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ROLE OF HEAT SHOCK PROTEINS IN DROUGHT TOLERANCE MECHANISM IN CHICKPEA

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Chickpea is highly drought-resistant and can withstand high temperatures and prolonged droughts, making it suitable for climate conditions in Ukraine, so increasing of chickpea drought tolerance is highly important. Heat shock proteins (HSP), especially small HSP (sHSP), are diverse and have evolved significantly, indicating their ancient origins and critical roles in plant stress responses. These proteins have undergone extensive gene duplication and divergence, leading to various functions and stress responses across different plant species. sHSP have conserved α -crystallin domain, and typically form large oligomeric complexes essential for their chaperone activity. They prevent protein aggregation and assist in protein refolding under stress. sHSPs are found in various cellular compartments, indicating specialized roles in different cellular environments. HSP regulation is controlled by heat shock factors (HSF), which activate in response to stress and bind to heat shock elements in HSP promoters. HSF are regulated at multiple levels, ensuring balanced stress adaptation and recovery. Identified HSF in chickpea are significantly upregulated during heat stress, indicating their critical role in stress tolerance. HSP, including sHSP like CaHSP18.5 and CaHSP22.7, are upregulated under drought stress in chickpea, contributing to improved membrane stability and antioxidative protection. Proteomic and transcriptomic analyses have identified key HSP that are differentially expressed in drought-tolerant chickpea genotypes. Cross-priming with mild drought stress can enhance the expression of HSP, providing potential strategy for improving both drought and heat tolerance in chickpea. MicroRNAs (miRNA) play crucial roles in regulating HSPs and other stress-responsive genes. miR408 and miR398 are significant in enhancing drought and heat tolerance by targeting specific genes and modulating HSP expression. The differential expression of various miRNA under drought conditions highlights their importance in multiple regulatory pathways.

Key words: *Cicer arietinum*, drought tolerance, variety, agricultural productivity, changing climate conditions, genes, small heat shock proteins.

Chickpea (*Cicer arietinum* L.) is a highly valued legume crop known for its significant nutritional benefits and economic importance. It is widely cultivated and consumed across the globe, particularly in developing countries. Chickpea is a rich source of high-quality protein, carbohydrates,

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dietary fiber, and essential vitamins and minerals, making it a crucial component of a balanced diet [1–3]. It contains essential amino acids, unsaturated fatty acids, and bioactive compounds like isoflavones and carotenoids, which contribute to its health benefits, including antioxidant, anti-inflammatory, and anti-diabetic properties [4]. Chickpea ranks third in global legumes production, with an annual yield of over 11.5 million tons, primarily centered in India [5].

Advances in chickpea breeding, including biofortification and the development of stress-tolerant varieties, are crucial for enhancing its nutritional quality and yield under extreme environmental conditions [6, 7]. Climate change is leading to more frequent and severe droughts, particularly in regions like Europe, North America, and China, which negatively impact crop yields and agricultural productivity [8]. Chickpea is highly drought-resistant and can withstand high temperatures and prolonged droughts, making it suitable for the climate conditions in Ukraine [9], so increasing of chickpea drought tolerance by techniques such as marker-assisted selection and genetical transformation is highly important. One of the promising targets are heat shock proteins (HSP). HSPs help maintain protein homeostasis by assisting in protein folding, assembly, translocation, and degradation under stress conditions, including drought [10]. HSPs are involved in the quality control of plasma membrane-resident pattern recognition receptors (PRRs) and intracellular resistance (R) proteins, which are crucial for plant immunity and stress responses, such as thermal and drought response [11].

HSPs phylogeny and evolution. HSPs are a diverse group of molecular chaperones that play crucial roles in protecting plants from stress-induced damage. Among them, small heat shock proteins (sHSPs) are particularly notable for their evolutionary diversity and functional significance. Plant sHSPs are highly diverse, with some species having up to 40 different sHSPs, which are categorized into multiple classes based on their cellular localization and function [12–15]. The sHSP gene families underwent significant lineage-specific expansions early in land plant evolution, with further diversification in seed plants and angiosperms [16]. Phylogenetic analyses reveal that gene duplication, sequence divergence, and gene conversion have played significant roles in the evolution of plant sHSPs [17]. The presence of sHSPs in both mosses and higher plants indicates that these gene families are ancient, evolving at least 450 million years ago [18]. sHSPs have diversified not only in sequence but also in function and cellular localization, suggesting that they may have different roles in stress responses and development. Some sHSPs are highly upregulated in response to heat and other stressors, while others are selectively expressed in seeds and pollen, or are constitutively expressed [19].

The chloroplast-localized sHSPs in mosses and angiosperms show unexpected evolutionary relationships, suggesting that these proteins evolved via gene duplication from nuclear-encoded cytosolic sHSPs rather than from cyanobacterial ancestors. In *Liriodendron chinense*, the HSP gene family has undergone segmental and tandem duplication events, contributing to its expansion and evolution, with many genes showing responsiveness to temperature stress [20].

The evolution of plant heat shock proteins, particularly sHSPs, is characterized by significant diversification and functional specialization. These proteins have ancient origins and have undergone extensive gene duplication and divergence, leading to a wide range of functions and stress responses. Despite their sequence variability, structural conservation suggests a stable evolutionary role in protecting plants from stress. Understanding the phylogeny and evolution of these proteins provides critical insights into plant adaptation to environmental challenges.

HSPs structure and functional mechanism. Plant small heat shock proteins (sHSPs) are a diverse and structurally complex group of proteins that play a critical role in plant stress tolerance. They function as molecular chaperones, preventing protein aggregation and assisting in protein refolding under stress conditions. The diversity and evolutionary expansion of sHSPs in plants highlight their importance in adapting to various environmental stresses. Understanding the structural and functional mechanisms of sHSPs, including their compartment-specific roles, is essential for developing strategies to enhance plant resilience to thermal stress. sHSPs share a conserved α -crystallin domain with a β -sandwich structure and a variable N-terminal domain [21].

These proteins typically form large oligomeric complexes, often with 12 or more subunits, which are crucial for their chaperone activity. The crystal structure of sHSPs reveals a hollow spherical complex with octahedral symmetry, composed of 24 monomers [22]. sHSPs act as molecular chaperones, binding to partially denatured proteins to prevent irreversible aggregation, and assist in refolding [23]. Different classes of sHSPs in the plant cytosol (Class I and Class II) exhibit varied mechanisms of target molecules protection, with Class II sHSPs maintaining oligomeric structures at high temperatures [24]. sHSPs are found in various cellular compartments, including the cytosol, chloroplasts, endoplasmic reticulum, and mitochondria, indicating specialized roles under different cellular environments. Chloroplast-localized sHSPs, such as Hsp21, associate with thylakoid membranes during heat stress, protecting photosystem II and electron transport [25].

HSPs regulation. The regulation of HSPs is primarily controlled by heat shock factors (HSFs), which are activated in response to stress. HSFs are essential regulators of HSP transcription. They bind to heat shock elements in HSP promoters, and mediate the dissociation of bound histones, leading to HSP transcription. HSFs are regulated at multiple levels, including transcriptional, post-transcriptional, and post-translational modifications, adding complexity to their function [26–28].

AtHSBP, a heat shock factor-binding protein in *Arabidopsis*, acts as a negative regulator of the heat shock response by interacting with HSFs and reducing their DNA-binding capacity. This regulation is crucial for seed development and recovery from heat stress. Genome-wide analyses have identified numerous HSFs and HSPs in various plant species, highlighting their conservation and diversification across different plant lineages. These studies provide valuable insights for breeding programs aimed at improving stress tolerance [29].

HSPs and HSFs play a critical role in managing stress responses, particularly heat stress. HSPs function as molecular chaperones, ensuring pro-

tein stability and preventing aggregation. HSFs regulate the transcription of HSPs through complex signaling pathways. The diversity of sHSPs and their specific roles in protecting cellular components, like photosystem II, underscore their importance in plant thermotolerance. Additionally, negative regulators like AtHSBP fine-tune the heat shock response, ensuring balanced stress adaptation and recovery. Understanding these mechanisms provides a foundation for developing stress-resistant plant varieties.

Study of Chidambaranathan et al. [30] had identified 22 HSFs in both desi and kabuli chickpea genomes. Specifically, CarHSFA2, A6, and B2 are significantly up-regulated in response to heat stress during the seedling and pod development stages. Comparative expression analysis in five different plants revealed that orthologs of CarHSFA2, A6, and B2 are also upregulated under heat stress, indicating the critical role of these HSFs in conferring heat tolerance in chickpea during pod development. Additionally, there is notable expression plasticity of HSFs under field conditions compared to control conditions. The identified heat stress-inducible HSFs in chickpea and the environmental influence on their expression require further detailed analysis.

HSPs in drought response in chickpea. HSPs, including small HSPs like CaHSP18.5 and CaHSP22.7, are upregulated in chickpea under drought stress, contributing to improved membrane stability and antioxidative protection [31–33]. Overexpression of specific HSPs, such as CaHsp25.9, in other plants like pepper, has shown enhanced drought tolerance by reducing reactive oxygen species (ROS) accumulation and increasing antioxidant enzymes activity [34].

Heat shock transcription factors (HSFs) like CarHSFB2 and MdHSFA8a are involved in regulating the expression of heat-responsive genes, which also play a role in drought tolerance. These factors help in the accumulation of flavonoids and activation of stress-responsive genes [35, 36].

Proteomic studies have identified several HSPs and other stress-related proteins that are differentially expressed in drought-tolerant chickpea genotypes. These proteins are involved in various physiological processes, including protein synthesis, intracellular traffic, and protective mechanisms [37–39]. Transcriptomic analyses have revealed that genes encoding HSPs and other stress-responsive proteins are upregulated in drought-tolerant chickpea genotypes, indicating their role in drought stress adaptation. Cross-priming with mild drought stress has been shown to enhance heat tolerance in chickpea by stimulating the expression of small HSPs and antioxidative protective mechanisms. This suggests a potential strategy for improving drought and heat tolerance simultaneously.

In the study of Juneja et al. [40], 18 Hsf and 42 Hsp genes were identified in desi chickpea, while 17 Hsf and 34 Hsp genes were identified in kabuli chickpea. Gene structure, conserved protein motif, and phylogenetic tree analyses were performed to classify and understand the evolutionary relationships between these genes. qRT-PCR results indicated the involvement of CaHsf and CaHsp genes in the heat stress response. Interaction network analysis revealed that HsfsA1 regulates the Hsp70 and Hsp18.2 genes, suggesting their role in various developmental processes. The regulation of CasHsp, CaHsp70, CaHsfs, CaHsp90, and CaHsp100

genes was further elucidated by identifying their miRNA targets, which include miR156, miR166, miR319, miR171, and miR5213, respectively. Additionally, it was observed that priming/pre-conditioning enhanced the plants' ability to withstand lethal stress and maintain cross-tolerance under both laboratory and field conditions.

Heat shock proteins (HSPs) and heat shock transcription factors (HSFs) play a significant role in enhancing drought tolerance in chickpea. These proteins help in maintaining membrane stability, reducing oxidative damage, and activating stress-responsive genes. Proteomic and transcriptomic analyses have identified key HSPs and other stress-related proteins that are upregulated in drought-tolerant genotypes. Cross-priming with mild drought stress can further enhance the expression of HSPs, providing a potential strategy for improving both drought and heat tolerance in chickpea.

Role of miRNA in HSPs regulation. MicroRNAs (miRNAs) are small non-coding RNAs that play crucial roles in regulating gene expression, including the modulation of heat shock proteins (HSPs) and other stress-responsive genes. Overexpression of miR408 in chickpea leads to increased drought tolerance by regulating drought-responsive genes, including DREB and other related genes [41, 42]. miR398 is induced by heat stress and downregulates its target genes (CSD1, CSD2, and CCS), enhancing thermotolerance by modulating heat shock proteins and heat stress transcription factors [43]. miR160 modulates the expression of heat shock proteins (HSP17.6A, HSP17.6II, HSP21, and HSP70B) and improves heat tolerance in *Arabidopsis*, suggesting a potential role in drought tolerance through similar mechanisms [44]. Differential expression of miRNAs (e.g., miR396, miR408, miR414, miR528, and miR1533) in chickpea under drought conditions indicates their role in regulating multiple pathways, including protein and nitrogen metabolism [45]. miRNAs play a pivotal role in regulating heat shock proteins and other stress-responsive genes, contributing to drought tolerance in chickpea. miR408 and miR398 are particularly significant, with miR408 enhancing drought tolerance by targeting plantacyanin and laccase, and miR398 improving thermotolerance by modulating heat shock proteins. The differential expression of various miRNAs under drought conditions highlights their importance in multiple regulatory pathways, making them potential targets for genetic manipulation to enhance drought tolerance in crops.

Conclusions. HSPs, especially small heat shock proteins (sHSPs), are diverse and have evolved significantly, indicating their ancient origins and critical roles in plant stress responses. These proteins have undergone extensive gene duplication and divergence, leading to various functions and stress responses across different plant species. sHSPs have a conserved α -crystallin domain and typically form large oligomeric complexes essential for their chaperone activity. They prevent protein aggregation and assist in protein refolding under stress. sHSPs are found in various cellular compartments, indicating specialized roles in different cellular environments.

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Understanding these mechanisms offers valuable strategies for developing stress-resistant chickpea varieties, which is crucial for sustaining agricultural productivity under changing climate conditions.

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РОЛЬ БІЛКІВ ТЕПЛОВОГО ШОКУ В МЕХАНІЗМІ ПОСУХОСТІЙКОСТІ НУТУ

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Нут може витримувати високі температури та тривалі посухи, що робить його придатним для вирощування в кліматичних умовах України, тому підвищення посухостійкості нуту внаслідок застосування методів селекції за допомогою маркерів та генетичної трансформації надзвичайно важливе. Протеїни теплового шоку (heat shock proteins, HSP), особливо малі HSP (small HSP, sHSP), різноманітні й значно еволюціонували, що свідчить про їхнє давнє походження і критично важливу роль у стресових реакціях рослин. Ці протеїни зазнали чималого генного дублювання та дивергенції, що привело до виникнення різних функцій та стресових реакцій у різних видів рослин. sHSP мають консервативний α -кристалічний домен і зазвичай утворюють великі олігомерні комплекси, необхідні для їхньої шаперонної активності. Вони запобігають агрегації протеїнів і допомагають у відновленні протеїнів під час стресу. sHSP знаходяться в різних клітинних компартментах, що вказує на їхню спеціалізовану роль у різних клітинних середовищах. Регуляція HSP контролюється факторами теплового шоку (heat shock factors, HSF), які активуються у відповідь на стрес і зв'язуються з елементами теплового шоку в промоторах HSP. Регулювання HSF відбувається на декількох рівнях, забезпечуючи збалансовану адаптацію до стресу та відновлення. Ідентифіковані HSF в нуті значно підвищують свою активність за теплового стресу, що вказує на їхню важливу роль у стресостійкості. HSP, включно sHSP, такі як CaHSP18.5 та CaHSP22.7, підвищують свою активність в нуті під час водного стресу, сприяючи покращенню стабільності мембран та антиоксидантного захисту. Протеомний та транскриптомний аналізи ідентифікували ключові HSP, які диференційовано експресуються у посухостійких генотипах нуту. Перехресне праймування з легким водним стресом може посилити експресію HSP, що є потенційною стратегією для покращення стійкості нуту до посухи та спеки. МікроРНК (miRNA) відіграють важливу роль у регуляції HSP та інших стресочутливих генів. miR408 та miR398 відіграють важливу роль у підвищенні стійкості до посухи та спеки націлюванням на конкретні гени та модуляції експресії HSP. Диференційована експресія різних міРНК за умов посухи підкреслює їхню важливість у численних регуляторних шляхах. Розуміння цих генетичних механізмів пропонує цінні стратегії для виведення стресостійких сортів нуту, що має вирішальне значення для підтримання продуктивності сільського господарства в умовах мінливого клімату.

Ключові слова: *Cicer arietinum*, посухостійкість, сорт, сільськогосподарська продуктивність, зміна кліматичних умов, гени, малі протеїни теплового шоку.

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