editing applications in chickpea.

While genotyping capabilities and genomic resources for chickpea have expanded rapidly, a major bottleneck remains in precise phenotyping, particularly for heat stress responses under field conditions. Addressing this challenge requires the development of low-cost HTP platforms that incorporate machine learning and AI tools. Such approaches are crucal for screening large germplasm collections and identifying climate-resilient chickpea varieties.

Conclusion and future perspective

The increasing frequency and intensity of heat stress events threaten global food security and agricultural sustainability (Callahan and Mankin 2022). With the global population projected to reach 9 billion by 2050, there is an urgent need to safeguard crop yields, including chickpea, under intensifying climate pressures. While considerable progress has been made in understanding chickpea's heat stress response, the molecular mechanisms conferring heat tolerance remain only partially understood. A comprehensive and integrated approach is required, including the systematic screening of genetically diverse chickpea genotypes across multiple gene pools to identify genomic regions linked to heat stress adaptation. Innovative technologies, such as speed breeding, offer opportunities to accelerate the development of heat-tolerant mapping populations. Combining GWAS with WGRS can facilitate the discovery of novel genomic regions and haplotypes associated with heat tolerance. These insights can be translated into breeding programs through marker-assisted and genomic selection, enhancing the adaptability of elite chickpea cultivars to high-temperature environments. The increasing availability of high-quality genome assemblies and pangenome data provides a valuable foundation for pinpointing causal genetic variants linked to heat stress resilience. Functional genomics approaches complement these efforts by identifying and validating candidate genes underlying major QTLs and revealing the molecular pathways involved in heat stress adaptation. Furthermore, recent advances in HTP techniques—including UAVs and multi-sensor platforms—combined with machine learning algorithms, enable rapid and precise phenotypic screening under field and controlled environments. These tools are instrumental for the efficient selection of heat-tolerant genotypes. Emerging genome editing tools, such as CRISPR/Cas9 and prime editing, now provide unprecedented opportunities for precisely manipulating genomic regions associated with heat tolerance. With improved transformation protocols, these tools could significantly advance chickpea improvement, helping to maintain productivity and resilience amid escalating heat stress challenges.

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Declarations

Competing interests The authors declare that the research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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