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REVIEW ARTICLE

Abiotic stress responses in pulses: Impact of drought and high temperature

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Abstract

Pulses, a vital food crop in India, play a significant role in nutritional security and agriculture. Despite India's prominence in global pulse production, achieving self-sufficiency in pulse production is challenged by escalating drought and rising temperatures. This review examines the responses of pulse crops to drought and high temperatures, highlighting vulnerabilities that affect seed germination, growth, biomass and reproductive traits. Drought and heat stress adversely impact seed germination, vigor and biomass accumulation while altering root and shoot characteristics. Physiological responses, including changes in photosynthesis, nutrient absorption and oxidative damage are explored alongside the implications for root nodule development under water stress. Recent molecular studies identify specific genes and proteins linked to heat tolerance in various legumes, such as green gram, wild creole bean and chickpea. The roles of microRNAs and transcription factors in modulating heat stress responses are emphasized. Additionally, heat stress-induced differential gene expression in cowpea nodules and soybeans impacts flowering pathways and key regulatory genes. Understanding these complex interactions between environmental stressors and pulse crop physiology is crucial for developing resilient varieties and sustainable agricultural practices amid climate change-induced challenges. Future research should focus on elucidating the molecular mechanisms of drought and heat tolerance, particularly stress-responsive genes, transcription factors and microRNAs. Advances in gene editing and genomics will aid in creating resilient pulse varieties, while comparative studies can refine breeding strategies to enhance drought and heat tolerance, ultimately supporting sustainable pulse production.

Keywords

abiotic stress; drought; high temperature; legumes; membrane stability; moisture stress; pulses

Introduction

Pulses are the second most important food crop in India after cereals. They play a crucial role in ensuring nutritional security in India and other developing nations. Pulses possess a diverse nutritional profile, including carbohydrates, proteins, fibers, amino acids and vitamins. They serve as a major protein source for the Indian population. Pulses have been referred to as "Poor man's meat" and "Rich man's vegetable" since they significantly contribute to the nutritional security of people (1-3). Beyond human consumption, pulses have been utilized for various agricultural purposes. They provide nutritious green fodder and feed for livestock and their cultivation enhances soil nitrogen status. Pulses play an important role in crop cultivation practices like crop rotation, intercropping and mixed cropping, which help maintain soil fertility. Pulses thrive well in a wide range of soil and climatic conditions (1-3). India plays a pivotal role in global pulse production and consumption, accounting for approximately 30-35 % of the total area and 27-28 % of total production Worldwide (1). Despite being the largest producer, India still imports pulses and has not yet achieved self-sufficiency (2). In the 2021-2022 agricultural year, India cultivated around 31.03 million ha of pulse crops, yielding approximately 27.69 million tonnes (4). The challenge lies in enhancing productivity to meet domestic demand and reduce import reliance, thereby ensuring sustainable food security (1, 2).

Nearly one-third of global land was affected by drought, presenting a persistent challenge to agriculture, with predicted increases in severity (5-7). While legumes exhibit moderate drought tolerance, they still suffer production losses under severe stress (6). Projections indicate that global temperatures will rise by 0.2 °C per decade, leading to an overall increase of 1.8 to 4.0 °C compared to current levels (8). In January 2024, the average global surface temperature exceeded the 20th century average by 1.27 °C, marking the warmest January on record and surpassing the previous record from January 2016 by 0.04 °C (Fig. 1) (9). Notably, January 2024 marked the 48th consecutive January, with temperatures consistently above the 20th century average (9). These climate changes exacerbate drought and high-temperature stresses, affecting all developmental stages of plants and significantly impacting crop productivity (10).

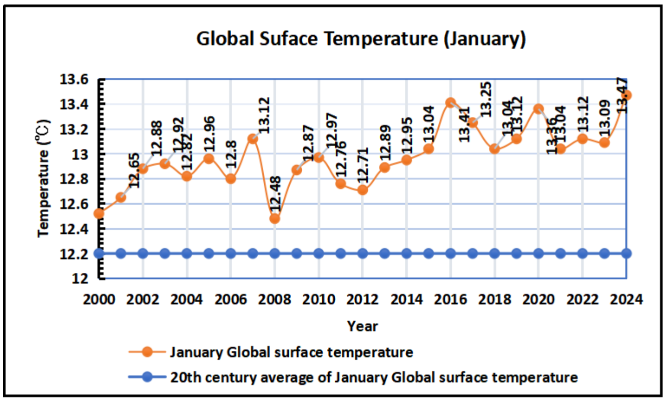

Fig. 1. Comparing the January global surface temperature of the past 25 years with the 20th century average (9).

To address these challenges, understanding the morphological, physiological, biochemical and molecular mechanisms underlying drought and high-temperature tolerance is essential for improving plant breeding and evolving plants that can adapt to future climate change effects. This review aims to explore the impacts of drought and high temperature on the morphological, physiological and biochemical traits of pulse crops, examining how these stresses influence growth, development and yield. By reviewing critical parameters such as leaf area, root development, photosynthetic efficiency and nutrient uptake, the review seeks to highlight adaptive responses across various pulse species under environmental stress. Furthermore, it will investigate molecular responses to drought, including the expression of drought-responsive genes, signaling pathways and stress-related proteins, ultimately providing insights into the mechanisms of drought and heat stress adaptation to support the development of more resilient pulse crop varieties.

Drought and high-temperature effect on morphological parameters

Studies demonstrated that drought and high-temperature stress induced significant morphological changes in pulses, including reduced leaf area, decreased dry mass and inhibited root growth. Common adaptive responses exhibited by pulses towards drought stress included smaller plant size, early maturation, increased leaf thickness and restricted leaf expansion, all of which help to maintain water balance (10, 22-29). Additionally, reduced leaf area and curling minimize transpiration, while trichomes reflect sunlight and help to lower leaf temperature, aiding in water conservation. Deep root systems further enable pulses to access moisture from deeper soil layers, enhancing drought tolerance (10, 24-28). Drought conditions were found to decrease the germination rates of green gram (11) and pigeon pea (12), along with adversely affecting seedling vigor in lentils (13). Water stress specifically hindered hypocotyl elongation in green gram, with a more pronounced effect in separated cotyledons (14). Moreover, plant growth was significantly hampered by drought, high temperatures or their combination, leading to reduced plant heights in mung bean (15, 16), cowpea (17), faba bean (18) and moth bean (19). High temperatures similarly caused a decrease in plant height for chickpeas (20, 21) and lentils (13, 22). The impact extended to plant biomass, which was decreased across various pulses, including pigeon pea, chickpea, cowpea and faba bean due to drought (12, 18, 23, 24) and in chickpea (25) and lentil (22) due to high temperatures. The combined stress further decreased biomass in black gram (26) and lentils (22).

Root development was variably affected by drought and high temperatures, with cowpeas showing enhanced root growth under drought (17). The root-to-shoot ratio increased in chickpea and cowpea, possibly due to longer roots under drought conditions as noted by (27) and (23) respectively, though moth bean showed reduced root length (19). Chickpea exhibited increased root length density at the expense of root diameter under water stress, with root volume remaining unaffected (24, 28). Root dry weight decreased in chickpeas and moth beans due to water stress (19, 29), while cowpeas and chickpeas saw increases in root dry weight under similar conditions (17, 28).

Above-ground drought reduced chickpea shoot length (27) but was increased by high temperature (25). Drought also led to lower shoot biomass in chickpeas and cowpeas (17, 29) and decreased shoot dry weight in both crops (17, 30). In cowpea, stem greenness was diminished by drought (17). Chickpea saw fewer branches due to drought but an increase with high temperatures (25, 27). In lentils, primary branch numbers remained stable under high temperatures and combined stresses, whereas secondary and tertiary branch numbers were notably reduced (22). Drought conditions have been found to significantly reduce the foliar presence in several legume species, including chickpea (27), faba bean (18), and Moth bean (19). Additionally, moth beans exhibited reductions in leaf dimensions under these conditions (19). Water scarcity also led to reduced leaf areas in mung bean (15), soybean (31, 32) and faba bean (18). In contrast, chickpeas experienced an increase in leaf area when exposed to higher temperatures (25). Cowpea and soybean showed decreases in leaf fresh weight and dry mass respectively, under drought stress (23, 32). Additionally, an increase in stomatal density and index was observed in cowpeas under such conditions (23).

Yield and related traits have also been severely impacted by drought, high temperatures and their combined effects. Early water deficits led to a decrease in the number of tillers per faba bean plant (18). The timing of flowering was affected in faba beans and cowpeas due to water stress (17, 33), while high-temperature stress shortened this period in lentils and chickpeas (13, 20-22). The adverse effects of drought and high temperatures also manifested in the acceleration of flowering in lentil (13, 22). Chickpea showed an increase in flower numbers under water deficit (27), but high temperatures can lead to significant yield losses across various pulses due to short-term exposure at critical growth stages such as flowering (34). For instance, heat stress during sporogenesis resulted in anther indehiscence in common beans (35) and the combined stress of drought and high temperatures hindered pollen germination in black gram (26).

The reproductive phase was particularly sensitive, with pollen and stigma viability, pollen tube growth, fertilization and embryogenesis all being negatively influenced by drought and high temperatures in common beans (36). High temperatures were found to shorten the period to pod initiation in chickpeas (21) and the grain-filling period in mung beans (37). Drought conditions led to earlier maturity in faba beans (18), while high temperatures had a similar effect on chickpeas and lentils (13, 20-22). Significant reductions were observed in the number of pods per plant in mung bean, soybean, chickpea, cowpea and faba bean due to drought (15-18, 27, 32, 38, 39). High temperatures also decreased pod numbers in chickpeas and lentils (13, 20-22). Interestingly, pod length in mung bean increased slightly under drought but decreased under high temperatures (16, 40). Drought also led to reductions in plant dry weight in soybean and cowpea (17, 32), while high temperatures specifically reduced pod dry weight in mung bean (40) but not in chickpeas (25).

Seed production was also affected, with drought and high temperatures reducing the number of seeds per pod and per plant in various species (15-17, 21, 38). However, seed weight remained unchanged under high temperatures in chickpeas (25). The hundred seed weight was decreased under both drought and high temperatures across several species (13, 15, 18, 20-22, 38, 39), despite a slight increase observed in mung bean under drought (16). Finally, overall yield metrics, including economic and biological yields as well as the harvest index were adversely affected across a range of legumes due to the stresses of water deficit, high temperatures and their combination, highlighting the significant impact of these environmental stressors on legume production (31, 38, 39).

Drought and high-temperature effect on physiological parameters

Photosynthetic parameters

Water stress affects various physiological processes like photosynthesis, photosynthates translocation, ion uptake, nutrient absorption and enzyme activity (41). The drought and high temperatures affect the photosynthetic process through decreased leaf expansion and decreased stomatal conductance, impairing the photosynthetic machinery and enhancing the leaf senescence (42-44). The drought decreased the stomatal conductance of chickpeas (39, 45) and soybean (31). The high temperature decreased the stomatal conductance in chickpeas (25, 46) and the combined drought and high temperature decreased it in mung beans (47). The abscisic acid (ABA) synthesis was triggered under drought conditions. The ABA produced causes the closure of stomata. Reduced stomatal conductance limits CO_2 availability, resulting in a lower activation state of rubisco, which decreases the rate of photosynthesis (42-45). The transpiration rate was reduced under water stress conditions in chickpeas (30, 39, 45) and soybean (31, 32). The combined water stress and high temperature reduced the transpiration rate in mung bean (47). The canopy temperature depression was reduced in chickpeas under water stress (39). Elevated leaf temperatures can exacerbate heat stress, leading to impaired enzymatic functions and metabolic processes associated with photosynthesis (39). The stomatal closure by drought leads to reduced CO_2 availability and makes plants susceptible to photo damage (43). The chickpea showed reduced internal CO_2 concentration (39) and also reduced CO_2 assimilation rate (30) under water deficit stress conditions. The stomatal closure leads to reduced intercellular CO_2 and thereby inhibits photosynthesis (48). Reduced CO_2 availability increases the risk of photorespiration, a process that diverts carbon from the Calvin cycle, resulting in decreased overall photosynthetic efficiency and energy loss (30, 43). The high temperature causes structural and functional disruption of chloroplast and its enzyme inactivation (49, 50). The prolonged CO_2 limitation leads to the production of reactive oxygen species, which damages the photosynthetic apparatus irreversibly. The damaged photosynthetic apparatus causes the reduction of photophosphorylation, which inhibits rubisco activity (43). The net photosynthetic rate was reduced under water deficit conditions in chickpeas (39, 45) and soybean (31, 32). The net photosynthetic rate was decreased in mung bean (40) and increased in chickpea (25) grown under high temperatures. The combined drought and high temperature decreased the net photosynthetic rate in mung bean (47).

The chlorophyll fluorescence (Fv/Fm ratio) decreased under drought (30, 51) and high temperatures (52). The combined drought and high temperature decreased the chlorophyll fluorescence in mung bean (47). The high temperature decreased the electron transport efficiency and quantum yield of chickpeas (53). The damage to photosynthetic apparatus during drought conditions was prevented through mechanisms like thermal dissipation, xanthophyll cycle, water-water cycle, D1 protein photo-destruction and dissociation of light-harvesting complexes (54, 55).

Relative water content

Relative water content (RWC) is a vital indicator of plant hydration status and it reflects the plant's ability to maintain water under drought stress. It directly impacts photosynthesis, growth and stress tolerance, with higher RWC linked to improved water retention, drought resilience and productivity. As a sensitive measure of plant water status, RWC responds quickly to environmental factors such as temperature and water availability, making it essential for assessing drought tolerance in pulse crops (15, 27). The RWC decreased under water deficit stress conditions in mung bean (15), chickpea (27), soybean (31), cowpea (23) and moth bean (19). The RWC remained unchanged in chickpeas under high temperatures (25), but recently (53) observed decreased RWC.

Membrane stability

The cell membrane is vital for maintaining cellular integrity and regulating water and nutrient transport and its stability is a key indicator of stress tolerance. Membrane stability often reflects a plant's ability to withstand adverse conditions. Minimizing membrane damage and maintaining membrane integrity is crucial for drought tolerance and thus, measuring cell membrane stability serves as an essential index for assessing plant resilience to environmental stresses (10, 12). The electrolyte leakage increased by drought conditions in pigeon peas (12) and chickpeas (27, 39). The membrane stability was affected negatively under water stress in mung bean (15), chickpea (27) and moth bean (19). The membrane injury index increased under high temperatures in chickpeas (56). The relative stress injury (RSI %) decreased in mung bean under high temperatures (57).

Plant pigments

The photosynthetic pigments are reduced and photosynthetic enzyme activity is altered under water-limited conditions (58, 59). Similarly, the photosynthetic pigments are reduced, the activity of photosystem II is impaired and RuBP regeneration is affected by high temperatures (60, 61). The reactive oxygen species (ROS) induced oxidative stress and inhibition of pigment biosynthesis leads to reduced photosynthetic pigment levels under stress (62). The soil-plant analysis development (SPAD) value of chlorophyll content decreased in chickpeas due to high temperature (52). The drought decreased chlorophyll content in chickpeas (27, 39, 51) and soybean (31). The high temperature decreased chlorophyll content in mung beans (57) and chickpeas (53). The chlorophyll stability index decreased in mung beans due to high temperature (57) and combined drought and high temperature (47). The high temperature decreased the carotenoid content in mung bean (57) and chickpeas (53).

Biochemical changes

Biochemical changes in pulses are vital for enhancing stress tolerance and adaptation to environmental stresses. These include the accumulation of osmoprotectants, antioxidants and stress-related proteins, which protect cellular structures, maintain metabolic balance and reduce oxidative damage caused by drought and heat. Stress conditions like drought trigger increased reactive oxygen species (ROS), leading to oxidative stress, reflected by elevated malondialdehyde (MDA) levels (12, 39, 53). Pulses counteract this by accumulating proline, glycine betaine and soluble sugars to maintain osmotic balance, though stress can also reduce the activity of enzymes essential for carbohydrate and nitrogen metabolism, impacting plant health (23-29, 45, 63-68). The leaf protein content was reduced by drought in mung bean (15) and chickpea (39). Contrastingly, the soluble protein increased in cowpeas during drought (23). The proline content was increased under drought in mung bean (15), chickpea (24, 27, 39, 45) and common pea (63). The proline content in chickpeas was increased by high temperature (25, 56). In chickpeas, the total sugar was increased by drought (27) and the high temperature either exerted no change (25) or decreased (56) the total sugar. The total soluble sugar in chickpeas increased by drought (39). In chickpeas, the high temperature increased, reducing sugar accumulation and decreasing the non-reducing sugar (56). The drought increased the glycine betaine content in chickpeas (27, 45). The osmolytes produced help the plants to increase their osmotic potential and thereby prevent their turgor losses (64).

The drought-induced lipid peroxidation thereby increased the MDA content in pigeon peas (12), chickpeas (27, 39) and cowpeas (23). The high temperature increased the MDA content in mung beans (40) and chickpeas (53).

Both the drought and high temperature increased the total anthocyanin content in chickpeas (27, 53). Similarly, both the drought (27) and high temperature (53) increased the flavonoid content in chickpeas. Drought also increased the phenolic content in chickpeas (27). The metabolites such as allantoin, L-arginine, L-histidine, L-isoleucine, L-proline and tryptophan were increased under drought conditions (51). Whereas the metabolites like alanine, aspartic acid, choline, phenylalanine, gamma-aminobutyric acid, tyrosine, guanine and glucosamine were decreased by drought conditions (51).

The drought condition decreased the activity of alpha-amylase, beta-amylase and total enzyme activity in common peas (63). The drought decreased the rubisco enzyme activity in soybeans (31). The reduced activity of the sucrose phosphate synthase and ADP-glucose pyrophosphorylase enzymes by high temperatures adversely affects starch and sucrose synthesis (65, 66). The heat stress-induced impairment of sucrose metabolism in leaves and anthers as well as the development of pollen grains, along with sucrose transporters inhibition, leads to reduced triose phosphate availability and reproductive failure (67, 68). The reduced activity of the nitrogen fixation-associated enzymes such as nitrogenase, asparagine synthetase, aspartate aminotransferase, glutamine synthetase, xanthine dehydrogenase and uricase were observed under decreased leaf water potential (69).

Antioxidant system

The production of ROS was triggered by the combined drought and high-temperature stresses. The presence of H_2O_2 was increased by water stress in pigeon peas (12) and chickpeas (39). The high temperature increased the H_2O_2 content in mung bean (40) and chickpeas (53). Similarly, The ROS contents like oxides, superoxide (O^-), hydroxyl radical (OH^-) and hydrogen peroxide (H_2O_2) were increased under combined drought and high-temperature stresses. The oxidants produced damage the cell membranes, cause lipid peroxidation, protein oxidation, enzyme inactivation, damage nucleic acids and eventually cause cell death (70-75). The increased ROS produced by the drought and high temperature negatively affects the chlorophyll pigments, chlorophyll fluorescence and photosynthetic rate (47). The reactive oxygen species and reactive nitrogen species produced by the high temperature affect protein synthesis, protein folding and stability, which disrupts plant growth (76).

The enzymatic antioxidants like *superoxide dismutase*, *peroxidase*, ascorbate *peroxidase*, *catalase* and guaiacol *peroxidase* and non-enzymatic antioxidants like ascorbic acids, glutathione, carotenoids, phenolic contents, proline were involved in regulating the cellular oxidants level through quenching and neutralizing them (72, 77-82). The antioxidant enzymes seemed to be increased under drought and high-temperature conditions. The *superoxide dismutase* activity was increased in chickpeas under drought (27, 39, 45) and also increased in mung bean under high temperatures (40). Similarly, the *catalase* activity was increased in chickpea under drought (27, 39, 45) and also increased in mung bean under high temperatures (40). The *peroxidase* enzyme activity was increased in chickpeas under drought conditions (39) and high temperatures (53). The ascorbate *peroxidase* activity was increased in chickpeas under drought conditions (27, 39, 45). The glutathione *reductase* activity was reduced in chickpeas under drought conditions (27). The chickpeas tolerated the heat stress through increased osmolytes and antioxidant production, which helped it to retain membrane integrity, protect macromolecules and sustain metabolism (83-85).

Nutrients level

Drought stress has significant impacts on nutrient absorption and also affects root nodule development (86). The nitrogen and phosphorus uptake, transport and redistribution are affected by drought, which leads to reduced plant growth (87). The shoot nitrogen content was decreased in soybeans under water stress (88). The total carbohydrate content of faba bean seeds was reduced when grown under water stress (18). The crude protein was increased in faba beans under drought (18) and decreased in lentils under high temperature and combined drought and high-temperature stress (13, 22). The water stress reduced the macronutrients and micronutrients of the common bean (89). The iron and zinc content of lentils was decreased by high temperature and the combined effect of drought and high temperature (13, 22). The Fig. 2 depicts the various morpho-physiological

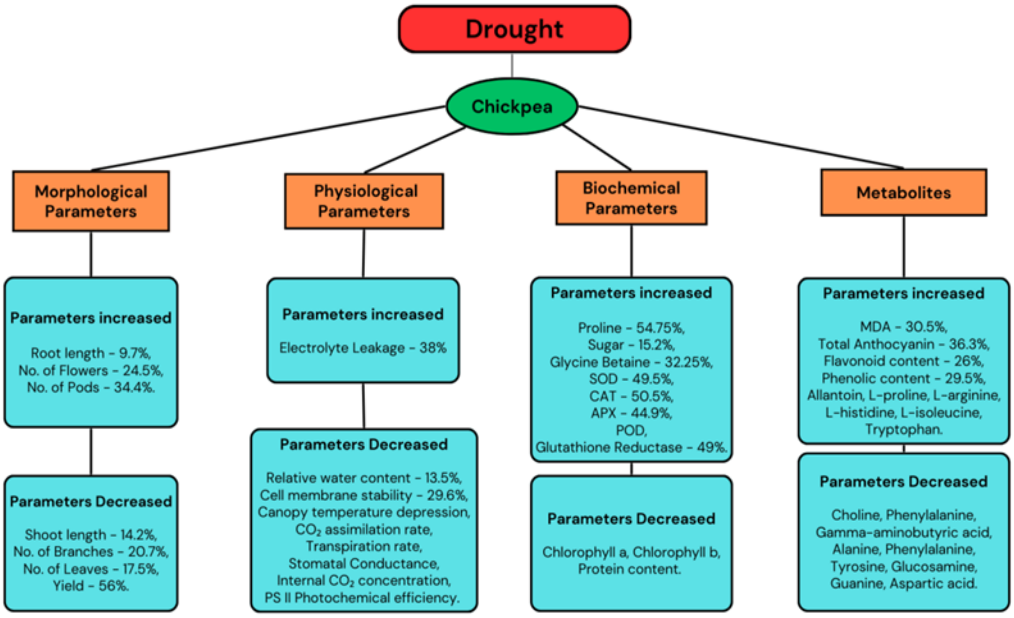

Fig. 2. The changes in various parameters observed in chickpea under drought (SOD - *Superoxide dismutase*, CAT - *Catalase*, APX - Ascorbate *Peroxidase*, POD- *Peroxidase*, MDA - Malondialdehyde) (27, 29, 30, 39, 45).

changes in chickpeas under drought conditions.

Drought and high-temperature stress on molecular mechanisms

Pulses exhibit several changes at the molecular level in response to drought by expressing drought-responsive genes. These responses encompass complex signaling cascades, transcriptional regulation and the activation of genes encoding osmoprotectants, membrane proteins and stress-related proteins, including heat shock proteins (HSP) and late embryogenesis abundant (LEA) proteins. Transcription factors and protein kinases play essential roles in orchestrating these responses through diverse signaling cascades. In heat-tolerant green gram genotype EC 398889, a protein band between 91-137 kDa was detected, while it was absent in heat-sensitive green gram genotype LGG460 (37). The protein band found was not characterized thoroughly and suggested that it may had some protective role under heat stress (37). In addition, the same heat-tolerant genotype also showed the expression of 101 kDa-sized heat shock protein (37). In the seedling stage of *Vigna glabrescens* genotype IC251372, a heat-tolerant wild creole bean, the *VrLEA-2, VrLEA-40, VrLEA47* and *VrLEA-55* genes were significantly upregulated under heat stress and formed the basis for heat tolerance (90).

In chickpea seedlings, the galactinol synthase (GolS) activity was increased under heat and oxidative stress and preferentially, *CaGolS1* transcript was found higher (up to 25-30 folds) than *CaGolS2* (91). Under drought stress, the expression of aquaporin genes *PIP2;2* and *NIP6;3* was upregulated in drought-tolerant chickpea genotype but down regulated in susceptible ones and thereby they positively related to the drought stress tolerance (92). It was identified 10 genes viz., *CaHS3, CaHS5, CaHS19, CaHS22, CaHS26, CaHS37, CaHS38, CaHS41, CaHS56* and *CaHS58* were helpful for putative heat -tolerant chickpea genotypes selection (93). Using the gene ontology classification system, (94) identified 32 potential genes in chickpeas associated with the response to heat stress, distributed across 4 linkage groups: 7 on *CaLG01*, 3 on *CaLG02*, 14 on *CaLG04* and 8 on *CaLG07* (Fig. 3). Within *CaLG01*, 6 out of seven genes were implicated in encoding heat shock proteins, while one gene encoded a pollen-specific leucine-rich repeat extension-like protein 1 (94). In *CaLG02*, among the 3 candidate genes, *Ca_16007* encoded a pollen-specific leucine-rich repeat extension-like protein 1, *Ca_22033* encoded an HSP-binding protein and *Ca_24649* encoded a truncated transcription factor CAULIFLOWER A-like (94). Within *CaLG04*, the 14 candidate genes consisted of 6 pollen-specific genes, 4 HSP-related genes, 3 genes encoding DnaJ heat shock amino-terminal domain proteins and one gene related to the protein PHOTOPERIOD-INDEPENDENT EARLY FLOWERING 1 isoform X1 (94). Lastly, in *CaLG07*, among 8 genes, 3 (*Ca_18924, Ca_16239* and *Ca_09277*) encoded HSP/HSF protein HSF24-like, 2 (*Ca_16434* and *Ca_16155*) encoded pollen-specific leucine-rich repeat extension-like protein 1/pollen receptor-like kinase 3, two (*Ca_10118* and *Ca_17996*) encoded protein EARLY FLOWERING 3/flowering time control protein FY and one (*Ca_13761*) encoded a calmodulin-binding heat-shock protein (94).

The *EMF1, EMF2, ERF1, NPGR1, BRC1/TCP18* and *BZR1* were posed to be candidate genes for high temperature-dependent effects in chickpeas (95). The genes related to adenylate isopentyl transferase and pathogenesis-related proteins were significantly regulated in leaves of tolerant chickpea genotypes but not in sensitive genotypes at a vegetative stage in response to heat stress (96). Intolerant chickpea genotypes leave, at the reproductive stage, about 14 genes that were involved in metabolic processes including CTP synthase-like and serine carboxypeptidase-like and those involved in encoding transcription factors including NAC family transcription factor 4, nuclear transcription factor Y and

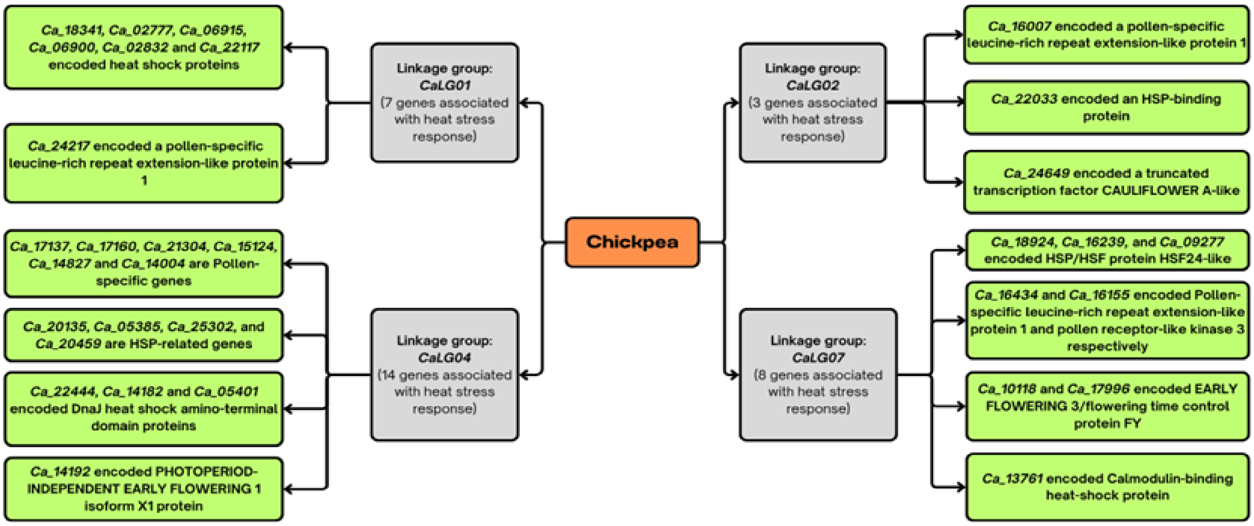

Fig. 3. Distribution of heat stress-associated genes in chickpea: linkage groups *CaLG01, CaLG02, CaLG04* and *CaLG07* (94).

transcription factor TGA4-like and also those genes involved in encoding for ABA-responsive protein ABR18-like and glycine-rich cell wall structural 1-like protein were regulated significantly under heat stress, but not in sensitive genotypes (96). In roots of tolerant chickpea genotypes, the genes that encoded cysteine-rich repeat secretary protein 38 and peroxidase 5-like were significantly upregulated and those genes that encoded E3 ubiquitin-ligase, dirigent protein 9-like and pectase lyase 1 were significantly downregulated, under heat stress at vegetative stage, but not in sensitive genotypes (96). In roots of tolerant chickpea genotypes, about 5 genes, including those encoding for glutamine-tRNA ligase, OBERON-like protein and ras-related protein RABE1c-like, were regulated significantly under heat stress at the reproductive stage, but not in sensitive genotypes (96). The genes that encoded for transcription factor families like *bHLH, bZIP, C2H2, ERF, HD-ZIP, MYB, MYB*-related, *NAC, MIKC-MADS* and *WRKY* were majorly found to be differentially expressed under heat stress in chickpea (96).

A small regulatory RNA of about 20-24 nucleotides derived from single-stranded stem-loop precursors is known to be microRNA and these microRNAs have a profound role in the regulation of genes (24). The upregulation of MicroRNA (*miRNA*) such as *miR167, miR168* and *miR171* up to more than three folds in root tissues of drought tolerant chickpea (Pusa362) conferred drought tolerance by directly targeting the auxin response factors, WD-repeat and scarecrow-like transcription factors respectively (24). In chickpea shoots, the *miR390* and *miR2118* were upregulated, which might target the *TAS3 SiRNA* and *TIR-NBS-LRR* genes respectively (24). The *TAS3 SiRNA* was involved in leaf growth, root growth and flowering time alterations through the regulation of *ARF* gene expression in Soyabean (97). The effective role of *miR2118* on drought tolerance in chickpeas was under conflict (24). Further, in drought-tolerant chickpeas, the novel *miRNA,* such as *nov_miR8* in root and *nov_miR2* in the shoot, were upregulated and targets the genes encoding laccase and GMP synthase, respectively (24). The GMP synthase regulated the signaling processes through the synthesis of purine nucleotides and thereby producing secondary messengers such as cyclic nucleotides (cGMP), which play an important role under abiotic stresses (24).

The genes *VuNSR1, VuNSR2, VuNSR3, VuNSR8, VuNSR13, VuNSR14, VuNSR15, VuNSR16* and *VuNSR19* were upregulated and the genes *VuNSR6, VuNSR9, VuNSR10* and *VuNSR20* were down regulated in cowpea nodules under heat stress (98).

In soybeans, the high temperature differentially regulated the major flowering genes of the photoperiodic pathway (99). The upregulation in the expression of floral activator genes such as *GmFT2a* and *GmFT5a* was observed in soybeans under high temperatures (99). Among the 26 annotated *GmCOL* genes in the genome of soybean, the *GmCOL5a/5b* and *GmCOL6a/6b* genes were highly upregulated, followed by *GmCOL11b* genes under high temperatures (99). Besides promoting the floral activators, the High temperature caused the suppression of floral repressor genes, including *E1 (GmGI1), E2 (GmGI2)* and its homolog *GmGI3*, in soybean (99). It was also found that the high temperature promoted the flowering in soybeans in a daylength-independent manner; that is, the high temperature helped the soybean to overcome the photoperiodic control of flowering (99).

Conclusion

Drought and high temperatures significantly impact pulse crops, influencing various physiological, morphological and biochemical parameters that affect plant growth, development and yield. Drought stress results in reduced germination rates, impaired seedling vigor and stunted growth in height and biomass across multiple pulse species. It also negatively impacts root development, shoot parameters and reproductive traits, such as flowering time and pod formation, ultimately leading to decreased yield and seed quality. High temperatures compound these effects, further diminishing plant height, biomass and pod numbers while disrupting critical physiological processes like photosynthesis, nutrient uptake and enzyme activities. Both stresses lead to lower photosynthetic rates, chlorophyll content and relative water content, coupled with increased oxidative stress and membrane damage. Biochemically, drought and heat stress alter the production of osmolytes, antioxidants and nutrient absorption, adversely affecting plant metabolism and yield.

Molecular studies underscore specific gene expressions related to heat and drought tolerance, highlighting the necessity for a deeper genetic understanding to develop resilient pulse crop varieties. This review innovatively integrates the effects of drought and high temperature across various pulses, providing a comprehensive analysis of plant physiology, morphology and biochemistry. It emphasizes key stress tolerance markers, such as stomatal conductance and membrane stability, while offering novel insights through protein characterization and gene expression analysis, particularly in green gram and chickpeas. The integration of advanced molecular techniques, including microRNA regulation and gene ontology, provides fresh perspectives on stress-responsive mechanisms, establishing a robust foundation for molecular breeding strategies aimed at developing climate-resilient pulse crops.

Future research should focus on elucidating the molecular mechanisms underlying drought and heat tolerance, particularly regarding stress-responsive genes, transcription factors and microRNAs. Characterizing these molecular components can yield valuable insights into plant adaptation to abiotic stresses. Additionally, advances in gene editing and genomics will facilitate the creation of pulse varieties with enhanced resilience. Comparative studies across species can further refine breeding strategies to improve drought and heat tolerance, ultimately contributing to sustainable pulse production amid changing climatic conditions.

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Authors' contributions

In the preparation of this manuscript, all authors made equal contributions to its writing, data verification, and interpretation. Each author reviewed and approved the final version of the manuscript.

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During the preparation of this manuscript, the authors used QuillBot, an AI-assisted writing tool, to reframe certain sentences to enhance the use of research-specific terminology. After utilizing this tool, the authors thoroughly reviewed and edited the content as necessary and take full responsibility for the accuracy and integrity of the final publication.

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