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Review

Genomic-Mediated Breeding Strategies for Global Warming in Chickpeas (*Cicer arietinum* L.)

Shailesh Kumar Jain [1], Eric J. von Wettberg [2], Sumer Singh Punia [1], Ashok Kumar Parihar [3,*], Amrit Lamichaney [3], Jitendra Kumar [3], Debjyoti Sen Gupta [3], Sarfraz Ahmad [1], Naveen Chandra Pant [1], Girish Prasad Dixit [1], Hatice Sari [4,5], Duygu Sari [5], Amar Ma'ruf [5], Pelin Toker [6] and Cengiz Toker [5,*]

[1] Department of Plant Breeding and Genetics, Sri Karan Narendra Agriculture University Jobner, Jaipur 303329, Rajasthan, India
[2] Plant and Soil Science and Gund Institute for the Environment, University of Vermont, Burlington, VT 05405, USA
[3] ICAR-Indian Institute of Pulses Research, Kanpur 208024, Uttar Pradesh, India
[4] Department of Crop and Soil Sciences, Washington State University, Pullman, WA 99164, USA
[5] Department of Field Crops, Faculty of Agriculture, Akdeniz University, TR-07070 Antalya, Türkiye
[6] Plant Breeding and Genetics, Faculty of Agriculture, Akdeniz University, TR-07070 Antalya, Türkiye
* Correspondence: ashoka.parihar@gmail.com (A.K.P.); toker@akdeniz.edu.tr (C.T.)

Abstract: Although chickpea (*Cicer arietinum* L.) has high yield potential, its seed yield is often low and unstable due to the impact of abiotic stresses, such as drought and heat. As a result of global warming, both drought and heat are estimated to be major yield constraints between one-quarter and one-third per annum. In the present review, genomic-mediated breeding strategies to increase resilience against global warming. Exacerbated drought and heat stresses have been examined to understand the latest advancement happening for better management of these challenges. Resistance mechanisms for drought and heat stresses consist of (i) escape via earliness, (ii) avoidance via morphological traits such as better root traits, compound leaves, or multipinnate leaves and double-/multiple-podded traits, and (iii) tolerance via molecular and physiological traits, such as special tissue and cellular abilities. Both stresses in chickpeas are quantitatively governed by minor genes and are profoundly influenced by edaphic and other environmental conditions. High-yield genotypes have traditionally been screened for resistance to drought and heat stresses in the target selection environment under stress conditions or in the simulacrum mediums under controlled conditions. There are many drought- and heat-tolerant genotypes among domestic and wild *Cicer* chickpeas, especially in accessions of *C. reticulatum* Ladiz., *C. echinospermum* P.H. Davis, and *C. turcicum* Toker, J. Berger, and Gokturk. The delineation of quantitative trait loci (QTLs) and genes allied to drought- and heat-related attributes have paved the way for designing stress-tolerant cultivars in chickpeas. Transgenic and "omics" technologies hold newer avenues for the basic understanding of background metabolic exchanges of QTLs/candidate genes for their further utilization. The overview of the effect of drought and heat stresses, its mechanisms/adaptive strategies, and markers linked to stress-related traits with their genetics and sources are pre-requisites for framing breeding programs of chickpeas with the intent of imparting drought tolerance. Ideotype chickpeas for resistance to drought and heat stresses were, therefore, developed directly using marker-aided selection over multiple locations. The current understanding of molecular breeding supported by functional genomics and omics technologies in developing drought- and heat-tolerant chickpea is discussed in this review.

Keywords: drought tolerance; heat tolerance; morphological and physiological traits; conventional breeding; QTLs; marker-assisted selection; omics technology; genetic engineering; chickpea

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1. Introduction

Significant crop yield losses are forecasted by the rise of global mean surface temperature (GMST) [1–3]. The increase in GMST due to global climate change not only triggers heat and drought stresses but also increases other abiotic and biotic stresses. Climate change will also increase variability in weather conditions. Heat accompanying drought stress is considered a major constraint on agricultural production [4]. Heat stress in agricultural lands can take two forms, one as acute heat shock and the other as medium or moderate heat stress. The former heat stress is referred to as lethal temperatures for plants from a few minutes to a few hours in midday. On the other hand, the later heat stress is known as chronically higher temperatures than optimum temperatures during the growing season [5]. Like heat stress, plants generally are subject to two types of drought stress. The first drought type is terminal drought, increasing from seedling to the end of maturity, while the second drought type is intermittent or unpredictable drought, stemming from insufficient and irregular rains during the growing season [6]. As a result of global warming, not only drought but also heat is estimated to be a major yield constraint in chickpeas. These two stresses are the main reasons for yield reduction, which is estimated to be a million tons per annum [7,8]. Since most chickpeas are grown under rainfed conditions, the crops in these scenarios are consistently exposed to terminal or intermittent drought and moderate heat stresses [9]. Under stressful circumstances, farmers rely on agronomic practices such as irrigation if available, tillage, and inter or mixed cropping to harvest moisture from the soil. Some farmers also prefer to grow their own landraces better adapted to the harsh environmental conditions despite poor yield. Such landraces have a wider genetic base compared to modern cultivars, which were selected for essential traits from wild progenitor species [10].

Improving drought and heat tolerance in chickpeas requires finding germplasm with greater tolerance for crosses to accessions that may have preferred agronomic traits [11]. Both cultivated chickpeas and wild relatives of chickpeas contain drought- and heat-resistant accessions. In cultivated chickpeas, there are two market classes, light colored and often larger-seeded Kabuli types, and dark-seeded and other smaller desi types. Harlan and de Wet [12] proposed a wide classification system that divided crop wild relatives into three gene pools: primary (GP1), secondary (GP2), and tertiary (GP3). The primary gene pool represents the wild progenitors and closely related species of the cultivated chickpeas. *Cicer arietinum* L., *C. reticulatum* Ladiz., and *C. echinospermum* P.H. Davis are in GP1, and easily crossing hybrids are generally fertile [13]. The crossability of *C. echinospermum* with cultivated chickpeas varies depending on the source population, and some authors have placed this species in the secondary gene pool due to this [13]. The secondary gene pool includes all biological species that are capable of crossing with the chickpea and are considered to be closely related. While gene transfer is feasible within this pool, barriers need to be overcome during the breeding process [14]. *C. bijugum* K.H. Rech., *C. judaicum* Boiss., and *C. pinnatifidum* Juab. and Spach recently discovered that the *C. turcicum* Toker, Berger, and Gokturk [15] species are in GP2. The tertiary gene pool consists of perennial wild species for which there is no known approach to successfully transfer genes from these wild species to cultivated chickpea varieties. This limited compatibility between the tertiary gene pool and cultivated chickpeas highlights the genetic barriers and challenges involved in incorporating the genetic diversity of these wild species into cultivated chickpea breeding programs (Figure 1).

Wild species play extremely important roles in both the identification of plant genomes and the genetic development of cultivars. In particular, wild species have contributed greatly to the solution of many fundamental problems, such as the origin, evolution, phylogenetic relationship, cytological status, and inheritance of genes of many field crops [16]. Wild chickpea species occur across different conditions and geographical locations and have great genetic diversity [17]. In previous studies, it has been reported that there is resistance to Ascochyta blight in *C. bijugum*, *C. echinospermum*, and *C. pinnatifidum* species [18,19]. Additionally, there is resistance to seed beetles and leafminers in *C. echinospermum* and *C. reticulatum* species [20–22]. Moreover, cold resistance has been observed in *C. bijugum*, *C. reticulatum*, *C. echinospermum*, and *C. pinnatifidum* species [23,24], while heat resistance has been noted in *C. turcicum* species [15]. *C. reticulatum* and *C. echinospermum* species are the wild relatives of chickpeas often used in the development of germplasm through traditional breeding methods due to their capability to produce fertile hybrids [25–27]. In the process of domesticating chickpeas, significant shifts in traits have been achieved, including reduced pod dehiscence, decreased levels of anti-nutritional compounds, larger grain size, and increased yield. Also, a random loss of alleles has occurred as a result of human selection, cultivation practices, and agricultural environments, dramatically reducing the effective population sizes of crops [28,29]. In essence, when humans select and cultivate plants for specific traits they want, it often results in a decrease in the genetic diversity of those plants in the regions of their genome that determine these desirable characteristics [30,31]. As a trade-off, the resistance to biotic and abiotic stresses has been diminished, and the overall variation has decreased (Figure 2). The cultivation bottlenecks have resulted in a decline in genetic diversity across numerous plant species, including chickpeas, leaving them susceptible to various stresses [32–36]. A primary objective of plant breeding is to identify advantageous alleles present in the wild relatives of the plant and incorporate them into modern varieties. The cultivation of chickpeas is mostly confined to rainfed conditions on marginal land accompanied by the limiting effect of several abiotic stresses; for instance, drought, terminal heat, cold, and salinity, which thus records very poor yield [5–7]. Of these abiotic stresses, drought is the most detrimental to the overall performance of this crop. It primarily leads to water stress due to reduced moisture availability in the soil and decreased soil water potential. In such situations, plants are unable to absorb sufficient water to meet their demand [37,38].

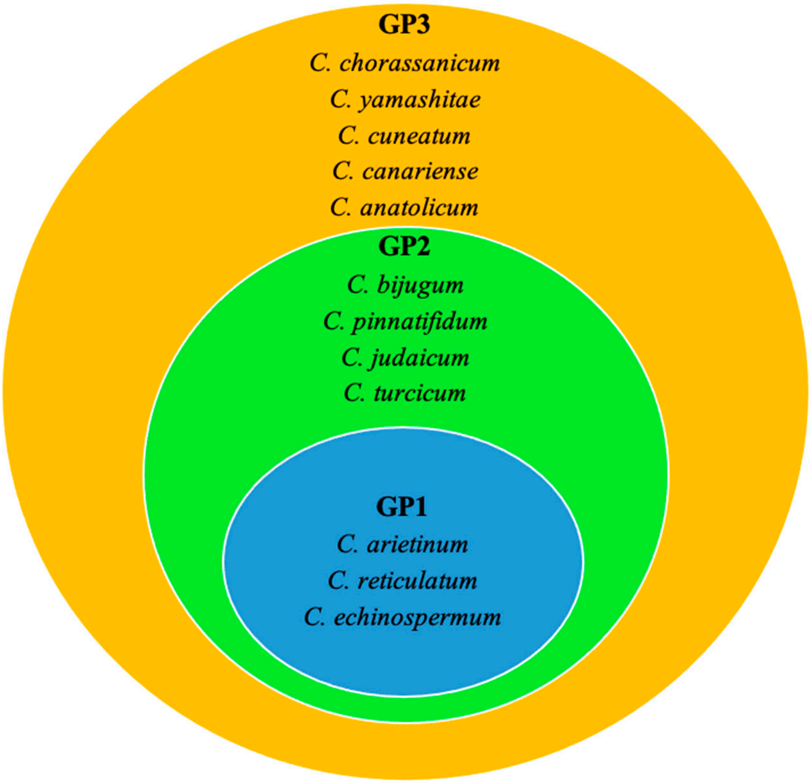

Figure 1. The gene pool in the genus *Cicer* according to their crossability with *C. arietinum* (from easiest to hardest, GP1, GP2, and GP3, respectively).

Due to the difficulties chickpeas face from susceptibility to abiotic and biotic stresses, the concept of a "crop ideotype" has gained importance, as it aims to develop desirable plant models with enhanced seed yield, oils, and other useful traits through strategic approaches referred by Siemens [39]. Donald [40] studied ideotypes for the first time in cereals, and revealed two important approaches: (i) "defect elimination", or the integration of disease resistance to a susceptible genotype from a resistant genotype, and (ii) "selection for yield", or the improvement of yield after crossing desirable parents [40]. Plant breeders tend to base selection on phenotype, whereas the genetic ideotype approach might help clarify the selection process. After a genetic ideotype is determined, it must be built into a breeding program as well [41]. There have been lots of ideotype determinations in chickpeas so far [42–45]. Ideotypes defined in accordance with the needs of farmers and agro-morphological and physiological features under drought and extreme temperature (heat and cold) conditions were reported by Toker et al. [5]. Although chickpeas are fit to grow in less soil moisture in drought-prone and heat environments, drought and heat stresses are essential limitations to chickpea production. In some climatic areas, such as Mediterranean regions, autumn sowing and early flowering could be recommended to make the winter rains beneficial in short rainy seasons under dryland cropping [46]. Water scarcity alone is responsible for about 70% of losses in agricultural yield globally [47]. In chickpeas, drought may occur at any growth phase, viz., sapling establishment, vegetative, and reproductive phase. Drought occurring during the reproductive stage is termed as terminal drought, and chickpea crops in rainfed situations often experience drought at the terminal stage, which mainly affects the quality and quantity of the harvest [48]. Notably, drought stress reduces chickpea yield by 40–50% [49].

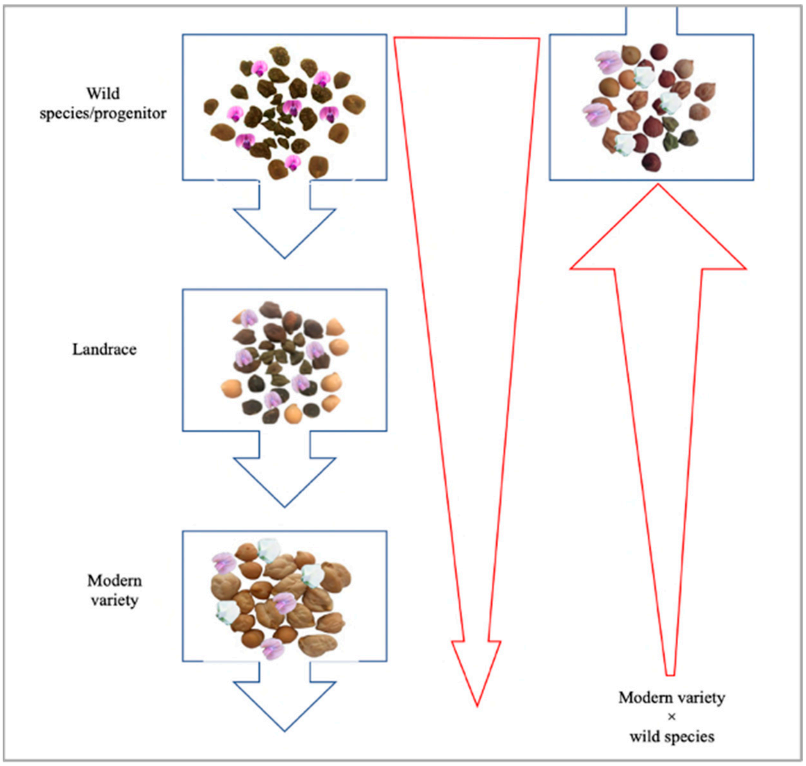

Figure 2. The reduced genetic diversity from wild species (progenitor) to modern chickpea varieties. The arrow indicates the reduced genetic diversity (left side). The arrow shows the increased genetic diversity when wild species are used in hybridization (right side).

Breeding drought-tolerant cultivars is important for harvesting potential yield in limited water conditions. To breed drought-tolerant cultivars, the proper exploration of the physiological, biochemical, and genetic mechanisms of the attributes imparting drought tolerance is quintessential. Drought tolerance is a multifaceted attribute, which has a polygenic nature of inheritance and often fluctuates by diversity and differences in plant phenology [50]. The generation of chickpea cultivars with early maturity is a leading approach for minimizing yield losses due to terminal drought stress. Moreover, the direct selection of improved genotypes with yield stability over multiple locations is another widely employed approach for identifying drought tolerant high-yield varieties of chickpeas. However, alternatively, indirect selection based on secondary morphological, physiological, and biochemical traits is also a strategy for breeding drought cultivars in chickpeas and is similar to other pulses. The availability of physical maps, functional genomic tools, whole genome sequence of chickpeas, and integrated molecular breeding and genetic engineering approaches will pave new opportunities for imparting tolerance to drought in chickpeas [51]. This review aims to enrich the current understanding of the mechanisms, physio-biochemical processes, and the omics technology of drought and heat tolerance for designing molecular breeding approaches to develop drought- and heat-tolerant chickpea cultivars. Previously, few review articles have been published that discussed separately different aspects, including the availability of genotypic variability, QTLs, molecular and physiological mechanisms, the impact of heat stress, the role of few genes, and the availability of candidate genes and breeding strategies for heat and drought tolerance in chickpeas [9,52–54]. However, the present review article comprehensively enriches our current understanding of the mechanisms, physio-biochemical processes, omics technology, and genes for heat and drought tolerance and their use for designing molecular breeding strategies for developing drought- and heat-tolerant chickpea cultivars.

2. Impact on Morpho-Physiological, Biochemical, and Molecular Parameters Due to Drought and Heat Stresses

The drought severity in chickpeas can be ascertained by considering different morpho-physiological and biochemical attributes [5,55–58] (Figure 3). Drought conditions during the seedling establishment stage could hamper the germination potential, rate, spread, and seedling development in chickpeas [59–61]. Stomatal conductance in chickpeas could decrease by 93% under acute drought [62]. A reduction in CO_2 assimilation, CO_2 diffusion, transpiration rate, relative water content (RWCs), and membrane strength is observed during drought situations in chickpeas [58]. A reduction in cell water potential, cell size, altered lipid biosynthesis and Rubisco, and ATP synthase activity, and an increase in the leakage of electrolytes from the cell, poor membrane integrity, and permanent cell damage are drought stress-associated abnormalities is observed. It reduces chlorophyll content and electron transport and causes the disruption of PS II, decreases assimilate translocation and carbon fixation, and ultimately hinders overall photosynthetic and other metabolic events [62]. During drought, nitrogen and carbohydrate metabolisms are reduced in chickpeas [63–66]. The reactive oxygen species (ROS) are produced under drought, causing severe oxidative damage. In drought conditions, antioxidant enzymes, for instance, superoxide dismutase (SOD), glutathione reductase, catalase, and peroxidase activities, vary in chickpeas [65].

Flowering to pod setting is the most delicate stage of chickpea to drought exposure. Chickpea crops planted in drought realize poor dry matter accumulation and harvest index compared to irrigated conditions [66,67]. Pod abortion in chickpeas due to water deficit conditions occurs more on secondary branches than primary branches. Pod production and viability are impacted the moment the water deficit begins. Notably, in the Kabuli market, types of pod abortion are greater than desi types [68]. Dehydration conditions disturb the vegetative, reproductive, and pod-filling period in chickpeas, which ultimately affects the size of the seeds. A drop in the number of flowers, pod setting, and amplified pod abortion is due to drought stress and resulted in reduced pod production in chickpeas. Likewise, the quantity of seeds by individual plants is reported to decline due to drought conditions [69]. Drought at early stages decreases chickpea growth, which leads to poor biomass accumulation and stunting [70], while during podding, poor pod set and increased abscisic acid (ABA) have been noticed [71]. Poor nodule formation and reduced biological nitrogen fixation have also been reported in response to drought in chickpeas, which ultimately lead to a sizable yield penalty [72,73].

Heat stress affects various chickpea growth stages from germination to grain yield. Likewise, heat stress affects various physiological processes such as transpiration, photosynthesis, respiration, osmotic regulation, and membrane thermo-stability [4,55]. Starting from germination, temperature becomes a limit in germination. According to Singh and

Dhaliwal [74], germination does not occur at temperatures above 45 °C. The temperature of 40/30 °C showed a decrease in biomass in tolerant and susceptible genotype experiments compared to the 35/25 °C temperature treatment [75]. The complexity of these effects is very important to review as information for steps to increase chickpea tolerance to heat stress. Compared to the vegetative stage, heat stress has a more severe impact on the reproductive stage. During the reproductive phase, in general, some of the effects caused by heat stress on chickpeas include increased flower abortion, a decreased number of flowers, pollen sterility, altered anther locule, a decreased stigma receptivity and fertilization, a reduced remobilization of photosynthate to seed, ovary abnormalities, and a decreased number of seeds and yield [52,76,77]. Chickpea accessions with multiple pods and compound leaf traits have an advantage in high-temperature stress compared to double pods with compound leaves and single pods with simple leaves with higher seed yields in Kabuli chickpeas [78]. Heat stress can result in damage to pollen and anther structures such as thickened anther epidermis, alterations in the number of anthers locules, and sterile pollen [77]. Pollen damage results in a decrease in chickpea production. There is a detrimental effect on the function of stigma and pollen fertility in chickpeas in growth experiments above 45 °C [79]. Screening of genotypes tolerant to high-temperature stress showed several genotypes tolerant to heat stress, as evidenced by a small decrease in pollen viability, pollen germination, high seed yield per plant, the presentation of pod set, photosynthesis ability, slight damage to membranes, oxidative processes, and leaf water status. Photosynthetic efficiency, chlorophyll, pollen viability, and pollen germination have a strong correlation with yield [80].

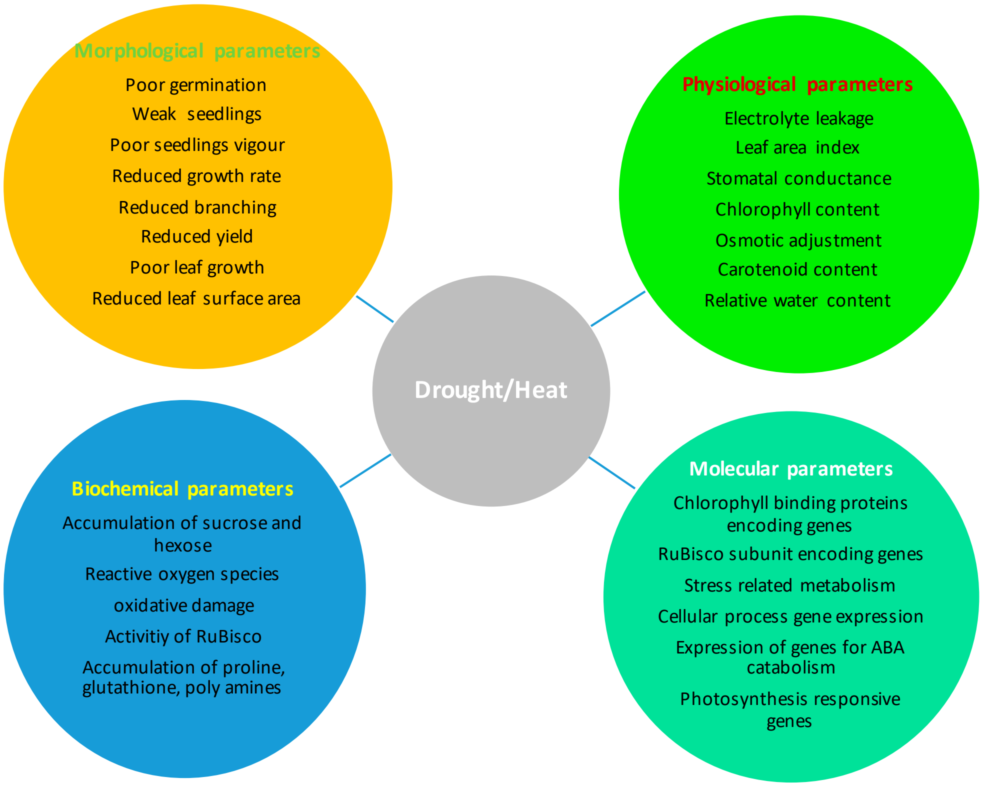

Figure 3. Morphological, physiological, biochemical, and molecular parameters based on drought stress.

In the physiological context, chickpeas are more sensitive to heat stress than other legumes on photosystem II (PSII) and membrane stability at 50 °C for 48 h. The Calvin cycle and PSII are considered to be the most heat-sensitive in the process of photosynthesis [81]. The most important enzyme in heat-sensitive carbon fixation is rubisco. Increasing temperature causes enzyme inhibition, which reduces carbon fixation. Heat results in the breakdown of this subunit in PSII, which causes a significant decrease in oxygen release as a result of partial damage to the manganese complex [82]. Heat can also cause an increase in the permeability of the thylakoid membrane, which makes the membrane more suitable to be damaged by reactive oxygen species (ROS), and the subsequent effect is that the photosynthetic apparatus is damaged [83]. Heat stress causes significant changes to several factors, including the formation, absorption, and energy transport of electrons along the cross-section of the reaction center [82]. Chlorophyll damage and chloroplast disruption induced leaf senescence in chickpeas at 35/16 °C for 10 days [84]. The decrease in chlorophyll content due to heat stress causes chlorosis in experiments > 32/20 °C during the reproductive stage [75]. The quantum yield or PSII was confirmed to be disturbed at 46 °C (during pod filling) as a form of damage to the photosynthetic system due to heat [85]. In other experiments, PSII damage was also confirmed in chickpeas at 50 °C for 48 h [81]. Associated with oxidative stress, ROS causes damage to membrane lipids, proteins, and DNA. Many physiological processes regulated by enzymes are sensitive to heat stress, which causes the disruption of metabolic pathways and uncouple enzymes by ROS [86].

3. Current Knowledge of Different Mechanisms Responsible for the Adaption of Chickpea Plants under Drought and Heat Conditions

Resistance mechanisms for heat and drought stresses in plants include (i) escape through earliness, (ii) avoidance through morphological traits, such as better root traits, compound leaves or multipinnate leaves, and double-/multiple-podded traits, and (iii) tolerance through physiological traits, such as special tissue and cell abilities [87,88]. Drought tolerance is a trait that involves different mechanisms to sustain plants under water deficit conditions (Figure 4). Initially, the mechanisms of drought resistance in plants have been described as drought escape and drought tolerance [88]. However, later on, drought tolerance mechanisms were grouped broadly as escape, avoidance, and tolerance [89]. Through quick phenological development, the plant finishes its life cycle through escape before the onset of severe water deficit in soils.

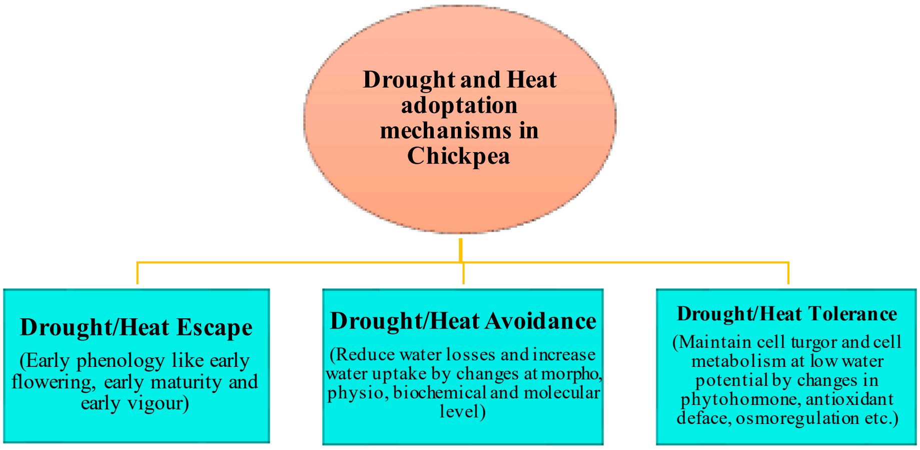

Figure 4. Adaptive strategy of chickpea plants under drought and heat stress.

Breeding for a short duration or early maturing varieties involves a drought escape mechanism and has proven its usefulness in improving yield under water deficit conditions [7,90]. Several varieties were developed [91]; however, all had lower yields compared to the best existing late-maturing varieties under well-watered conditions, as they cannot accumulate enough total plant biomass due to a reduced total photosynthetic period [91]. Early vigor is also considered a mechanism for escaping drought in certain plant species [92]. Early flowering and maturity give plants a way to mature early in cases of terminal drought, and subsequently prevent yield loss [70,93].

In the case of avoidance, plants maintain both water uptake and water loss to prevent crop losses during drought. Deep root systems for absorbing water from lower strata of soil and a smaller leaf area for restricting losses of water through transpiration are the ideal characters for drought avoidance in chickpeas and are extensively embraced for the improvement of genetic potential. The positive alignment between grain yield and root biomass under a moisture stress state has been demonstrated in chickpeas [94]. Therefore, deep root systems can absorb subsoil water below 30 cm soil depths and offer exciting possibilities to increase yield under terminal drought stress. Thus, increased root depth or expending the root system, reduced epidermal conductance, leaf rolling or folding, spreading type habit, and the presence of cuticular wax on surfaces all aid in maintaining optimum water potential [75].

Plants that are tolerant to drought can better maintain turgor, even at low water potential, thus performing optimal metabolic activities under water deficit conditions through protoplasmic tolerance or synthesis of osmoprotectants or compatible solutes. Osmotic adjustment is a vital physiological parameter that controls the absorption of water and maintenance of cell turgor pressure during moisture stress circumstances [95] and has an encouraging association with grain yield in chickpeas [96–98]. Membrane stability, chlorophyll, and high water use efficiency are other important physiological parameters that help genotypes in mitigating drought stress [99–101]. Proline is an example of a harmonious solute that provides a safeguard to plants against oxidative damage by ROS under drought but is not explored as a screening tool in chickpeas for drought resistance [92]. Polyamines, a secondary metabolite, are usually produced during high temperature/drought stress [66,102] and provide some degree of stress tolerance under these adverse conditions. Synthesis of phytohormones like auxin, cytokinins, and gibberellins decline, whereas the corresponding levels of ABA and ethylene tend to upsurge due to drought. Under moisture deficit conditions, ROS induces oxidative impairment to cellular macromolecules and cell structure, i.e., lipid peroxidation. Enzymatic and non-enzymatic antioxidants serve as a defense mechanism against ROS-induced damage in the plant cells and have proven to be an adoptive response in plants in water-limiting situations [103,104].

Mechanisms of adaptation to heat stress in chickpeas can take three forms: heat release mechanisms, heat avoidance mechanisms, and heat tolerance mechanisms [105]. In the first mechanism, heat tolerance is initial and of short duration. This form of adaptation occurs in chickpea flowering. Early flowering and ripening occur under high-temperature stress. It has been observed in south Indian and Mediterranean species in the months with high temperatures [5]. Observations have shown mechanisms to avoid heat stress, such as leaf orientation, transpiration modulation, and radiation reflection [105]. The next mechanism, tolerance, involves the composition of membrane lipids, membrane integrity, heat shock proteins (HSPs), and osmoprotectants. Oxidative stress and cellular membrane integrity cause significant injury to heat stress-sensitive genotypes [75,87,106]. Salicylic acid (SA) plays an important role in tolerance to high-temperature stress in chickpeas and other plants. The application of SA can reduce the induction of membrane damage due to heat stress in chickpeas. The presence of SA also changes the content of proline and proteins by inducing several stress enzymes such as the activity of catalase (CAT), ascorbate peroxidase (APOX), and peroxidase (POX) [107]. Abscisic acid (ABA) has also been confirmed to provide heat tolerance. Giving ABA to chickpeas reduces oxidative damage, as measured by the content of hydrogen peroxide and malondialdehyde compared to the presence of the biosynthetic inhibitor fluridone (FLU) [108].

4. Genetic Knowledge of Traits Responsible to Chickpea Drought and Heat

Several morpho-physiological traits have been reported by various researchers [7,57,90,99,109–124] to impart drought tolerance in chickpeas, as presented in Table 1. However, large genetic variability for these traits is reported among chickpea genotypes [125]. Inheritance of these traits was reported to be under the control of a large number of oligo and/or poly genes along with different gene interactions [50]. For example, leaf characters are mostly governed by oligo genes [126].

Table 1. Marker traits associated with drought tolerance in chickpeas.

Marker Trait	Mechanism	Ref.
Early flowering and maturity	Escape	[7,90,109,110]
Root traits like a prolific root system, length, density, dry weight, diameter, surface area, and volume	Avoidance	[111–115]
Carotenoid concentrations and ion accumulation (Na+ and K^+)	Tolerance	[116]
Water use efficiency	Tolerance	[99,117–119]
Osmotic adjustment	Tolerance	[118,120]
Relative water content	Tolerance	[116]
Chlorophyll content	Tolerance	[57,116]
Shoot biomass, canopy temperature depression, and leaf area index	Avoidance	[113]
Stomatal conductance	Tolerance	[121]
ABA regulation	Tolerance	[122]
Antioxidant scavenging enzymes, proline, and molecular chaperones	Tolerance	[57,123,124]

The initial vigor in chickpeas is impacted by two genes having duplicate dominant epistatic modes of action [127], while root traits, i.e., length, dry weight, and density, showed polygenic inheritance with additive gene action [128]. Breeding for short-duration chickpea cultivars is an important strategy for combating terminal drought stress. Therefore, inheritance knowledge of early flowering can help to breed the early maturing genotypes in chickpeas. A recent study reports a major recessive gene governing early blossoming [110]. However, many of the traits conferring drought tolerance are governed by polygenes and additive gene effects [8]. These initial findings about the genetic mechanism of drought tolerance are based on approaches, like generation mean analysis and diallel analysis, relying majorly on yield and yield attributes at drought and irrigated conditions [129].

The use of genetic diversity in the species for the target traits is the main goal for plant breeding. Different breeding strategies including traditional breeding, modern molecular breeding, OMICS-based, and transgenic approaches generate genetic variation in the crops and then introduce the genes related to the traits of interest into the new cultivars [130,131]. Therefore, the collection of genetic variation, the selection of plants presenting desirable genes from different parents, and monitoring selected lines are the three main principles of a breeding program [132]. In earlier times, the selection of landraces was used by chickpea breeders for developing new varieties, while hybridization has been preferred recently [133]. However, these techniques include traditional breeding approaches and are still not adequate for ensuring global food security for the future world population. The progress in modern techniques can have a big role in increasing the genetic gain in yield under environmental stress conditions [8]. In this context, the utilization of chickpea genetic and genomic resources can lead to increased yield and the development of heat stress-tolerant cultivars [133,134]. Thus, the incorporation of traditional and modern molecular techniques is necessary for accelerating breeding programs in chickpeas.

5. Selection Indices and the Identification of Donors for Drought Tolerance

Selection for drought tolerance is tricky due to the strong association between genotypes and the environment along with restricted information about the role and function of different tolerance mechanisms. Hence, different drought resistance indices have been used by researchers to evaluate genetic differences for developing drought-tolerant genotypes. To appraise the behavior of plants under drought, certain selection indexes are important indicators [135]. These are mean productivity (MP), geometric mean productivity (GMP), the stress stability index (SSI), the stress tolerance index (STI), the yield index (YI), the superiority index (SI), drought tolerance efficiency (DTE), and the abiotic tolerance index (ATI) [135–139]. During the recent past [7,38,43,49,91,110,114,115,140–147], trait-specific donors have been identified for those traits, which deciphered the inheritance and genetics of resistance/tolerance under drought stress in chickpeas. Important genetic sources were identified based on different morphological, physiological, and biochemical traits (Table 2).

Table 2. Donor for drought tolerance in chickpeas.

Tolerant Sources (Donors)	Basis for Tolerance	Ref.
ICC 4958	Length, dry weight, and density of root	[140]
ICCC 37, ICCV 2, ICCV 10, and ICCV 90629	Early phenology traits	[48,141]
ICC series: 4958, 1356, 3512, 8261, 4872, 15697, and 13523	Deep root systems and root length density	[142]
ICC 10480 and ICC 5680	Narrow fewer pinnules and smaller leaf areas	[143]
H208, RS11, H355, RS10, S26, and G24 Azerbaijan 583	Deep root, root mass, and root volume	[43]
ICC 4958 and ICC 8261	Deep root, rapid rates of root development and water extraction, and drought adaptive root traits	[91,143]
ICC 4958	Root volume and root length	[43]
ACC317 and ACC316	Early phenological trait	[7]
ICC 7571	Harvest index and DRI	[144]
RSG 143-1, RSG 973, and CSJ 73	Drought susceptibility index, WUE, plant dry matter, and low membrane injury	[145]
ICCV 10 and ICC 14778	Better partitioning and superior yield	[114]
ICC 16374B, ICC 9586, ICC 15510, and ICC 867	Deep rooting	[115]
FLIP 87-59 C	Stress yield	[146]
RSG 991, RSG 888, and RSG 973	Root penetration depth, WUE, and plant dry matter	[145]
ICC 4958	Osmotic regulation	[147]
IG5844, IG5856, IG5883, IG5867, IG5884, IG5887, IG5894, IG5896, IG5906, IG5908, ILWC 118, ICC 17207, and ILWC 21	Relative water content (RWC), membrane stability index (MSI), and drought tolerance index	[49]
IG5844a, 5856, 5867, 5884, 5887, 5894, 5896, 5906, and 5908	(MSI) and (RWC)	[7,41]
ICC 8261 and ICC 4958	Root traits	[91]

6. Breeding Tactics for Enhancing Drought Tolerance in Chickpeas

Different breeding strategies including conventional breeding, current modern molecular breeding, OMICS-based and transgenic approaches may be utilized to manipulate the genetic background of chickpea genotypes toward drought tolerance (Figure 5). These breeding techniques could be helpful in the ideotype improvement of chickpea crops, which will serve as a tool for combating drought.

6.1. Breeding of Drought- and Heat-Tolerant High-Yield Varieties Using Traditional Breeding Approaches

Enhancing drought tolerance in crops deploying traditional breeding is a worthy approach and has been utilized as a prime tactic for the improvements of crops [148]. Conventional breeding techniques essentially require heritable variation for the exploitation of variability to emanate drought-tolerant chickpeas [149]. The breeding accomplishments are usually limited due to their polygenic behavior, low heritability, and inadequate knowledge of the concerned physiological dimensions [8,110,125,150,151]. Most breeding programs for incorporation of drought tolerance are concentrated on selection, i.e., selecting cultivars with higher yield under drought stress. This selection focuses primarily on yield or the physiological/secondary parameters. In chickpeas, certain marker traits serve as promising parameters and may be helpful for screening a large number of genotypes (Table 1). The most essential criterion of these marker traits is a strong genotypic association with grain yield and high heritability coupled with low G × E interaction. The utilization of some secondary traits, like leaf water potential and osmotic adjustment, may greatly enhance the selection efficiency. Some genotypes/donors capable of escaping and avoiding drought are identified considering various marker traits through different selection strategies and are available for further breeding programs in chickpeas (Table 2). The selection of higher yields under moisture stress conditions is regularly practiced to identify drought-resistant genotypes [152]; however, it achieved limited genetic gain while following this procedure exclusively [153]. If the source for drought tolerance is available for germplasm lines or cultivated varieties, the pedigree and bulk methods of breeding could be used. If the source of resistance is in the wild species, then backcross breeding is desirable. Pedigree, mass-pedigree, and single-seed descent breeding approaches are ideal for the incorporation of major alleles/QTLs from donor to recipient parent. It has also been suggested that multiple cross-approaches may be used to combine different desired attributes simultaneously after the source genotypes have been identified. A trait-based breeding approach may also be utilized to enhance crop productivity compared to yield under stress condition-based evaluation [154].

Figure 5. Breeding strategy for the development of drought- and heat-tolerant genotypes in chickpeas.

It is clearly known that the yield-related traits such as plant height, the number of pods per plant, the number of seeds per pod, biological yield, the harvest index, grain yield, 100-seed weight, and abiotic stress tolerance are multigenic and quantitatively inherited. These traits are greatly influenced by the genotype (G) and the environment (E) interactions (G × E) [155]. However, over the past fifty years, conventional breeding approaches such as plant introduction, hybridization, and mutation have made it possible to reveal the yield and abiotic stress tolerance traits in chickpea cultivars [156].

Chickpeas are self-pollinated crops, and pure line selection from landraces has been the most used method for chickpea breeding. Fixing genetic variation in inbred chickpea lines is the main objective for breeding. However, it takes about 7–8 years or more. The long-day nature of chickpeas can reduce the length of the breeding cycle, and they successfully produce two generations per year in either off-season nurseries or glasshouse facilities. The recent technology known as "speed breeding" reduces the generation time by an extension of the photoperiod to produce six or seven generations per year in chickpeas [157]. Cultivated chickpeas are a good source of important genes for heat tolerance. Recent studies indicated a large genotypic variation for heat tolerance in chickpeas in the reproductive stage [11,158]. Several heat-tolerant genotypes including landraces (ICC 637, ICC 762, ICC 1180, ICC 1205, ICC 2065, ICC 4567, ICC 4958, ICC 8950, ICC 10393, ICC 15618, and ICC 16524), breeding lines (ICC 5221, ICCV 07108, ICCV 92809, ICCV 07109, ICC 15567, ICCV 07110, and ICCL 83105), and elite cultivars (GG 2, ICCV 92069, JG 6, PhuleG 12, Vaibhav, ICCV 89314, Rajas, ICCL 83149, ICCC 37, DigVijay, ICCL 87207, KPG 59, ICCL 83110, ICCL 82108, Pusa 547, and Pusa 391) were showed in Table 3 [7,112–116,159]. The study by Kaushal et al. [76] reported temperatures above 35/20 °C. Day/night did not decrease the pods set in heat-tolerant chickpea genotypes but it caused flower abortion in sensitive genotypes. A greater pod set was observed in heat-tolerant genotypes (ICC 1205 and ICC 15614) compared to heat-sensitive genotypes (ICC 4567 and ICC 10685) [77]. Based on physiological and biochemical studies [76,133], ICCV 92944 was described as a heat-tolerant genotype. ICCV 92944, ICC 1205, and ICC 4958 chickpea genotypes have been reported as sources of heat stress tolerance under field conditions [133].

Table 3. Sources of heat tolerance in chickpeas.

Sources	Genotype	Ref.
Landraces	ICC 637, ICC 762, ICC 1180, ICC 1205, ICC 2065, ICC 4567, ICC 4958, ICC 8950, ICC 10393, ICC 15618, and ICC 16524	[114,159]
Breeding lines	ICCV 07104, ICCV 07105, ICCV 07108, ICCV 07109, ICCV 07110, ICCV 07115, ICCV 07117, ICCV 07118, and ICCV 98902	[112,115,159]
Elite cultivars	GG 2, ICCV 92069, JG 6, PhuleG 12, Vaibhav, ICCV 89314, Rajas, ICCL 83149, ICCC 37, DigVijay, ICCL 87207, KPG 59, ICCL 83110, ICCL 82108, Pusa 547, and Pusa 391	[116,159]
Wild *Cicer* relatives	*C. anatolicum*, *C. microphyllum*, *C. montbretii*, *C. oxydon*, *C. reticulatum*, and *C. songaricum*	[7]

Mutagenesis approaches have successfully been used in chickpeas because of their narrow genetic diversity, small flowers, and hybridization difficulties. For example, Toker [160] used gamma rays in 10 *Cicer* species to improve heat stress tolerance and observe mutant lines that were more tolerant to the heat than their parents. Mutagenesis creates genetic variation with the main objective of increasing yield and stress tolerance. The joint FAO/IAEA Centre of Nuclear Techniques in Food and Agriculture reports a total of 27 mutant high-yield chickpea cultivars that have been recently released that are tolerant to abiotic stresses.

6.2. Exploitation of Wild Relatives through Pre-Breeding for Drought and Heat Tolerance

The unavailability of resistance sources in the cultivated species is a prime limitation in chickpea improvement toward drought tolerance. However, the crop wild relatives (CWR), *C. reticulatum*, *C. bijugum*, *C. echinospermum*, *C. judaicum*, and *C. pinnatiifidum*, are identified as the potential genetic sources for the incorporation of resistance to several abiotic stresses [15]. The genetic potential of CWR may be exploited by developing the pre-breeding lines using different approaches. Since *C. reticulatum* is fully crossable with *C. arietinum*, it can be used in introgression programs. The exploitation of the remaining cross-incompatible species can be performed through specialized techniques, including tissue culture. Introgressing useful genes into agronomically acceptable backgrounds through pre-breeding has emerged as an economic tool in the recent past [137,161]. The CWR of chickpeas is reported to show considerable tolerance to drought [23,162]. Numbers of drought-tolerant genotypes were developed by transferring genes of drought tolerance into cultivated chickpeas from *C. reticulatum* [7,94]. For example, the interspecific crosses attempted in India by various NARS institutions have incorporated useful abiotic stress resistance in chickpeas [49]. However, a poor seed set (1.69%) of such crosses is an important issue limiting the utility of introgression breeding.

Pre-breeding has recently emerged as a highly cost-efficient tool for the introgression of useful genes from wild relatives. Crop wild relatives are important sources of genetic diversity for increasing the narrow genetic pool of cultivated crops [163] and have been used for biotic and abiotic stress tolerance [17,23,29,163–165]. The barriers to interspecific hybridization have limited the use of wild species. Only two species, *C. reticulatum* Ladiz. and *C. echinospermum* P.H. Davis, can be crossed easily with the cultivated chickpea [166]. Alien gene introgression into the cultivated chickpea has not been successfully carried out so far because of sexual incompatibility with the other *Cicer* species in the second and third gene pools [167]. However, hybrid seedlings have already been reported in interspecific crosses between cultivated chickpeas and some wild *Cicer* species, such as *C. bijugum* K.H. Rech, *C. judaicum* Boiss., and *C. pinnatifidum* Jaub. and Sp. [168–171]. However, an exploitation of the remaining cross-incompatible species can be performed through appropriate tissue culture techniques. Although there are many heat-tolerant sources in the cultivated chickpea, the tolerance of many accessions of perennial wild *Cicer* species such as *C. anatolicum* Alef., *C. microphyllum* Benht., *C. montbretii* Jaub et Sp., *C. oxydon* Boiss. Et Hoh., and *C. songaricum* Steph ex DC. were found to be highly tolerant to heat stress compared with the cultivated chickpea. *C. pinnatifidum* and *C. reticulatum* performed similarly under heat conditions when they were compared to the heat-tolerant cultivated checks [7]. Moreover, several accessions of wild *Cicer* species such as *C. anatolicum* (PI 561078, PI 383626, WG-14183), *C. microphyllum* (PI 532928), *C. montbretii* (WG-14189), *C. oxydon* (PI 561103), and *C. songaricum* (WG-4574) were detected as sources of heat tolerance.

6.3. Exploitation of QTLs/Genes for Drought and Heat Tolerance Employing Marker-Assisted Breeding

The majority of the traits that impart tolerance to drought are quantitatively inherited and show polygenic inheritance. These traits show complex inheritance patterns due to interactions among genes. An elaborated genetic understanding of drought tolerance-related attributes is a basic requirement for exploiting them in regular breeding programs. In this context, molecular markers offer an extraordinary opportunity for locating QTLs controlling these traits, as they are not impacted by external environmental conditions [172]. To map the genes or QTLs pertaining to drought tolerance in various crops, different sorts of molecular markers (e.g., SSR, RFPL, AFLP, and RAPD in the past, and SNPs today) have been embraced [173–175]. In chickpeas, utilizing SSR/EST (expressed sequence tags) marker genes/QTLs have been associated with drought tolerance and responsive attributes [154,176–181]. Bi-parental mapping populations developed by different researchers [36,72,136,164,165,167–171] facilitated the depiction of markers allied to different QTLs for drought-tolerant attributes in chickpeas (Table S1). Tightly linked markers of a targeted QTL are helpful for developing near-isogenic lines; they improve our understanding of the underlying mechanism of drought tolerance and facilitate introgression into adaptive cultivars. Marker-assisted breeding (MAB) efforts have assisted in developing drought-tolerant chickpea varieties by incorporating large root systems [154]. Thudi et al. [176] introgressed QTLs controlling this trait in three popular varieties of chickpeas by using a marker marker-assisted backcrossing approach (MABC). This technique was utilized to transfer drought tolerance from ICC 8261 into chickpea cultivars "Chefe" and "KAK 2" [133]. This drought-tolerant population was developed in the background of "JG 11" by deploying a "QTL hotspot" harboring numerous QTLs for drought tolerance from ICC 4958 [154]. The same source (ICC 4958) was used in Ethiopia to emanate a drought-tolerant cultivar in the background of JG 11 (Geletu) by introgressing a QTL hotspot using the MABC, which recorded a 15% higher yield over the check variety "Teketay". The use of marker-assisted recurrent selection has been initiated during the last decade in chickpea crops to identify and emanate drought-tolerant genotypes [159]. Recently, the first MAB chickpea variety (Pusa 10216) was developed by transferring drought-tolerant genes from ICC 4958 to Pusa 372, which showed about a 16% increase in yield over Pusa 372 in drought conditions across India [177,178].

As heat stress is a complex trait controlled by many genes/QTLs, the screening and selection process for heat-tolerant genotypes is difficult and time-consuming in the field [52,179]. Genotype × environment (G × E) interaction also limits the selection of heat-tolerant genotypes. In recent years, significant advances have been made in developing novel genetic tools for genetic diversity analysis, gene/QTL mapping, the construction of linkage maps, and marker-assisted selection (MAS) [180–182]. Several studies have been carried out earlier to identify the quantitative trait loci (QTLs) for heat stress tolerance [51,159,177,183,184] (Table 4).

Table 4. List of some major QTLs associated with traits related to heat tolerance in chickpeas.

Stress	Trait	LG	Markers/Locus	Cross/Genotypes	Ref.
Heat	SY	CaLG05	Ca5_44667768-Ca5_46955940	ICC 4567 × ICC 15614	[183]
	CC	CaLG06	CPGR206-H3G031	DCP 92-3 × ICCV 92944	[184]
	MSI	CaLG05	NCPGR267	Desi genotypes	[185]
	MSI	CaLG06	H2L102	Desi genotypes	[185]
	MSI	CaLG07	TS 53	Desi genotypes	[185]

LG: linkage group, SY: seed yield, CC: chlorophyll content, MSI: membrane stability index.

The study by Paul et al. [183] was conducted to identify QTLs related to heat tolerance in chickpeas using 292 RILs derived from the cross ICC 4567 (heat sensitive) × ICC 15614 (heat tolerant). Different late-sown and normal-sown environments were used for phenotyping RILs. Heat tolerance-related traits including days to 50% flowering, podding behavior, the number of pods, the number of seeds, seed yield, the harvest index, and 100-seed weight were identified. Under heat-stress environments, a high variation in the number of pods, number of seeds, seed yield, and harvest index were observed compared to the controlled environment. Combining the high-density genetic map, four QTLs for heat tolerance-related traits were detected on CaLG05 and CaLG06. Jha et al. [184] identified a total of 77 QTLs for heat tolerance-related traits such as 100 seed weight, days to pod initiation, the nitrogen balance index, and chlorophyll content. Over 30% phenotypic variation for 100-seed weight and days to pod initiation were explained in a genomic region on CaLG07. Kushwah et al. [51] identified 28 QTLs related to heat tolerance using 187 RILs developed from the cross GPF 2 (heat tolerant) × ILWC 292 (heat sensitive). Stable QTLs for days to flowering can be one of the dominant factors contributing to heat tolerance.

6.4. OMICS-Based Technology and Transgenesis Approach for Drought and Heat Tolerance in Chickpeas

"Omics" is an amalgamation of different modern approaches, viz., proteomics, genomics, metabolomics, and transcriptomics. The advancement in different omics approaches has considerably enhanced molecular/genetic perception of any stress and facilitated recognition of QTL/gene(s) and the pathways regulated during drought conditions [154,186–189]. Using different genomic approaches, a number of genes controlling different mechanisms underlying drought tolerance have been recognized in chickpeas

(Table S1). These genes provide opportunities to use them in developing improved drought-tolerant cultivars using different genomic approaches, including genome editing and genomic-assisted breeding.

Genomics generates molecular markers that can be used in the analysis of genetic diversity and mapping of the QTLs/genes for drought tolerance and pertaining traits. These linked markers hold great promise for the manipulation of QTLs through MAS, leading to drought-tolerant cultivar development [186]. Further, high-throughput sequencing technologies have facilitated the mapping of QTLs and the construction of genetic linkage maps of many vital traits, including tolerance to drought in chickpeas [4,187,190]. The data generated under genomics are frequently utilized by breeders in MAS for drought tolerance in chickpeas.

In chickpeas, transcriptional profiling under drought stress using EST sequencing, SAGE, and cDNA microarray analysis has been embraced to understand the magnitude of gene expression in susceptible and tolerant genotypes [191–196]. These efforts have led to the detection of the network of genes controlling drought tolerance. Out of 20,162 ESTs generated in chickpeas, 105 were recorded to have differential expression under drought [195]. At the start of the last decade, Deokar et al. [192] reported 5494 drought-responsive ESTs when compared between a susceptible and tolerant genotype. A transcriptome study in chickpeas identified 3969 and 2623 differentially expressed and 52 and 88 specifically expressed genes in foliage and root tissues, respectively, in drought conditions [196]. A SuperSAGE-based transcriptome analysis identified 7532 differentially expressed transcripts in chickpea genotypes grown in drought and normal conditions [191]. Transcriptome studies of oxylipin synthesis genes unveil early initiation of jasmonates in chickpea roots during drought stress. With the use of the advanced Illumina HiSeq 2000 platform for transcriptome analysis in chickpeas, 4053 (early reproductive) and 1330 (late reproductive) differentially expressed genes were detected in drought-stressed conditions [188]. An Illumina TrueSeq-based transcriptome analysis in chickpeas led to the identification of 169 (root) and 261 (shoot) differentially expressed genes [197]. Kumar et al. [198], using the Illumina platform, identified a total of 1624 genes with different levels of expression for mannitol dehydrogenase, serine hydroxymethyl transferase, cytochrome, galactinol-sucrose galactosyl transferase, and down regulatory genes, like abscisic acid 8′-hy-droxylase, calmodulin-like proteinAP2-EREBP, bHLH, bZIP, C3H, MYB, NAC, WRKY, and MADS in chickpeas under drought stress. Recently, a gene expression atlas (CaGEA) of *Cicer arietinum* was constructed from the ICC 4958 (drought-tolerant) genotype [199]. The non-coding RNAs (ncRNAs) play a vital character in the mechanism of drought tolerance in chickpeas as regulatory elements of gene expression. The small ncRNAs regulate various developmental processes through controlling transcriptional and post-transcriptional gene expression [200]. For example, micro RNA (miR408) resulted in the overexpression of the DREB and other drought-responsive genes and improved tolerance of drought [201]. Recently, a total of 285 non-coding circRNAs have been identified in chickpeas under drought conditions; of which, 11, 46, and 228 were intronic, exonic, and intergenic circRNAs types, respectively [202]. The identified mRNAs showed diverse plant responses like stress tolerance, signal transduction, transcriptional control, response to auxin, GTPase, hydrolase, and oxidoreductase activity.

Proteomics offers a means to categorize the patterns of accumulation of protein under stress [203]. The identification of differentially expressed proteins and understanding their expression patterns under drought conditions will assist in formulating strategies to enhance drought tolerance [204]. The integration of physiological understanding and proteomic analysis is a vital tactic to understand the molecular responses of crops during water deficit exposure [205]. Drought-responsive proteins allied with signal transduction and cell wall modification were identified under water deficit in chickpeas. The differentially expressed 147 proteins may be involved in a variety of functions; for example, gene transcription and replication, molecular chaperones, chromatin remodeling, and cell signaling [206]. About 134 differentially expressed proteins have been recognized in the chickpea drought-tolerant cultivar JG 62, which included the known and novel dehydration-responsive proteins [207]. Cevik et al., [208] recognized 24 differently expressed proteins under drought stress related to proline and sucrose synthesis, cyctosolic fructose-bisphosphate aldolase, and glutamine synthetase in *C. reticulatum*. Various genes were identified in chickpeas under water deficit stress, which is responsible for controlling hormone signaling [189]. In a recent report, significant deviations in mitochondrial protein complement were noticed that have a crucial role in carbon fixation and oxidative phosphorylation in chickpeas [209].

Metabolomic research in plants has provided valuable insights into plant metabolism regulation and responses to drought stress. At water deficit stress, a significant variation was observed in the levels of the key metabolites of different cellular metabolic pathways, such as glycolysis, the TCA cycle, carbohydrates, proteins, and hormone metabolism [210–212]. The metabolites that show marked variation in their accumulation pattern typically under water deficit stress are proline, sugars, and gamma-aminobutyric acid (GABA), as these help plants with osmotic pressure regulation during dehydration [213–215]. On a similar note, differential alterations in the magnitude of various metabolites, viz., L-proline, allantoin, choline, L-histidine, phenylalanine, L-arginine, and GABA, provided a basis of adaptation during dehydration in chickpeas [212]. Thus, progress made in recent years in the stream of omics provides precious information on the configuration and behavior of chickpea genomes, which aids in improving the understanding of their response during drought conditions and subsequent varietal improvement.

The molecular pathways underlying heat tolerance in chickpeas have been extensively studied using advanced OMICS-based technologies such as genomics, transcriptomics, proteomics, and metabolomics. These technologies have enabled scientists to identify crucial genes, proteins, and metabolic pathways involved in heat stress responses, shedding light on the intricate regulatory networks governing these processes. Transcriptomics, an OMICS-based technology focused on analyzing gene expression patterns through high-throughput sequencing, has been employed in chickpea research. Several transcriptome studies have investigated how chickpea genes respond to heat stress by examining changes in their expression levels. For instance, Kudapa et al. [199] utilized RNA sequencing to analyze the transcriptomes of different chickpea tissues (leaves, roots, and flowers) across six genotypes exhibiting varying levels of heat responsiveness. Their study resulted in a vast number of reads, which were then mapped against the chickpea genome. Through this analysis, they identified thousands of differentially expressed genes (DEGs), including novel ones, such as heat stress-related heat shock proteins (HSPs). The researchers also discovered a collection of stress-responsive genes and genetic markers that could be utilized in breeding programs to develop heat-tolerant chickpea varieties. HSPs play a crucial role in heat stress responses by preventing protein denaturation and aggregation, as well as assisting in protein refolding and degradation [216].

Yadav et al. [217] employed transcriptome sequencing to identify differentially expressed HSP18.5 and HSP22.7 genes in response to heat stress in chickpeas. Their findings indicated that these genes were upregulated under heat stress conditions, suggesting their potential role in heat stress tolerance. Additionally, Bhogireddy et al. [218] investigated the involvement of non-coding RNAs, including mRNAs and long non-coding RNAs (lncRNAs), in the response to heat stress in chickpeas. Through their study, they discovered 894 putative lincRNAs in leaf and root tissues under heat stress conditions, along with 61,110 mRNA-targeting genes associated with stress response, signaling, and metabolic processes. In a recent study by Kudapa et al. [219], the transcriptomic response of chickpeas to heat stress was analyzed using RNA-seq. The researchers identified 14,544 DEGs in response to heat stress, with significant enrichment observed in key pathways such as photosynthesis, stress response, and hormone signaling. Moreover, they identified several transcription factors (bHLH, ERF, WRKY, and MYB) that may play a role in regulating the heat stress response in chickpeas.

Proteomic methods have also been employed to study differential stress responses in plants. Researchers have identified proteins that respond to heat stress as well as genotype-specific proteins in various chickpea genotypes, aiming to gain a deeper understanding of heat tolerance adaptation mechanisms. Parankusam et al. [220] utilized gel-free proteomics to identify 482 heat-related proteins in a thermotolerant chickpea genotype. Through this analysis, they uncovered several candidate genes associated with thermotolerance. Similarly, Makonya et al. [221] investigated heat stress and found that the heat-tolerant genotypes exhibited an increase in specific proteins related to protein synthesis, defense, and transport during the flowering stage. These proteins included sucrose-phosphate synthase, sucrose-phosphatase, HSP70, ribulose bisphosphate carboxylase/oxygenase activase, plastocyanin, and protoporphyrinogen oxidase. Furthermore, Parankusam et al. [220] identified 482 heat-responsive proteins, including HSPs such as 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). These proteins were associated with heat tolerance in the tolerant chickpea genotype. The utilization of OMICS-based technologies has significantly advanced our understanding of the molecular mechanisms underlying chickpea heat tolerance. Genomics, transcriptomics, proteomics, and metabolomics have allowed for the identification of key genes, proteins, and metabolic pathways involved in heat stress responses, providing valuable insights into the complex regulatory networks governing these processes.

The utilization of transgenomics or transgenics offers a specific gene-based approach for pinning the apparatuses of stress tolerance in crops. Over the years, numerous transgenic technologies were employed for drought tolerance refinement that involves the manifestation of various functional gene-encoding enzymes related to osmoprotectants synthesis [222], LEA proteins [223], detoxification enzymes [224], and modifying membrane lipids profiles [225]. Transgenic technology has been already used to improve drought tolerance and yield in food crops. The incorporation of gene ZmNF-YB2 TFs and SNAC1 and SNAC2/OsNAC6 into transgenic maize and rice, respectively, improved drought tolerance [226,227]. A choline oxidase gene (*codA*), responsible for the synthesis of glycine-betaine from choline, was targeted at chickpea chloroplasts to improve photosynthetic machinery and handle oxidative damage by ROS [186]. H_2O_2 is accountable for improving the antioxidant machinery in the transgenic chickpea chloroplasts [228]. Transgenes were developed by utilizing various genes isolated either from the same genome or from other genomes and have shown the potential to induce stress resistance in plants. The *P5CSF129A* gene encodes P5CS responsible for the overproduction of proline [186], which plays a significant role in combating drought in chickpeas. The overexpression of *DREB1A* derived from *Arabidopsis thaliana* was utilized to increase the tolerance of drought in transgenic chickpeas [229]. A few candidate genes identified in chickpeas, viz., aquaporins [230], *bZIP, MYB, WRKY* [181], ASR, DHN and DREB and *DREB2A* [176], Efl-1 [231], *REF6* [159], *MyB, AP2/ERF,* and *XPB1* [192], have great potential in drought resistance breeding in chickpeas. Thus, transgenomics offers new and exciting avenues of varietal improvement in chickpeas.

7. Candidate Genes Related to Drought and Heat Tolerance

Several candidate genes have been studied [198,201,232–246] to find their effect on drought mitigation strategies in chickpeas (Table 5). A calmodulin-binding transcription activator (CAMTA) has a role in the mitigation of drought stress by augmenting the actions of antioxidant enzymes [246]. Gene editing for genes involved in imparting drought tolerance, like *Reveille 7* (*RVE7*) and *4-coumarate ligase* (*4CL*), have been found to be encouraging [245]. Notably, *4CL* is a part of the lignin biosynthesis pathway, and *RVE7* is an MYB transcription factor that regulates the circadian rhythm. The knockout or non-functioning of selected genes in the chickpea using DNA-free CRISPR/Cas9 editing demonstrated greater precise editing of the *RVE7* gene than the *4CL* gene. These genes need to be studied in more detail. Similarly, increased cytokinin oxidases/dehydrogenases (*CKX*) in root and advanced chickpea transgenic lines were studied, and it was found that transformed plants have enhanced long-term drought tolerance and an increased root-to-shoot biomass ratio [244]. Transcriptional factor CarERF116 differentially expressed and upregulated several stress-related genes involved in resistance to osmotic stress and decreased sensitivity to ABA at the time of seed germination [242]. *P5CSF129A,* which is involved in the osmoregulation and encoding of the mutagenized Δ1-pyrroline-5-carboxylate synthetase (P5CS) for the excess production of proline, was used in chickpeas [232]. Furthermore, the transgenic events were evaluated for transpiration efficiency (TE), stomatal conductance, photosynthetic activity, and root length during water deficit. The results were positive; however, there are a lot of things to be resolved, like the overexpression of this gene, which causes stress conditions. Many other candidate genes used either through transgenesis or gene editing in chickpeas are presented in Table 5.

Despite thorough physiological studies on chickpea heat stress, the candidate genes and molecular pathways linked to heat resistance have received little attention. The response of the heat-tolerant chickpea to heat stress may be significantly influenced by the gene encodings for bHLH, ERF, WRKY, MYB, C2H2, and NAC. The tolerant chickpea genotypes showed significant differential regulation in genes involved in calcium signaling pathways, which include calcium-permeable stress-gated cation channel 1, calcium-binding protein, and calmodulin-like protein [219]. This suggests that these genes may play a crucial role in the plant's ability to tolerate stress, possibly through the regulation of calcium levels within the cell. Understanding the mechanisms involved in stress tolerance can help in the development of strategies to improve crop productivity under adverse environmental conditions.

Under heat stress conditions, a significant number of HSPs, including HSP 90.5, HSP 83, and small HSPs [219], and HSP18.5 and HSP22.7 [217], have been reported to be differentially upregulated in tolerant chickpea genotypes in response to heat stress. These findings suggest that HSPs play a crucial role in the plant's response to heat stress by protecting proteins from damage and facilitating their proper folding and assembly. Jha et al. [184] found that 32 candidate genes in QTL regions that encode heat shock protein genes, heat shock transcription factors, and pollen-specific genes are involved in controlling flowering time. Understanding the molecular mechanisms involved in stress tolerance can aid in the development of crops that are better adapted to harsh environmental conditions.

In conclusion, molecular studies play a critical role in understanding the underlying mechanisms of heat stress in chickpeas. With the rise in global temperatures, heat stress has become a major constraint for crop production, and the development of heat-tolerant varieties is essential to ensure food security. Molecular studies have enabled researchers to identify the key genes and pathways involved in heat stress response in chickpeas, providing insights into the molecular mechanisms that regulate tolerance to these stresses. The availability of genome sequences of 3366 accessions of chickpeas [247] provide an opportunity to identify the allelic variability for these candidate genes controlling the physiological/biochemical traits imparting drought and heat tolerance in chickpeas. The germplasm lines that carried the allelic variants of these genes can be validated under stress conditions. This information can be used to develop molecular markers that can be used in breeding programs by selecting recombinants having the genes controlling physiological traits imparting heat/drought tolerance along with improved yielding ability, leading to the development of heat-/drought-tolerant varieties. Moreover, editing these candidate genes paves the way for the identification of novel allelic variants for traits imparting drought and heat tolerance in chickpeas [54]. Therefore, molecular studies have great potential to contribute to the development of sustainable agricultural practices and the production of resilient crops that can withstand the challenges of a changing climate.

Table 5. Genes involved in drought tolerance in chickpeas.

S.N.	Gene Name	Promoter	Functional Remarks	Reference
1	P5CSF129A	CaMV 35S	Osmoregulatory gene encoding the mutagenized D1-pyrroline-5-carboxylate synthetase (P5CS) for the over production of proline.	[232]
2	CarNAC	-	A potential regulatory gene contributing to the differential tissue-specific drought tolerability.	[233–235]
3	CaTLP1	CaMV 35S	*CaTLP1* is upregulated by dehydration, and its stress-responsive function is associated with an ABA-dependent network.	[236]
4	Dehydration-responsive element-binding protein 1A (DREB1A) and 2A (DREB2A) genes	Atrd29A	*rd29A* influences *DREB1A* on mechanisms underlying water uptake, stomata response, transpiration efficiency, and rooting architecture in water-stressed plants.	[201,237]
5	Rd17, Rd29a, and Rd29b genes	miR408	DREB1A and DREB2A transcription factors act on Rd17, Rd29a, and Rd29b genes andregulate their expression levels under drought conditions.	[201]
6	CaIMP	-	Regulating phytic acid levels to confer drought tolerance in natural populations of chickpeas.	[238]
7	CaRRP1	-	Secretome analysis reveals dynamic extracellular remodeling that was used to maintain cell structure and biogenesis, in addition to acting in signaling events crucial for cellular homeostasis during stress adaptation.	[239]
8	CaCIPK25	-	Gene expression in chickpeas increases upon salt, dehydration, and different hormonal treatments and is involved in root development and abiotic stress tolerance.	[240]
9	1R-MYB	-	The 1R-MYB transcription factors play an important role in co-regulating drought tolerance in chickpea roots.	[241]
10	CarERF116 gene	CaMV 35S	Transcriptional factor CarERF116 differentially expressed and upregulates several stress-related genes involved in resistance to osmotic stress and reduced sensitivity to ABA during seed germination.	[242]
11	Probable mannitol dehydrogenase, serine hydroxymethyltransferase 4-like, 17.5 kDa class I heat shock protein-like, cytochrome P450 81E8-like, galactinol-sucrose galactosyltransferase-like, xyloglucan endotransglucosylase/hydrolase protein 23, abscisic acid 8′-hydroxylase 1-like, calmodulin-like protein 11, and proline dehydrogenase 2 mitochondrial-like genes	-	The *C. arietinum* drought-responsive genes (CaDRGs) modulate the expression of transcription factors (TFs) AP2-EREBP, bHLH, bZIP, C3H, MYB, NAC, WRKY, and MADS under simulated drought conditions.	[198]

Table 5. *Cont.*

S.N.	Gene Name	Promoter	Functional Remarks	Reference
12	Abscissic acid and the stress-ripening (ASR) gene	-	Play a role in drought tolerance in chickpeas.	[243]
13	CaCKX6	CaWRKY31	Increased cytokinin oxidases/dehydrogenases (CKX) activity in root and advanced chickpea transgenic lines exhibited a higher root-to-shoot biomass ratio and enhanced long-term drought tolerance.	[244]
14	4CL (4-coumarate ligase) and RVE7 (Reveille 7)	-	First report of CRISPR/Cas9-mediated DNA-free editing of 4CL and RVE7 genes for drought tolerance.	[245]
15	CAMTA (calmodulin-binding transcription activator) gene	-	The *CAMTA* gene overexpression in response to drought and salinity stress has shown enhanced activities of various antioxidant enzymes (ascorbate peroxidase (APX), catalase (CAT), glutathione S-transferase (GST), superoxide dismutase (SOD), and monodehydroascorbate reductase (MDHAR)).	[246]

8. Limitations and Future Directions

Drought and heat are serious constraints on the potential yield of chickpeas, particularly since this crop is mostly grown on marginal land under rainfed situations with inadequate or no inputs. Global climate change is exacerbating severe drought and heat conditions, as well as increasing unpredictability. The following are limitations for breeding heat-/drought-tolerant cultivars in chickpeas:

- Heat and drought tolerance are complex in nature because multiple traits are involved to control the tolerance to these stresses;
- Low heritability of the traits imparting drought and heat tolerance due to high G × E interactions limit the breeding of high-yield cultivars with heat and drought tolerance;
- There is still a lack of knowledge on the major physiological/biochemical/morphological traits imparting heat and drought tolerance. This could be due to the unavailability of precise screening methods for these traits;
- The molecular mechanism underlying these traits is not known properly and, which limits the scope for molecular breeding for these traits;
- The traits imparting drought and heat tolerance are controlled by many genes, and a network of genes is involved to control these traits. Therefore, major QTLs/genes are not well-characterized for these traits;
- Only a small percentage of accessions have been screened for their performance under water-limited conditions and high-temperature conditions despite the availability of a range of chickpea germplasm.

However, recent advances in genomics have provided opportunities for designing breeding strategies for developing heat- and drought-tolerant cultivars in chickpeas. The phenology is the most important mechanism, and the pod set is the primary yield component to be considered in heat tolerance breeding. Therefore, serious efforts are required for the accurate characterization of the existing germplasm against these traits, as well as drought and heat stress tolerance utilizing high-throughput screening techniques. Molecular mapping-based QTL identification and transcriptome analysis have paved the way to dissect the complexity of traits imparting drought and heat tolerance (Table S1) [91,248–254]. This led to the identification of major QTLs or candidate genes for heat and drought tolerance in chickpeas [154]. The candidate genes provide the opportunity to develop functional markers from important genes in the future and will be used in future chickpea breeding programs [54]. The sequencing of chickpea landraces and varieties led to the characterization of pangenomes, which may help to more accurately identify the alleles associated with traits imparting in drought and heat tolerance [255] and accurate genes for genome editing using CRISPR-clustered, regularly interspaced, short palindromic repeat technology [256]. Several genes have been identified for drought and heat tolerance in other crop species. These genes are available for developing heat- and drought-tolerant transgenic chickpeas [54]. For example, transgenic chickpea lines carrying *AtDREB1a* identified earlier from *Arabidopsis thaliana* for abiotic stress tolerance showed better performance under water stress conditions [257]. Genome editing has proved its efficiency in the development of climate-resilient cultivars of different crops [258]. In chickpeas, two genes (i.e., RVE7 and 4CL) identified for drought tolerance have been used first time for gene editing [246]. Knock-outs of these genes showed an association with the drought tolerance mechanisms, leading to the laying of a foundation for future genome editing options in the chickpea [259].

The identification of physio-biochemical and molecular traits is important for a proper understanding of the overall apparatus of drought and heat tolerance. Additionally, the refinement of selection norms for different adaptive/physiological attributes is required when addressing the issues of drought and heat stresses. To achieve this, a threshold level of stress should be defined to ensure a similar experimental approach during experiments conducted across various locations. Next-generation sequencing has made the discovery of beneficial alleles easier, facilitating the eventual pyramiding of several beneficial alleles conferring tolerance against drought and heat stresses. The use of robust screening techniques and new and novel breeding tools, such as molecular breeding coupled with the recently available phenomics platforms and "omics" approaches, is essential to enhance the effectiveness and efficiency of selection, such that considerably higher genetic gains are achieved. Finally, interdisciplinary approaches are required for integrating the experience of crop breeders, physiologists, and molecular biologists, which should help to understand and analyze the dynamic behavior of plants against drought and heat stresses, thereby exploiting the full potential of chickpeas. Thus, holistic approaches serve the purpose and help to develop better drought- and heat-tolerant genotypes of chickpeas and may aid in addressing food insecurity and malnutrition-related challenges, in addition to providing protein-rich quality food for millions of consumers across the globe.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/agriculture13091721/s1, Table S1: Different QTLs reported in chickpea under drought stress.

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