

Uday C Jha  
Harsh Nayyar  
Shiv Kumar Agrawal  
Kadambot H. M. Siddique *Editors*

# Developing Climate Resilient Grain and Forage Legumes

 Springer

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Editors

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*Editors*

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# Improving Chickpea Genetic Gain Under Rising Drought and Heat Stress Using Breeding Approaches and Modern Technologies

Uday C Jha, Harsh Nayyar, Rintu Jha, Prasant Kumar Singh, Girish Prasad Dixit, Yogesh Kumar, Biswajit Mondal, Avinash Kumar Srivastava, Eric J. B. von Wettberg, Pronob J. Paul, Ajaz A. Lone, Srinivasan Samineni, Sailesh K. Tripathi, and Kadambot H. M. Siddique

## Abstract

Increasing grain legume production, particularly for chickpea, will provide essential “plant-based dietary protein” and other micronutrients under the changing global climate. Drought and terminal heat stress limit plant growth and

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negatively affect various phenological events, causing severe yield losses. Among various strategies for improving stress tolerance, the judicious utilization of available genetic variation in the chickpea gene pool could minimize the adverse effects of drought and heat stress, sustaining chickpea yields. In addition, advancements in chickpea genomic resources, from molecular markers, namely, SSR, SNP, and INDELs and tools for association genetics, RNA-seq, to the availability of chickpea genome sequences and efforts of global chickpea germplasm resequencing allow us to identify loci and haplotypes contributing to drought and heat tolerance across the whole genome. Thus, molecular markers have enabled the successful transfer of drought-tolerant traits to elite chickpea cultivars using marker-assisted and haplotype-based breeding approaches. Likewise, the role of drought- and heat-responsive proteins and metabolites could significantly improve our understanding of the molecular mechanisms of drought and heat tolerance in chickpea via proteomics and metabolomics. Moreover, emerging novel breeding technologies (e.g., genomic selection, speed breeding, and genome editing) could enhance the necessary genetic gain to feed the increasing global population under an abruptly changing global climate.

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**Keywords**

Chickpea · Drought · Heat · Molecular marker · Genetic variability

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## 1.1 Introduction

Chickpea is a highly nutritious grain legume crop that contributes to global food security, providing essential amino acids and micronutrients to the global human population (Jukanti et al. 2012). Chickpea ameliorates soil nitrogen content by fixing atmospheric N<sub>2</sub> through symbiotically efficient rhizobacteria (Graham and Vance 2003), enriching soil nitrogen for subsequent crops in the rotation (Marques et al. 2020a). Global climate change and shifting production practices frequently expose chickpea to terminal drought and heat stress, causing severe yield losses (Jha et al. 2014a). Efficient utilization of chickpea germplasm resources, including landraces, wild relatives, and improved breeding lines, could sustain chickpea yields under drought and heat stress. Despite the genetic complexity of drought and heat tolerance mechanisms, various genomic resources—including draft genome sequences, resequencing panels, and segregating populations—have been developed in the last decade to elucidate the genetic determinants governing drought and heat tolerance (Thudi et al. 2014; Jha et al. 2018a, 2021a; Paul et al. 2018b; Jain et al. 2013; Varshney et al. 2013a, 2019). Furthermore, molecular markers have enabled the successful transfer of drought-tolerant traits to elite chickpea cultivars using a marker-assisted breeding approach (Roorkiwal et al. 2020). Thus, haplotype-based breeding could introduce desired allelic combinations to improve drought and heat stress tolerance in chickpea. Functional genomics could be used to pinpoint drought and heat-tolerant candidate gene(s) and their putative functions. Likewise,

proteomics and metabolomics could greatly improve our current knowledge on various proteins and metabolites produced in response to drought and heat stress (Khan et al. 2019a, b). The knowledge to be gained from these approaches can be quickly harnessed due to the power of novel breeding technologies including genomic selection, haplotype-based breeding, speed breeding, and genome editing (Meuwissen et al. 2001; Hickey et al. 2019; Samineni et al. 2019; Bohra et al. 2020; Badhan et al. 2021). These approaches combined with knowledge on the genetic basis of stress tolerance traits should improve crop breeding to help meet the challenge of feeding the growing global population under climate change.

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## 1.2 Impacts and Anomalies Associated with Drought Stress in Chickpea

Drought stress alone causes up to 50% yield losses in chickpea (Varshney et al. 2014). Chickpea frequently faces terminal drought stress as it is mostly grown under rainfed conditions in semiarid and arid regions (Gaur et al. 2012). Drought stress can occur at any stage of the plant growth cycle, with terminal drought the most common across the major production areas in South Asia, East Africa, and Mediterranean climates. Key physiological and biochemical, and developmental processes—photosynthesis, RuBisCo activity, carbohydrate synthesis, TCA cycle, respiration, and root growth—are seriously affected under drought stress, restricting plant growth (Yordanov et al. 2003; Parry et al. 2002; Guo et al. 2018). Drought stress during germination and vegetative growth decreases stomatal conductance, chlorophyll synthesis, plant vigor, and biomass accumulation (Krishnamurthy et al. 2013a, b; Purushothaman et al. 2015, 2016; Pang et al. 2017b). Drought stress during reproductive growth significantly affects anther formation, pollen formation, pollen fertility, pollen tube germination, and fertilization (Leport et al. 1999), resulting in improper pod formation, seed development, and seed filling, and ultimately significant yield losses. Moreover, drought stress affects nitrogen fixation by decreasing nitrogenase activity due to reduced expression of the *nifK* gene (Serraj et al. 1999; Nasr Esfahani et al. 2014).

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## 1.3 Impact of Heat Stress on the Reproductive Process in Chickpea

Rising global temperatures are challenging chickpea growth and development processes, leading to profound yield losses of at least 10–15%, or 53–330 kg/ha (Kalra et al. 2008; Upadhyaya et al. 2011; Kaushal et al. 2013; Jha et al. 2014b, 2017). Heat stress affects plant growth processes during vegetative, reproductive, and maturity phases (Devasirvatham et al. 2015; Bhandari et al. 2020). Heat stress hastens plant phenological events, decreasing biomass accumulation and grain filling, and ultimately causing yield losses (Kaushal et al. 2013). The reproductive stage is the most vulnerable to heat stress (Jagadish et al. 2021) because it severely impairs all

reproductive processes (Devasirvatham et al. 2013; Jha et al. 2017). Increased atmospheric temperatures beyond normal during anthesis affect anther formation, the pollination process, including pollen germination and pollen tube formation, fertilization, and pod formation (Kaushal et al. 2013; Devasirvatham et al. 2013, 2015; Bhandari et al. 2020). Consequently, heat exposure inhibits proper seed development, resulting in shriveled seed and thus severe yield losses (Devasirvatham et al. 2013, 2015). Furthermore, nodule development and biological nitrogen fixation processes are impeded under heat stress, negatively impacting plant growth.

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## 1.4 Genetic Resources for Drought and Heat Stress Tolerance

Harnessing genetic variability from various wild gene pools, landraces, and improved breeding lines could be the most eco-friendly and economic approach for developing abiotic stress tolerance, including drought and heat stress tolerance.

Several promising chickpea genotypes conferring drought tolerance have been identified based on various phenological, physiological and yield-related traits (Kumar and Rao 1996; Krishnamurthy et al. 2003; Shah et al. 2020). Drought stress can be mitigated by hastening plant phenological processes before the onset of terminal drought stress. The advantage of early phenology to tackle drought stress can be harnessed by transferring this trait into high-yielding yet drought-sensitive elite chickpea genotypes, for example, ICC96029, ICC96030, ICCV2, ACC316, and ACC317 (Kumar and Rao 1996; Kumar and Abbo 2001; Krishnamurthy et al. 2003; Canci and Toker 2009a) (see Table 1.1). However, early phenology can come with a yield penalty. Root system architecture—an important parameter manifesting plasticity under various environmental stresses, including drought—could be harnessed to develop drought tolerance in plants. Numerous studies have identified chickpea genotypes harboring improved root traits under drought stress. For example, ICC495 and ICC8261, with high root biomass and rooting depth (Krishnamurthy et al. 2003; Kashiwagi et al. 2008) have been judiciously used in chickpea breeding programs to develop drought-tolerant genotypes (Varshney et al. 2014). Targeting root traits for improving drought tolerance, Khandal et al. (2020) recently manipulated cytokinin levels to increase lateral root development and root biomass, attributing to drought tolerance in chickpea. Several promising chickpea lines exhibit improved photosynthesis, stomatal conductance, chlorophyll fluorescence, and other physiological traits under water stress (Toker et al. 2007; Makonya et al. 2020; Shah et al. 2020).

Several biochemicals, including various sugars, osmolytes, antioxidants, and other biochemicals, are produced in response to drought stress. Based on these parameters, MCC 544, MCC 696 and MCC 693 (Mafekheri et al. 2010), ILC482 (Mafakheri et al. 2011), Bakhar-2011 (Farooq et al. 2018), and D0091-10, K010-10, and D0085-10 (Shah et al. 2020) have been identified as potentially stress tolerant and useful as parents for crosses. In terms of yield and yield-related traits, ICC 14778, ICCV 10 (Ramamoorthy et al. 2016), ICC8950 (Awasthi et al. 2013),

**Table 1.1** List of chickpea genotypes contributing to heat and drought stress tolerance

Stress	Resistance source	Origin/reported from	Tested field/ laboratory/ greenhouse	Trait used for selection imparting stress tolerance	References
Drought stress	ICC 96029	India	Field	Earliness	Kumar and Rao (1996)
	ICCV 2	India	Field	Earliness	Kumar and Abbo (2001)
	ICC 4958	India	Field	Root and root-related traits	Kashiwagi et al. (2008), Krishnamurthy et al. (2003), Kashiwagi et al. (2005)
	<i>C. anatolicum</i> , <i>C. microphyllum</i> , <i>C. songaricum</i> , <i>C. oxydon</i> , <i>C. montbretii</i>	Turkey	Field	Low wilting under water stress	Toker et al. (2007)
	ICC 8261	India	Field	Root and root-related traits	Gaur et al. (2008)
	ACC316, ACC317	Turkey	Field	Earliness	Canci and Tokar (2009a)
	ILC482	Iran	Field	Osmolyte regulation	Mafakheri et al. (2011)
	ICC 7571	India	Field	High harvest index	Kashiwagi et al. (2013)
	ICC 14778, ICCV 10	India	Field	Grain yield trait	Ramamoorthy et al. (2016)
	ICC8950	India	Laboratory	High antioxidant defense capacity, and high seed yield	Awasthi et al. (2017)
	ICC 16374B, ICC 15510, ICC 9586, ICC 867	India	Field	Deeper root for acquiring water	Chen et al. (2017)

(continued)

Table 1.1 (continued)

Stress	Resistance source	Origin/reported from	Tested field/laboratory/greenhouse	Trait used for selection imparting stress tolerance	References
	ICC 14778, ICCV 10	India	Field	Root growth	Ramamoorthy et al. (2017)
	Neelam	Australia	Greenhouse	Improved seed yield	Pang et al. (2017a)
	Bakhar-2011	Australia	Laboratory	Increased proline, trehalose content	Farooq et al. (2018)
	Acc#7	University of Cape Town, South Africa	Greenhouse	Increased shoot biomass, Pn, Fv/Fm, and RWC; smaller root diameter	Makonya et al. (2020)
	D0091-10, K010-10, D0085-10, K005-10, D0078-10, 08AG016, 08AG004, D0080-10, 09AG002, K002-10, D0099-10	Pakistan	Growth chamber and field	Cell membrane stability, proline content, glycine betaine, nitrate reductase	Shah et al. (2020)
	CH55/09	Pakistan	Field	Stable yield	Arif et al. (2021)
	<i>C. reticulatum</i> (Kalkan_64, Savur_63)	University of California	Laboratory	Metabolic pathways, viz., phenylpropanoid metabolism	Moenga et al. (2020)
Heat stress	ILC482, Annegiri, ICCV10		Laboratory	Cell membrane	Srinivasan et al. (1996)
	ICCV88512 and ICCV88513	India	Field	Grain yield	Dua (2001)
	ACC316and ACC317		Field	Earliness	Canci and Tokor (2009a)
	ICC1205	India	Field and laboratory	High pollen viability	Devasirvatham et al. (2010)
	ICC4958, ICC4991, ICC6279, ICC6874, ICC7441, ICC8950	India	Field	Earliness, seed yield/plant	Krishnamurthy et al. (2011)

ICC14346	India	Field	Earliness	Upadhyaya et al. (2011)
ICC14778	India	Field	Cooler canopy	Zaman-Allah et al. (2011a, b)
ICCV92944	India	Field	Earliness	Gaur et al. (2012)
ICC15614	India	Field and laboratory	High pollen viability	Devasirvatham et al. (2012, 2013), Kaushal et al. (2013)
BG 256	India	Laboratory	Seed yield	Jumrani and Bhatia (2014)
ICC8950	India	Laboratory	Physiological, biochemical and yield traits	Awasthi et al. (2014)
Katila, Vaibhav, Avrodhi	India	Field	Increased grain yield	Jha and Shil (2015)
RVG 203, JAKI 9218, JG 130, ICCV0 7118, ICC1356	India	Field	Increased grain yield	Jha et al. (2015, 2018b, c, 2019a, b)
ICC 14778, ICC 15618	India	Field	Improved yield	Varshney et al. (2019)
<i>Cicer turcicum</i>	Antalya, Turkey	Screenhouse	High pod set	Toker et al. (2021)

FLIP03-145C, ILC 3182, and ILC 588 (Hamwieh and Imtiaz 2015), ICC 7571 (Kashiwagi et al. 2013), Neelam (Pang et al. 2017a), and CH55/099 (Arif et al. 2021) were identified as promising genotypes conferring drought tolerance; these genotypes could be used as donors for transferring yield and yield-related traits into elite yet drought-sensitive chickpea cultivars.

Heat stress is emerging as a serious abiotic stress in chickpea, especially during the reproductive stage (Jha et al. 2014a). Several chickpea genotypes have been identified that exhibit heat tolerance based on various parameters (Gaur et al. 2012; Jha et al. 2018b; Bhandari et al. 2020). Heat-tolerant lines can be selected based on yield parameters using various selection indices (e.g., heat tolerance index, tolerance index, heat susceptibility index) by growing genotypes under timely and late-sown conditions. Using this screening method, several potential heat-tolerant chickpea lines (e.g., RVG 203, RSG 888, JAKI 9218, GNG 469, IPC 06-11) have been reported (Jha et al. 2018b). Likewise, ICCV92944, RVG203, JAKI9218, ICC1356, and JG130 showed improved yield performance under heat stress (Gaur et al. 2012; Jha et al. 2015, 2018b, c). Within Ethiopian germplasm, DZ-Cr-0034 was identified as heat tolerant in multisite trials in Ethiopia and India (Getahun et al. 2021). Assessing yield and yield-related traits of breeding lines at multiple locations will provide further impetus for selecting heat-tolerant lines under a range of target environments. In this context, JAKI 9218 showed promising results under heat stress (Jha et al. 2019b).

Earliness is an important heat escape mechanism. ACC316, ACC317 (Canci and Toker 2009a), and ICCV92944 (Gaur et al. 2012) were identified for their earliness to escape heat stress. Likewise, ILC482, Annegiri, ICCV10, ICC8950, and ICC14778 were identified as promising genotypes in terms of various physiological traits contributing to heat tolerance (Srinivasan et al. 1996; Zaman-Allah et al. 2011a, b; Awasthi et al. 2014). Screening for pollen and pollen-related traits under heat stress at the reproductive phase could be important for selecting heat-tolerant chickpea lines. Based on these traits, ICCV92944, ICC15614, ICC1205, and ICC07110 were identified as heat-tolerant in both the field and a growth chamber (Kaushal et al. 2013; Awasthi et al. 2014; Devasirvatham et al. 2015; Bhandari et al. 2020) (see Table 1.1). Significant genetic variation for various phenological, morphophysiological, and yield-related traits was found in the ICC15614 × ICC4567, and DCP92-3 × ICCV92944 mapping populations under heat stress (Paul et al. 2018a; Jha et al. 2021a, b).

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## 1.5 Crop Wild Relatives (CWRs): A Hidden Reservoir of Drought and Heat Tolerance in Chickpea

Judicious exploitation of CWRs in crop breeding programs could broaden the genetic base of improved breeding lines for sustaining grain yield and plant adaptation under challenging environments (Coyne et al. 2020; von Wettberg et al. 2018). Likewise, various CWR accessions of chickpea are being incorporated into breeding programs for developing abiotic stress tolerance, including drought and heat



tolerance. An evaluation of various chickpea CWRs—*C. anatolicum*, *C. microphyllum*, *C. montbretti*, *C. oxydon*, and *C. songaricum*—under water stress revealed their potential for conferring drought tolerance (Toker et al. 2007). Similarly, an assessment of various annual *Cicer* species for drought and heat stress tolerance identified better adaptation of four *C. reticulatum* accessions and one *C. pinnatifidum* accession under drought and heat stress (Canci and Toker 2009b); these *Cicer* species could be used to introgress “adaptive traits” contributing to drought and heat stress tolerance into elite chickpea cultivars. To date, only *C. reticulatum* and some *C. echinospermum* are compatible with cultivated chickpea (e.g., Kahraman et al. 2017). However, with an increased understanding of the nature of genome organization in the genus (Varshney et al. 2021), it may be feasible to cross more distantly related *Cicer* species, such as *C. pinnatifidum*.

Recent studies harnessing new collections of *C. reticulatum* and *C. echinospermum* from southeastern Turkey (von Wettberg et al. 2018; Coyne et al. 2020) have identified new sources of drought and heat tolerance (e.g., Talip et al. 2018; von Wettberg et al. 2018; Marques et al. 2020b; Getahun et al. 2021). Initial analyses of these collections identified multiple populations from lower elevation, more exposed sites with greater drought tolerance (e.g., von Wettberg et al. 2018). Some higher elevation sites showed greater cold tolerance (Mir et al. 2021), but interestingly, a lower elevation, low water availability site was among the most cold-tolerant parents. This suggests that wild populations may exhibit interesting patterns of cross-tolerance among abiotic and biotic stresses (von Wettberg et al. 2014).

To harness variation beyond *C. reticulatum* and *C. echinospermum*, which have far narrower environmental distributions than other *Cicer* species (Coyne et al. 2020), it makes sense to continue looking at other wild taxa. Recently, Toker et al. (2021) reported *C. turcicum* as a species exhibiting better reproductive function under heat stress. Ongoing work is assessing the potential to cross this species with cultivated chickpea (Toker, pers. comm). Besides CWRs, “adaptive loci” of landraces conferring plant phenotypic plasticity and adaptation under various hostile environments could be harnessed to develop climate-resilient genotypes. Considering this, Varshney et al. (2019) identified ICC 14778 and ICC 15618 as two chickpea genotypes possessing gene(s) that contribute to chickpea adaptation in hot environments.

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## 1.6 Genomic Resources for Drought and Heat Tolerance

During the last decade, unprecedented advances in developing chickpea genomics resources have enabled the mapping of various breeding importance traits, including drought and heat stress (Thudi et al. 2014; Jha 2018; Jha et al. 2020).

Understanding the genetic basis of traits has improved with the advent of SSR markers. Several drought-related traits QTLs were identified on different linkage groups by employing SSR markers (Rehman et al. 2011; Varshney et al. 2014; Hamwieh et al. 2013). Comprehensive phenotyping of various drought-relevant

traits in two biparental mapping populations evaluated at multiple locations underpinned a QTL hotspot on CaLG04 (Varshney et al. 2014). Subsequently, the availability of SNP markers developed through genotyping-by-sequencing (GBS) technology-enabled partitioning of this QTL hotspot into *QTL-hotspot\_a* (harboring 15 genes) and *QTL-hotspot\_b* (harboring 11 genes) (Kale et al. 2015). Furthermore, Jaganathan et al. (2015) refined this QTL-hotspot genomic region to 14 cM, harboring several novel SNPs in the ICC1882 × ICC4958 mapping population using GBS technology. To identify drought tolerance QTLs, Sivasakthi et al. (2018) elucidated 13 M-QTLs related to plant vigor (rather than drought tolerance *per se*) on LG4 coinciding with the QTL hotspot and one M-QTL contributing to stomatal conductance on LG3 under drought stress. The availability of the chickpea genome sequence assisted in pinpointing the candidate gene(s) underlying these drought stress QTLs (Jaganathan et al. 2015; Kale et al. 2015; Srivastava et al. 2016).

Jha et al. (2019a) shed light on the genetic control of heat tolerance in chickpea using a diallel analysis based on phenological and yield parameters assessed under heat stress. The authors reported the presence of both additive and nonadditive gene action controlling heat tolerance. Thus, the availability of molecular markers, especially SSRs and SNPs, further improves our understanding of the genetics of heat tolerance (Thudi et al. 2014; Jha et al. 2019c, 2021a, b).

Assaying the F<sub>2</sub>-derived DCP92-3 × ICCV92944 mapping population using SSR markers identified one QTL controlling primary branch number and one QTL linked to chlorophyll content under heat stress (Jha et al. 2019c). Paul et al. (2018b) mapped yield-related QTLs (pod number per plant, seed number per plant, biomass, and percentage pod set) on CaLG05 and CaLG06 chromosomes under heat stress by genotyping the ICC15614 × ICC4567 mapping population using GBS technology. Likewise, deploying the GBS-derived 788 SNP markers in the DCP92-3 × ICCV92944 mapping population identified 37 major QTLs related to various physiological and yield-related traits evaluated under heat stress (Jha et al. 2021b) (see Table 1.2). The authors also elucidated 28 candidate genes related to HSPs underlying the identified QTLs. Moreover, a large set of global germplasm offers great opportunity to capture significant marker-trait associations for heat-tolerant traits across the whole genome using genome-wide association mapping (Thudi et al. 2014; Varshney et al. 2019). Based on this approach, several MTAs for various phenological, physiological, and yield-related traits evaluated under heat stress have been uncovered in chickpea (Thudi et al. 2014; Jha et al. 2017, 2018a, 2021a; Varshney et al. 2019).

Using 81 SSR markers assayed in 71 chickpea genotypes, several significant MTAs related to physiological traits, namely, membrane stability index and chlorophyll content were identified under heat stress (Jha et al. 2018a). Likewise, GWAS performed on a set of 182 chickpea germplasm using 120 SSR markers elucidated a plethora of significant MTAs for various phenological, physiological, and yield and yield-related traits phenotyped under heat stress (Jha et al. 2021a) (see Table 1.2). Apart from this, various root traits contributing to higher water use efficiency and the QTL hotspot from ICC4958 to elite chickpea cultivars, such as JG11, ICCV10, RSG888, Pusa 372, Pusa 362, and JAKI9218, have been transferred using

**Table 1.2** List of QTLs related to drought and heat-stress tolerance in chickpea

Stress	Mapping approach	Population name and size	QTLs/MTA	Marker type	No. markers used	LG group	References
Drought	Biparental	ILC588 × ILC3279, RILs (155)	15 QTLs	SSR	97	LG1, LG3, LG4, LG7, LG8	Rehman et al. (2011)
	Biparental	ILC588 9 × ILC3279, RILs (181)	93 QTLs	SSR		LG3, LG4	Hamwich et al. (2013)
	Biparental	JG 11 × ICC4958, BC	QTL-hotspot	SSR, AFLP		–	Varshney et al. (2013b)
	Biparental	ICC 4958 × ICC1882, RILs (264)	QTL-hotspot	SSR	551	CaLG04	Varshney et al. (2014)
		ICC 283 × ICC 8261, RILs (288)	312 significant MTAs	DArT, SNP	1072 DArTs +651 + 113 + 36 SSRs	CaLG04	Thudi et al. (2014)
	Biparental	ICC 4958 × ICC 1882, RILs (232)	164 main-effect QTLs	SNP, CAPS, dCAPS,	743 SNPs +232 SSRs+21 DArTs	CaLG04	Jaganathan et al. (2015)
			QTL-hotspot	SSR	7 EST-SSRs, 4 genic molecular markers		
	Biparental	ICC 4958 × ICC 1882, RILs (232)	QTL-hotspot_a (15 genes)	SNP	53,223 SNPs	CaLG04	Kale et al. (2015)
			QTL-hotspot_b (11 genes)			CaLG08, CaLG07	
	Biparental	ICC 4958 × ICC 1882	3 candidate genes	SNP		CaLG01, CaLG04	Singh et al. (2016)

(continued)

**Table 1.2** (continued)

Stress	Mapping approach	Population name and size	QTLs/MTA	Marker type	No. markers used	LG group	References
	Biparental	ICC 4958 × ICC 17163	6 candidate genes	SNP		CaLG2, CaLG3, CaLG4, CaLG5, CaLG6, CaLG7	Srivastava et al. (2016)
	Biparental	CC 4958 × ICC 1882, RILs (232)	21 major QTLs	SNP	241 SSRs, 1007 SSRs and 1557 SNPs	CaLG01, CaLG03, CaLG04, CaLG05, Ca LG06, CaLG07, Ca LG08	Sivasakthi et al. (2018)
	Super GWAS		38 significant MTAs	SNP	1,44,000	Ca3, Ca4, Ca5, Ca6	Li et al. (2018)
Heat	Biparental	ICC 4567 × ICC 15614, RILs (292)	4 QTLs	SNP	271		Paul et al. (2018b)
	GWAS	71 genotypes		SSR	81		Jha et al. (2018a)
	Biparental	DCP92-3 × ICCV92944, F2 (206)	2 QTLs	SSR	78		Jha et al. (2019c)
	GWAS			SNP			Varshney et al. (2019)
	GWAS	182 genotypes	24 + 14 MTAs under normal condition; 17 + 34 MTAs in heat-stressed environment	SSR	120 SSRs	LG1 to LG8	Jha et al. (2021a)
	Biparental	DCP92-3 × ICCV92944	77 QTLs	SNP	788	LG1-LG8	Jha et al. (2021b)

marker-assisted backcrossing approach to improve drought tolerance in chickpea (Varshney et al. 2013b; Roorkiwal et al. 2020; Bharadwaj et al. 2020).

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## 1.7 Functional Genomics Approach for Uncovering Candidate Genes for Drought and Heat Tolerance

In the last decade, advances in functional genomics approaches, especially RNA-seq and earlier related technologies, have been used to identify several candidate gene (s) and their relevant function contributing to drought and heat stress in chickpea (Badhan et al. 2018; Mahdavi Mashaki et al. 2018). Earlier work using microarray technology identified several thousand genes expressed in response to drought stress (Mantri et al. 2007; Varshney et al. 2009). Varshney et al. (2009) reported 20,162 ESTs responding to drought stress. Likewise, Deokar et al. (2011) obtained 3062 unigenes responding to drought stress in a suppression subtraction hybridization study. Subsequently, high throughput RNA-seq technology assisted in unveiling a plethora of transcription factors (TFs), including WRKY, NAC, MYB, AP2-EREBP, and bHLH, controlling drought stress tolerance (Badhan et al. 2018; Mahdavi Mashaki et al. 2018; Kumar et al. 2019). Myriad of DEGs has been investigated using RNA-seq studies in chickpea to explore the role of various differentially expressed genes (DEGs) in response to drought stress (Kumar et al. 2019; Bhaskarla et al. 2020; Sagar et al. 2021). Recently, the roles of phospholipases D genes (Sagar et al. 2021) and oxylipin biosynthesis genes (Bhaskarla et al. 2020) contributing to drought stress response were elucidated in a functional genomic study (see Table 1.3). Agarwal et al. (2016) uncovered five HSP 90 genes contributing to heat stress tolerance based on the results of an RNA-seq study on reproductive tissues treated with heat stress. Thus, transcriptomic studies have facilitated the deciphering of candidate gene(s) and complex network of gene (s) and their functional role in attributing plant adaptation to drought and heat stress in chickpea.

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## 1.8 Proteome and Metabolome Dynamics for Resolving Drought and Heat Tolerance in Chickpea

Proteomics could enhance our understanding of drought stress tolerance by providing insight into the proteins produced in response to drought stress (Parankusam et al. 2017). Drought-responsive participatory proteins obtained under drought stress include cellular proteins involved in glycolysis, protein synthesis, TCA cycle, signal transduction, protecting cells from reactive oxygen species (ROS)-related damage, heat shock proteins, and cellular osmotic adjustment (Gupta et al. 2020; Vessal et al. 2020). Vessal et al. (2020) reported the participatory activity of RuBisCo, ATP synthase, carbonic anhydrase, L-ascorbate peroxidase, auxin-binding protein contributing to drought stress tolerance in chickpea. Similarly, a comparative proteomics analysis revealed 75 proteins—related to oxidative stress

**Table 1.3** List of differentially expressed gene(s) under drought and heat stress identified by functional genomic approaches

Stress	Tissue used	Transcriptomic technique used	Differentially expressed gene (s) with putative function	References
Drought	Leaves and flowers		Repression of aquaporin-like membrane channel protein; inhibition of auxin-repressed proteins	Mantri et al. (2007)
	Roots	SuperSAGE	7532 unitags and 880 unitags involved in ROS scavenging activity under water stress	Molina et al. (2008)
	Roots	ESTs	20,162 ESTs, dehydrin DHN3, late embryogenesis abundant (LEA) genes coexpressed under drought stress	Varshney et al. (2009)
	Shoots and roots	Suppression subtractive hybridization	3062 unigenes; upregulation of myoinositol-1-phosphate synthase (MIPS) and pyrroline-5-carboxylate synthetase (P5CS) genes helps in drought stress tolerance; regulation of Myb, ERF-2, NAC, bZIP, HD-ZP, etc. could participate in drought tolerance	Deokar et al. (2011)
	Roots	ESTs	44,639 tentative unique sequences involved in regulating various stress-responsive TFs and HSPs under drought stress	Hiremath et al. (2011)
	Roots	RNA-seq	4053 and 1330 regulate TFs (bHLH, AP2-EREBP and MYB HB, WRKY and NAC) under water stress	Garg et al. (2016)
	Roots and shoots	RNA-seq	–	Srivastava et al. (2016)
	Leaves from shoots at apical meristem stage	RNA-seq	1562 genes, 2592 genes related to controlling expression of MYB-related protein, ethylene response under water stress	Badhan et al. (2018)
	Roots and shoots	RNA-seq	261 and 169 genes, TFs (bHLH, leucine-rich repeat), aldo/ keto reductase, potassium channel, chlorophyll A-B binding protein, inositol polyphosphate-related phosphatase	Mahdavi Mashaki et al. (2018)
	–	RNA-seq	1624 genes including regulation of mannitol dehydrogenase, serine hydroxymethyl-transferase 4-like, cytochrome P450 81E8-like and galactinol-	Kumar et al. (2019)

(continued)

**Table 1.3** (continued)

Stress	Tissue used	Transcriptomic technique used	Differentially expressed gene (s) with putative function	References
			sucrose galactosyltransferase-like, AP2- EREBP, bHLH, bZIP, C3H, MYB, NAC, WRKY TFs under water-scarce environment	
	Roots	RNA-seq	Upregulation of stress-responsive transcription factors, kinases, ROS signaling and scavenging, transporters, root nodulation, and oxylipin biosynthesis genes	Bhaskarla et al. (2020)
	Roots	qRT-PCR	<i>Ca_06899</i> , <i>Ca_18090</i> , <i>Ca_22941</i> , <i>Ca_04337</i> , <i>Ca_04069</i> , <i>Ca_04233</i> , <i>Ca_12660</i> , <i>Ca_16379</i> , <i>Ca_16946</i> , and <i>Ca_21186</i>	Singh et al. (2016)
	Leaves Seedling	RNA-seq SqRT-PCR	Genes involved in phenylpropanoid biosynthesis pathway were upregulated in tolerant genotype <i>WRKY</i> , <i>DREB2A</i> , and <i>CarNAC3</i> genes	Moenga et al. (2020) Borhani et al. (2020)
	–	qRT-PCR	Phospholipases D genes differentially expressed in response to drought stress	Sagar et al. (2021)
Heat	Flowers, shoots, roots	RNA-seq	Five HSP 90 genes	Agarwal et al. (2016)

tolerance, HSPs, cellular metabolism, ROS metabolism—involved in drought stress tolerance in chickpea (Gupta et al. 2020).

A comparative proteomics analysis revealed that proline and sucrose biosynthesis-related proteins, glutamine synthetase, and cytosolic fructose-bisphosphate aldolase were involved in drought stress tolerance in *C. reticulatum* than *C. arietinum* (Cevik et al. 2019). A proteomics analysis of reproductive tissue identified 154 proteins differentially expressed in two contrasting heat-tolerant genotypes under heat stress; the actively participating proteins included 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 (Parankusam et al. 2017). Further study is needed to decipher the role of various proteins related to drought- and heat-sensing and signal transduction pathways contributing to drought and heat tolerance in chickpea.

Likewise, metabolomics profiling could be harnessed to obtain insights into the various metabolites generated in response to drought and heat stress, allowing plants to survive under these stresses (Khan et al. 2019a, b). Metabolomic analysis of two

contrasting chickpea genotypes under water stress revealed the accumulation of various metabolites (e.g., choline, phenylalanine, gamma-aminobutyric acid, alanine, phenylalanine, tyrosine, glucosamine, guanine, and aspartic acid) attributed to drought stress adaptation (Khan et al. 2019a). Khan et al. (2019b) reported the accumulation of various metabolites (proline, L-arginine, L-histidine, L-isoleucine, and tryptophan) in the leaves of chickpea genotypes treated with plant growth-promoting rhizobacteria (PGPR) and various plant growth regulators (PGRs) under drought stress. The PGPR- and PGR-treated plants also had enhanced riboflavin accumulation, L-asparagine, aspartate, and glycerol in leaves. The same research group also witnessed the increased accumulation of malonate, 5-oxo-L-proline, and trans-cinnamate in genotypes treated with PGPR and PGR, which was attributed to drought tolerance (Khan et al. 2019c). Hence, these drought- and heat-responsive metabolites allow chickpea to maintain growth and development and ultimately survive in drought- and heat-stress environments.

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## 1.9 Emerging Modern Breeding Tools for Accelerating Genetic Gain in Chickpea

Traditional breeding approaches have significantly improved chickpea yield but these approaches alone will not meet the rising demand for chickpea due to the growing human population (Langridge and Fleury 2011). The augmentation of several novel breeding tools, such as genomic selection, could predict the genetic merit/phenotypic performance/breeding value of various untested progenies developed in crossing programs using various prediction/statistical models, thus reducing the breeding cycle and assisting in the selection of superior progenies with improved genetic gain (Meuwissen et al. 2001). Such an approach has been used to predict genetic gain in chickpea under drought stress (Li et al. 2018). Speed breeding/rapid generation has been recently introduced to grow three to four crop generations per year in chickpea, thus allowing faster development of new cultivars (Hickey et al. 2019; Samineni et al. 2020). Likewise, genome editing tools could be used to manipulate nucleotide sequences (addition/deletion) at targeted locations without the intervention of transgene (Nasti and Voytas 2021). This technology has been used to develop drought-tolerant chickpea by editing *4-coumarate ligase (4CL)* and *Reveille 7 (RVE7)* genes attributed to water stress tolerance (Badhan et al. 2021). In addition, the multiparent advanced generation intercross (MAGIC) population scheme was developed at ICRISAT, India, to broaden the genetic base by capturing high allelic diversity and increasing resilience to various abiotic stresses, including drought and heat stress. Potential diverse founder parents, including ICC 4958, JG 130, ICCV 10, JAKI 9218, JG 130, JG 16, ICCV 97105, and ICCV 00108 were included in the crossing programme for this scheme (Samineni et al. 2017). The recombinant inbred lines from these parents could map drought- and heat-tolerant QTLs with higher resolution and improve chickpea genetic gain under harsh environments. A similar hybrid-nested association mapping and backcross introgression approach has been used to harness variation in recent crop wild relative



collections (von Wettberg et al. 2018), crossing a diverse panel of wild parents into elite cultivated lines.

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### 1.10 Scope of High Throughput Phenotyping for Capturing the Precise Phenotypic Response of Drought and Heat Stress in Plants

As drought and heat stress are governed by multiple gene(s)/QTLs and greatly influenced by  $G \times E \times M$  interactions, measuring their accurate response remains challenging (Hein et al. 2021; Smith et al. 2021). The evolution of various phenomics facilities in the last decade has dramatically advanced our understanding, measuring the drought and heat stress response both spatially and temporally. Advances in nondestructive methods, including sensor-based technologies, image-based platforms, unmanned aerial vehicles, and drone-based technologies, have assisted in measuring drought and heat stress responses at a large scale under target environments in the field (Houle et al. 2010; Fiorani and Schurr 2013; Furbank and Tester 2011; Großkinsky et al. 2015; Hein et al. 2021). Among image-based techniques, Red–Green–Blue images can measure plant area and color, time of day of flowering, yield, and yield parameters (Sadeghi-Tehran et al. 2017; Xiong et al. 2017). Likewise, infrared is used to assess plant temperature, and SPAD meters, hyperspectral radiometers, and field spectroradiometers are used to assess photosynthesis efficiency (Peng et al. 2017). Moreover, emerging deep learning and machine learning approaches could be used to measure drought and heat stress responses to develop better drought- and heat-tolerant chickpea lines.

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### 1.11 Conclusion and Future Perspective

With global climate change, frequent episodes of drought and heat stress are becoming a major concern, exacerbating chickpea yield losses. A thorough screening of chickpea germplasm is urgently needed in the target environment to increase chickpea resilience to drought and heat stress. As drought and heat stress sometimes occur concurrently, the selection of traits conferring combined drought tolerance should be targeted and transferred into elite chickpea lines for increased resilience to drought and heat tolerance. Concomitantly, studies should focus on pre-breeding activities and exploration of landraces with inherent drought and heat tolerance capability (Rani et al. 2020). Marker-assisted breeding schemes allow us to transfer the genomic regions conferring drought and heat tolerance into elite chickpea cultivars, thus improving the genetic gain of elite chickpea cultivars (Roorkiwal et al. 2020).

Efforts to resequence global chickpea germplasm and a pangenomics approach could underpin the novel causal variants attributing drought and heat tolerance in chickpea (Varshney et al. 2021). Likewise, genomic selection will assist in predicting superior progenies conferring drought and heat tolerance based on the

prediction model and thus reduce breeding cycles. In parallel, MAGIC and NAM populations are being developed to increase resilience and broaden the genetic base. In addition, rapid generation advancement and genome editing technology could be used to design a more climate-resilient chickpea to sustain global food security.

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