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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

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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 hightemperature 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 shortterm 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 grainfilling 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 CO₂ 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 CO₂ availability and makes plants susceptible to photo damage (43). The chickpea showed reduced internal CO₂ concentration (39) and also reduced CO₂ assimilation rate (30) under water deficit stress conditions. The stomatal closure leads to reduced intercellular CO₂ and thereby inhibits photosynthesis (48). Reduced CO₂ 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 waterlimited 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

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, Lisoleucine, L-proline and tryptophan were increased under drought conditions (51). Whereas the metabolites like alanine, aspartic acid, choline, phenylalanine, gammaaminobutyric 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 H₂O₂ content in mung bean (40) and chickpeas (53). Similarly, The ROS contents like oxides, superoxide (O⁻), hydroxyl radical (OH⁻) and hydrogen peroxide (H₂O₂) 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 changes in chickpeas under drought conditions.



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).

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 (GoIS) activity was increased under heat and oxidative stress and preferentially, *CaGoIS1* transcript was found higher (up to 25-30 folds) than *CaGoIS2* (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 extensionlike 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 transcription factor TGA4-like and also those genes



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

involved in encoding for ABA-responsive protein ABR18like 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 *GmGl3*, 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 stressresponsive 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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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.

References

- Mishra P, Al Khatib AM, Lal P, Anwar A, Nganvongpanit K, Abotaleb M, et al. An overview of pulses production in India: retrospect and prospects of the future food with an application of hybrid models. National Academy Science Letters. 2023 Oct;46(5):367-74. https:// doi.org/10.1007/s40009-023-01267-2
- Hazra KK, Basu PS. Pulses. In: Trajectory of 75 years of Indian Agriculture after Independence. Singapore: Springer Nature Singapore. 2023;189-230. https://doi.org/10.1007/978-981-19-7997-2_9
- Kumar N, Hashim M, Nath CP, Hazra KK, Singh AK. Pulses in conservation agriculture: An approach for sustainable crop production and soil health. Journal of Food Legumes. 2023;36 (1):1-9.https://doi.org/10.59797/jfl.v36.i1.138
- Kumar A, Sharma AK, Yadav RK, Meitei S, Arora N, Gaur DK. Agricultural statistics at a glance 2022. Directorate of Economics and Statistics, Department of Agriculture Cooperation and Farmer Welfare, Ministry of Agriculture and Farmers Welfare, Govt. of India. 2022;40-41. Available at: https://desagri.gov.in/documentreport/agricultural-statistics-at-a-glance-2022/.
- Zhang L, Yu X, Zhou T, Zhang W, Hu S, Clark R. Understanding and attribution of extreme heat and drought events in 2022: current situation and future challenges. Advances in Atmospheric Sciences. 2023;40(11):1941-51.https://doi.org/10.1007/s00376-023 -3171-x
- Wang T, Sun F. Integrated drought vulnerability and risk assessment for future scenarios: An indicator-based analysis. Science of the Total Environment. 2023; 900:165591. https://

doi.org/10.1016/j.scitotenv.2023.165591

- Mahto SS, Mishra V. Increasing risk of simultaneous occurrence of flash drought in major global croplands. Environmental Research Letters. 2023;18(4):044044. https://doi.org/10.1088/1748-9326/ acc8ed
- IPCC. Climate change 2007: The physical science basis. Contribution of working group I to the fourth assessment report of the IPCC. In: Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL (eds). Cambridge, UK: Cambridge University Press; 2007:996.
- NOAA. NOAA National Centers for Environmental Information, Monthly Global Climate Report for January 2024. Published online February 2024, retrieved on February 28, 2024 from https:// www.ncei.noaa.gov/access/monitoring/monthly-report/ global/202401.
- Kamatchi KM, Anitha K, Kumar KA, Senthil A, Kalarani MK, Djanaguiraman M. Impacts of combined drought and hightemperature stress on growth, physiology and yield of crops. Plant Physiology Reports. 2024;29(1):28-36. https:// doi.org/10.1007/s40502-023-00754-4
- Anitha K, Senthil A, Kalarani M, Senthil N, Marimuthu S, Djanaguiraman M, Umapathi M. Exogenous melatonin improves seed germination and seedling growth in green gram under drought stress. J Appl Nat Sci. 2022;14(4):1190-97. https:// doi.org/10.31018/jans.v14i4.3818
- 12. Shahana T, Rao PA, Ram SS, Sujatha E. Mitigation of drought stress by 24-epibarassinolide and 28-homobrassinolide in pigeon pea seedlings. Int J Multi Curr Res. 2015;3:905-11.
- El Haddad N, Choukri H, Ghanem ME, Smouni A, Mentag R, Rajendran K, Hejjaoui K, et al. High-temperature and drought stress effects on growth, yield and nutritional quality with transpiration response to vapor pressure deficit in lentil. Plants. 2021;11(1):95.https://doi.org/10.3390/plants11010095
- Raina SK, Govindasamy V, Kumar M, Singh AK, Rane J, Minhas PS. Genetic variation in physiological responses of mung beans (*Vigna radiata* (L.) Wilczek) to drought. Acta Physiol Plant. 2016;38:1-12. https://doi.org/10.1007/s11738-016-2280-x
- Bangar P, Chaudhury A, Tiwari B, Kumar S, Kumari R, Bhat KV. Morphophysiological and biochemical response of mung bean (*Vigna radiata* (L.) Wilczek) varieties at different developmental stages under drought stress. Turk J Biol. 2019;43(1):58-69. https:// doi.org/10.3906/biy-1801-64
- Ghanbari M, Javan SM. Study the response of mung bean genotypes to drought stress by multivariate analysis. Int J Agric Innov Res. 2015;3(4):2319-1473.
- Santos R, Carvalho M, Rosa E, Carnide V, Castro I. Root and agromorphological traits performance in cowpea under drought stress. Agronomy. 2020;10(10):1604. https://doi.org/10.3390/ agronomy10101604
- Al-Suhaibani N. Influence of early water deficit on seed yield and quality of faba bean under arid environment of Saudi Arabia. Am-Eurasian J Agric Environ Sci. 2009;5(5):649-54.
- Meena MK, Malik A, Singh R, Singh AP, Naik S, Meena RK, et al. Morphological and biochemical changes in moth bean during drought stress. Int J Environ Climate Change. 2023;13(11):187-201. https://doi.org/10.9734/ijecc/2023/v13i113158
- Kumar N, Nandwal A, Yadav R, Bhasker P, Kumar S, Devi S, et al. Assessment of chickpea genotypes for high temperature tolerance. Indian J Plant Physiol. 2012;17(3&4):224-32.
- Tare S, Yasin M, Sikarwar RS, Puri P, Malik V. Dissection of genetic variability, correlation of seed yield and yield contributing traits in chickpea (*Cicer arietinum* L.) in different temperature conditions. The Pharma Innovation Journal. 2023;12(2):1702-07.
- 22. Choukri H, Hejjaoui K, El-Baouchi A, El Haddad N, Smouni A, Maalouf F, et al. Heat and drought stress impact on phenology,

grain yield and nutritional quality of lentil (*Lens culinaris* Medikus). Front Nutr. 2020;7:596307.https://doi.org/10.3389/fnut.2020.596307

- Jayawardhane J, Goyali JC, Zafari S, Igamberdiev AU. The response of cowpea (*Vigna unguiculata*) plants to three abiotic stresses applied with increasing intensity: Hypoxia, salinity and water deficit. Metabolites. 2022;12(1):38.https://doi.org/10.3390/ metabo12010038
- Singh L, Kohli D, Gaikwad K, Kansal R, Dahuja A, Paul V, et al. Effect of drought stress on morphological, biochemical, physiological traits and expression analysis of microRNAs in drought-tolerant and sensitive genotypes of chickpea. Indian J Genet Plant Breed. 2021;81(02):266-76.http:// dx.doi.org/10.31742/IJGPB.81.2.9
- 25. Sangeeta Khetarpal SK, Madan Pal MP, Sneh Lata SL. Effect of elevated temperature on growth and physiological characteristics in chickpea cultivars. Indian Journal of Plant Physiology. 2009;14 (4):377-83.
- 26. Katiyar A, Singh P. Biochemical studies of selected pulses in response to heat, photoperiods and carbon nanoparticles. Indian Res J Genet Biotechnol. 2015;7(01):77-83.
- Keerthi Sree Y, Lakra N, Manorama K, Ahlawat Y, Zaid A, Elansary HO, et al. Drought-induced morpho-physiological, biochemical, metabolite responses and protein profiling of chickpea (*Cicer arietinum* L.). Agronomy. 2023;13(7):1814.https://doi.org/10.3390/ agronomy13071814
- Ramamoorthy P, Lakshmanan K, Upadhyaya HD, Vadez V, Varshney RK. Root traits confer grain yield advantages under terminal drought in chickpea (*Cicer arietinum* L.). Field Crops Res. 2017;201:146-61.https://doi.org/10.1016/j.fcr.2016.11.004
- 29. Khan N, Bano A, Zandi P. Effects of exogenously applied plant growth regulators in combination with PGPR on the physiology and root growth of chickpea (*Cicer arietinum*) and their role in drought tolerance. J Plant Interact. 2018;13(1):239-47.https://doi.org/10.1080/17429145.2018.1471527
- Rahbarian R, Khavari-Nejad R, Ganjeali A, Bagheri A, Najafi F. Drought stress effects on photosynthesis, chlorophyll fluorescence and water relations in tolerant and susceptible chickpea (*Cicer arietinum* L.) genotypes. Acta Biol Cracoviensia. Ser Bot. 2011;53(1).https://doi.org/10.2478/V10182-011-0007-2
- Shafiq I, Hussain S, Hassan B, Shoaib M, Mumtaz M, Wang B, et al. Effect of simultaneous shade and drought stress on morphology, leaf gas exchange and yield parameters of different soybean cultivars. Photosynthetica. 2020;58(5).https://doi.org/10.32615/ ps.2020.067
- Silva JA d, Carvalho LG d, Andrade FR. Gas exchange and water stress index in soybean cultivated under water deficit and soil compaction. Rev Ceres. 2022;69:218-26.https:// doi.org/10.1590/0034-737x202269020013
- Abdellatif KF, El Sayed A, Zakaria AM. Drought stress tolerance of faba bean as studied by morphological traits and seed storage protein pattern. J Plant Stud. 2012;1(2):47.https:// doi.org/10.5539/jps.v1n2p47
- Gull R, Bhat TA, Sheikh TA, Wani OA, Fayaz S, Nazir A, et al. Climate change impact on pulse in India - A review. J PharmacognPhytochem. 2020;9(4):3159-66.
- 35. Porch T, Jahn M. Effects of high-temperature stress on microsporogenesis in heat-sensitive and heat⊠tolerant genotypes of *Phaseolus vulgaris*. Plant Cell Environ. 2001;24(7):723-31.https://doi.org/10.1046/j.1365-3040.2001.00716.x
- Kumar M, Siddique KH. Metabolic engineering for understanding abiotic stress tolerance in plants. In: Molecular Response and Genetic Engineering for Stress in Plants, Volume 1: Abiotic stress. Bristol, UK: IOP Publishing. 1 2022;2-1.https://doi.org/10.1088/978 -0-7503-4921-5ch2

- Basu PS, Pratap A, Gupta S, Sharma K, Tomar R, Singh NP. Physiological traits for shortening crop duration and improving productivity of greengram (*Vigna radiata* (L.) Wilczek) under high temperature. Front Plant Sci. 2019;10:1508.https:// doi.org/10.3389/fpls.2019.01508
- Siahbidi MMP, Aboughadareh AP, Bazdar A, Naghavi MR. Investigation of water deficit stress effects on yield and yield components of four soybean cultivars at different growth stages. Int J Biosci. 2013;3:104-09.http://dx.doi.org/10.12692/ijb/3.8.104-109
- Tiwari PN, Tiwari S, Sapre S, Tripathi N, Payasi DK, Singh M, et al. Prioritization of physio-biochemical selection indices and yieldattributing traits toward the acquisition of drought tolerance in chickpea (*Cicer arietinum* L.). Plants. 2023;12(18):3175.https:// doi.org/10.3390%2Fplants12183175
- 40. Rakavi B, Sritharan N. Physiological response of green gram under heat stress. J PharmacognPhytochem. 2019;8(1S):181-85.
- Ahmad HM, Wang X, Fiaz S, Azeem F, Shaheen T. Morphological and physiological response of *Helianthus annuus* L. to drought stress and correlation of wax contents for drought tolerance traits. Arab J Sci Eng. 2021;1-15.https://doi.org/10.1007/s13369-021-06098-1
- 42. Farooq M, Wahid A, Kobayashi N, Fujita D, Basra S. Plant drought stress: effects, mechanisms and management. Sustainable Agriculture. 2009;153-88.https://doi.org/10.1051/agro:2008021
- Lawlor DW, Cornic G. Photosynthetic carbon assimilation and associated metabolism in relation to water deficits in higher plants. Plant Cell Environ. 2002;25(2):275-94.https:// doi.org/10.1046/j.0016-8025.2001.00814.x
- Wahid A, Gelani S, Ashraf M, Foolad MR. Heat tolerance in plants: an overview. Environ Exp Bot. 2007;61(3):199-223.https:// doi.org/10.1016/j.envexpbot.2007.05.011
- Awari V, Dalvi U, Lokhande P, Pawar V, Mate S, Naik R, Mhase L. Physiological and biochemical basis for moisture stress tolerance in chickpea under pot study. Int J Curr Microbiol Appl Sci. 2017;6 (5):1247-59.https://doi.org/10.20546/ijcmas.2017.605.135
- Jain AK. Heat sensitivity on physiological and biochemical traits in chickpea (*Cicer arietinum* L.). Adv Environ Res. 2014;3(4):307-19.https://doi.org/10.12989/aer.2014.3.4.307
- 47. Kuppusamy A, Alagarswamy S, Karuppusami KM, Maduraimuthu D, Natesan S, Ramalingam K, et al. Melatonin enhances the photosynthesis and antioxidant enzyme activities of mung bean under drought and high-temperature stress conditions. Plants. 2023;12(13):2535.https://doi.org/10.3390/plants12132535
- Chaves MM, Flexas J, Pinheiro C. Photosynthesis under drought and salt stress: regulation mechanisms from whole plant to cell. Ann Bot. 2009;103(4):551-60.https://doi.org/10.1093/aob/mcn125
- Cui L, Li J, Fan Y, Xu S, Zhang Z. High temperature effects on photosynthesis, PSII functionality and antioxidant activity of two *Festuca arundinacea* cultivars with different heat susceptibility. Bot Stud. 2006;47(1):61-69.
- Dekov I, Tsonev T, Yordanov I. Effects of water stress and hightemperature stress on the structure and activity of photosynthetic apparatus of *Zea mays* and *Helianthus annuus*. Photosynthetica. 2000;38:361-66.https://doi.org/10.1023/A:1010961218145
- Khan N, Bano A, Rahman MA, Rathinasabapathi B, Babar MA. UPLC-HRMS-based untargeted metabolic profiling reveals changes in chickpea (*Cicer arietinum*) metabolome following long -term drought stress. Plant Cell Environ. 2019;42(1):115-32.https://doi.org/10.1111/pce.13195
- Jha UC, Devi P, Prakash V, Kumar S, Parida SK, Paul PJ, et al. Response of physiological, reproductive function and yield traits in cultivated chickpea (*Cicer arietinum* L.) under heat stress. Front Plant Sci. 2022;13.https://doi.org/10.3389/fpls.2022.880519

- Arslan Ö. The role of heat acclimation in thermotolerance of chickpea cultivars: Changes in photochemical and biochemical responses. Life. 2023;13(1):233. https://doi.org/10.3390/ life13010233
- Demmig-Adams B, Adams III WW. Photoprotection in an ecological context: the remarkable complexity of thermal energy dissipation. New Phytol. 2006;172(1):11-21. https:// doi.org/10.1111/j.1469-8137.2006.01835.x
- Niyogi KK. Photoprotection revisited: genetic and molecular approaches. Annu Rev Plant Biol. 1999;50(1):333-59. https:// doi.org/10.1146/annurev.arplant.50.1.333
- Arunkumar R, Sairam R, Deshmukh P, Pal M, Khetarpal S, Pandey SK, et al. High temperature stress and accumulation of compatible solutes in chickpea (*Cicer arietinum* L.). Indian J Plant Physiol. 2012;17:145-50.
- 57. Chand G, Nandwal A, Kumar N, Devi S, Khajuria S. Yield and physiological responses of mung bean *Vigna radiata* (L.) Wilczek genotypes to high temperature at reproductive stage. Legume Res. 2018;41(4):557-62. https://doi.org/10.18805/LR-3795
- Fu J, Huang B. Involvement of antioxidants and lipid peroxidation in the adaptation of two cool-season grasses to localized drought stress. Environ Exp Bot. 2001;45(2):105-14. https:// doi.org/10.1016/S0098-8472(00)00084-8
- Monakhova O, Chernyad'ev I. Protective role of kartolin-4 in wheat plants exposed to soil drought. Appl BiochemMicrobiol. 2002;38:373-80. https://doi.org/10.1023/A:1016243424428
- Camejo D, Jiménez A, Alarcón JJ, Torres W, Gómez JM, Sevilla F. Changes in photosynthetic parameters and antioxidant activities following heat-shock treatment in tomato plants. Funct Plant Biol. 2006;33(2):177-87.https://doi.org/10.1071/fp05067
- 61. Wise R, Olson A, Schrader S, Sharkey T. Electron transport is the functional limitation of photosynthesis in field-grown Pima cotton plants at high temperature. Plant Cell Environ. 2004;27(6):717-24. https://doi.org/10.1111/j.1365-3040.2004.01171.x
- Prasad P, Pisipati S, Momčilović I, Ristic Z. Independent and combined effects of high temperature and drought stress during grain filling on plant yield and chloroplast EF-Tu expression in spring wheat. J Agron Crop Sci. 2011;197(6):430-41. https:// doi.org/10.1111/j.1439-037X.2011.00477.x
- 63. Al-Jebory El. Effect of water stress on carbohydrate metabolism during *Pisum sativum* seedlings growth. Euphrates J Agric Sci. 2012;4(4):1-12.
- Bhargava A, Carmona FF, Bhargava M, Srivastava S. Approaches for enhanced phytoextraction of heavy metals. J Environ Manage. 2012;105:103-20. https://doi.org/10.1016/j.jenvman.2012.04.002
- Rodriguez P, Torrecillas A, Morales M, Ortuno M, Sánchez-Blanco M. Effects of NaCl salinity and water stress on growth and leaf water relations of *Asteriscus maritimus* plants. Environ Exp Bot. 2005;53 (2):113-23. https://doi.org/10.1016/j.envexpbot.2004.03.005
- Zhao FC, Jing LQ, Yan FB, Lu DL, Wang GY, Lu WP. Effects of heat stress during grain filling on sugar accumulation and enzyme activity associated with sucrose metabolism in sweet corn. 2013;1644-51.https://doi.org/10.3724/SP.J.1006.2013.01644
- 67. Kaushal N, Awasthi R, Gupta K, Gaur P, Siddique KH, Nayyar H. Heat-stress-induced reproductive failures in chickpea (*Cicer arietinum*) are associated with impaired sucrose metabolism in leaves and anthers. Funct Plant Biol. 2013;40(12):1334-49.https:// doi.org/10.1071/FP13082
- Kaushal N, Bhandari K, Siddique KH, Nayyar H. Food crops face rising temperatures: an overview of responses, adaptive mechanisms and approaches to improve heat tolerance. Cogent Food Agric. 2016;2(1):1134380. https:// doi.org/10.1080/23311932.2015.1134380
- 69. Kaur A, Sheoran I, Singh R. Effect of water stress on the enzymes of nitrogen metabolism in mung bean (*Vigna radiata* Wilczeck)

nodules. Plant Cell Environ. 1985;8(3):195-200. https:// doi.org/10.1111/1365-3040.EP11604608

- Choudhury S, Panda P, Sahoo L, Panda SK. Reactive oxygen species signaling in plants under abiotic stress. Plant Signal Behav. 2013;8(4):e23681.https://doi.org/10.4161/psb.23681
- 71. Hirt H. Foreword II. In: Improving Crop Resistance to Abiotic Stress. Wiley-VCH. 30 March 2012. 10.1002/9783527632930
- Jincy M, Jeyakumar P, Boominathan P, Manivannan N, Varanavasiappan S, Prasad VBR. Impact of drought and high temperature stress on oxidants and antioxidants in greengram (*Vigna radiata* (L.) Wilczek). J PharmacognPhytochem. 2019;8 (3):1809-13.
- Meriga B, Reddy BK, Rao KR, Reddy LA, Kishor PK. Aluminiuminduced production of oxygen radicals, lipid peroxidation and DNA damage in seedlings of rice (*Oryza sativa*). J Plant Physiol. 2004;161(1):63-68.https://doi.org/10.1078/0176-1617-01156
- Miller G, Shulaev V, Mittler R. Reactive oxygen signaling and abiotic stress. Physiol Plant. 2008;133(3):481-89.https:// doi.org/10.1111/j.1399-3054.2008.01090.x
- Suzuki N, Koussevitzky S, Mittler R, Miller G. ROS and redox signalling in the response of plants to abiotic stress. Plant Cell Environ. 2012;35(2):259-70. https://doi.org/10.1111/j.1365-3040.2011.02336.x
- Mittler R, Zandalinas SI, Fichman Y, Van Breusegem F. Reactive oxygen species signalling in plant stress responses. Nat Rev Mol Cell Biol. 2022;23(10):663-79.https://doi.org/10.1038/s41580-022-00499-2
- Anderson JA, Padhye SR. Protein aggregation, radical scavenging capacity and stability of hydrogen peroxide defense systems in heat-stressed vinca and sweet pea leaves. J Am Soc Hortic Sci. 2004;129(1):54-59. https://doi.org/10.21273/JASHS.129.1.0054
- Bohnert HJ, Shen B. Transformation and compatible solutes. Sci Hortic. 1998;78(1-4):237-60.https://doi.org/10.1016/S0304-4238 (98)00195-2
- Hasanuzzaman M, Bhuyan MB, Zulfiqar F, Raza A, Mohsin SM, Mahmud JA, Fujita M, Fotopoulos V. Reactive oxygen species and antioxidant defense in plants under abiotic stress: Revisiting the crucial role of a universal defense regulator. Antioxidants. 2020;9 (8):681. https://doi.org/10.3390/antiox9080681
- Hassan M, Mansoor S. Oxidative stress and antioxidant defense mechanism in mung bean seedlings after lead and cadmium treatments. Turk J Agric For. 2014;38(1):55-61. https:// doi.org/10.3906/TAR-1212-4
- Kaur N, Kaur J, Grewal SK, Singh I. Effect of heat stress on antioxidative defense system and its amelioration by heat acclimation and salicylic acid pre-treatments in three pigeon pea genotypes. Indian J Agric Biochem. 2019;32(1):106-10. http:// dx.doi.org/10.5958/0974-4479.2019.00014.5
- Zafar SA, Hameed A, Ashraf M, Khan AS, Li X, Siddique KH. Agronomic, physiological and molecular characterisation of rice mutants revealed the key role of reactive oxygen species and catalase in high-temperature stress tolerance. Funct Plant Biol. 2020;47(5):440-53. https://doi.org/10.1071/fp19246
- Parankusam S, Bhatnagar-Mathur P, Sharma KK. Heat responsive proteome changes reveal molecular mechanisms underlying heat tolerance in chickpea. Environ Exp Bot. 2017;141:132-44. https:// doi.org/10.1016/j.envexpbot.2017.07.007
- Rani A, Devi P, Jha UC, Sharma KD, Siddique KH, Nayyar H. Developing climate-resilient chickpea involving physiological and molecular approaches with a focus on temperature and drought stresses. Front Plant Sci. 2020;10:1759.https://doi.org/10.3389/ fpls.2019.01759
- Yadav S, Kushwaha HR, Kumar K, Verma PK. Comparative structural modeling of a monothiol GRX from chickpea: Insight in iron–sulfur cluster assembly. Int J Biol Macromol. 2012;51(3):266-

73. https://doi.org/10.1016/j.ijbiomac.2012.05.014

- 86. Raghu N, Patil J, Meena M, Suma T, Rathod P. Physiological approaches for yield improvement in chickpea (*Cicer arietinum* L.) under drought condition. 2023.
- Rouphael Y, Cardarelli M, Schwarz D, Franken P, Colla G. Effects of drought on nutrient uptake and assimilation in vegetable crops. In: Plant Responses to Drought Stress: From Morphological to Molecular Features; 2012.171-95.https://doi.org/10.1007/978-3-642-32653-0_7
- Ayman E, Sorour S, Morsi A, Islam M, Saneoka H. Role of osmoprotectants and compost application in improving water stress tolerance in soybean (*Glycine max* L.). Int J Curr Res. 2016;8:25949-54.
- Kiymaz S, Abaci-Bayar AA, Beyaz R. The effect of water stress on nutrient elements in soil and leaf of common bean (*Phaseolus vulgaris* L.). J Agric Fac Gaziosmanpaşa Univ (JAFAG). 2020;37 (3):130-40.https://doi.org/10.13002/jafag4697
- 90. Singh CM, Kumar M, Pratap A, Tripathi A, Singh S, Mishra A, et al. Genome-wide analysis of late embryogenesis abundant protein gene family in *vigna* species and expression of *VrLEA* encoding genes in *vigna glabrescens* reveal its role in heat tolerance. Front Plant Sci. 2022.https://doi.org/10.3389/fpls.2022.843107
- Salvi P, Kamble NU, Majee M. Stress-inducible galactinol synthase of chickpea (CaGolS) is implicated in heat and oxidative stress tolerance through reducing stress-induced excessive reactive oxygen species accumulation. Plant Cell Physiol. 2018;59(1):155-66.https://doi.org/10.1093/pcp/pcx170
- Azeem F, Bilal A, Rana M, Muhammad A, Habibullah N, Sabir H, et al. Drought affects aquaporins gene expression in important pulse legume chickpea (*Cicer arietinum* L.). Pak J Bot. 2019;51(1):81-88.http://dx.doi.org/10.30848/PJB2019-1(30)

- Rodríguez-Vera A, Acosta-Gallegos J, Ruiz-Nieto J, Montero-Tavera V. Selection by genetic expression profiles of desi and kabuli chickpea (*Cicer arietinum* L.) genotypes tolerant to high temperature stress. Legume Res Int J. 2021;44(1):60-66.http:// dx.doi.org/10.18805/LR-541
- Jha UC, Nayyar H, Palakurthi R, Jha R, Valluri V, Bajaj P, et al. Major QTLs and potential candidate genes for heat stress tolerance identified in chickpea (*Cicer arietinum* L.). Front Plant Sci. 2021;12:655103. https://doi.org/10.3389/fpls.2021.655103
- Li Y, Lake L, Chauhan YS, Taylor J, Sadras VO. Genetic basis and adaptive implications of temperature-dependent and temperature-independent effects of drought on chickpea reproductive phenology. J Exp Bot. 2022;73(14):4981-95.https:// doi.org/10.1093/jxb/erac195
- 96. Kudapa H, Barmukh R, Garg V, Chitikineni A, Samineni S, Agarwal G, Varshney RK. Comprehensive transcriptome profiling uncovers molecular mechanisms and potential candidate genes associated with heat stress response in chickpea. Int J Mol Sci. 2023;24 (2):1369.https://doi.org/10.3390/ijms24021369
- Liu H, Yu H, Tang G, Huang T. Small but powerful: function of microRNAs in plant development. Plant Cell Rep. 2018;37:515-28. https://doi.org/10.1007/s00299-017-2246-5
- Simões-Araújo JL, Rodrigues RL, Liliane BA, Mondego JM, Alves-Ferreira M, Rumjanek NG, Margis-Pinheiro M. Identification of differentially expressed genes by cDNA-AFLP technique during heat stress in cowpea nodules. FEBS Lett. 2002;515(1-3):44-50. https://doi.org/10.1016/s0014-5793(02)02416-x
- 99. No DH, Baek D, Lee SH, Cheong MS, Chun HJ, Park MS, et al. Hightemperature conditions promote soybean flowering through the transcriptional reprograming of flowering genes in the photoperiod pathway. Int J Mol Sci. 2021;22(3):1314. https:// doi.org/10.3390/ijms22031314