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Understanding the Role of Molecular Chaperones in Plant Stress Tolerance Mechanisms

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INTRODUCTION

Abiotic stresses the major constrains affecting sustainable agricultural production throughout the world. Abiotic stress including extreme temperature, drought, oxidative stress, salinity and toxicity are the primary cause of crop loss and significantly reducing global crop yield up to 50 %. Series of morphological, biochemical, physiological and molecular changes have been observed in plants under stressed condition. Most of the cellular and molecular mechanism associated with physiological and biochemical mechanisms of the plants are unable to face the environmental threats at every stage of growth and development. These changes significantly affect proper growth and development of plants under diverse environmental conditions. Some phenological development in plants like stomatal closure, deeper root system, and cuticular waxes significantly reduces the effect of environmental stresses. These phenological development cellular defense mechanism in the plants and plays vital role in reducing the effect of climatic conditions through development of tolerance mechanism (Roy, et al., 2019). In this series, molecular chaperons have been found to responsive when plants are subjected to stress conditions like high temperature, drought and salinity. Wide range of cellular pathways associated with molecular chaperons has been studies by the researchers to understand the mechanism of tolerance in plants under high temperature and water deficit condition. Chaperones prevent stress-induced aggregation by binding to non-native proteins, keeping them in folding-competent states until they can be refolded or degraded (Lindquist and Craig 1988).

Moreover, Chaperones prevent stress-induced aggregation by binding to non-native proteins, keeping them in folding-competent states until they can be refolded or degraded. Most of the molecular chaperons are ubiquitous proteins found in plant and animal cells. Several *hsp* genes that have been identified at various domain of heat-sock proteins contributing wide variety of stresses such as UV light, heat, cold, wound healing and some other biotic stresses. Most of the *hsp* genes associated with heat-sock proteins contributing to the cellular homeostasis and stressed condition (Wang, et al., 2024). Molecular chaperons are very crucial for the development of tolerance in plants against stresses. Most of the molecular chaperons are able to stabilize proteins and folders that prevent misfolding of the proteins during abiotic stresses. Heat-sock proteins (HSPs) are the well-known group of the molecular chaperons involved in maintaining cellular homeostasis through protein folding, trafficking, and degradation under abiotic stresses like heat, drought and salinity (Al-Whaibi, 2011). Several classes of heat-sock proteins such as HSP60, HSP70, and HSP90 have been identified in the plants are able to maintain the damaged proteins by heat and drought (Bosl, et al., 2006). Every stage of the plans growth and development including seed germination to maturity stages have been found to damage by high temperature and water deficit condition are managed by these molecular chaperons. Increase in chaperon's level in plants under heat and drought condition directly enhancing plant resilience and accelerates stress tolerance mechanism. In the present article, authors have tried to explore the various classes of molecular chaperons and their strategic role in the abiotic stress tolerance mechanism in plants.

2. Classes of plant chaperons

Heat-sock proteins (molecular chaperons) are generally observed in all living organism including bacteria, plants and animals. The number of and classes of molecular chaperons varies from organism to organism. Molecular chaperons are found in most of the cellular organelles like endoplasmic reticulum, mitochondria, cytoplasm, chloroplast and nucleus (Wang, et al., 2024). Based on the molecular weight, most of the heat-sock proteins are categorized in to five major classes: (i) small heat shock proteins (ii) HSP60 (iii) HSP70 (iv) HSP90 and (v) HSP100. Some molecular chaperons are indentified as co-chaperons like HSP40. HSP40 play very important role and assisting HSP70 for proper functioning under teat and drought stress.

Table 1: Major classes of plant chaperons and their function under stressed condition

HSP Class	Primary Stress Function	Specific Plant Examples
Small HSPs	Holding misfolded proteins for later refolding.	Protect Photosystem II during heat stress.
HSP60	Provide safe cage for isolated protein folding in organelles.	Vital for the stability and assembly of Rubisco.
HSP70	Bind with hydrophobic stretches to facilitate folding and transport.	Involved infection defense and hormone signaling.
HSP90	Regulates maturation of signaling *kinases* and receptors.	Buffers genetic variation and stabilizes R proteins in immunity.
HSP100	Unfold large protein aggregates formed during severe heat.	Established heat tolerance in seedlings.

2.1. Hsp 70 family: Hsp 70 with co-chaperons built a set of prominent cellular molecules that assist with wide range of protein assistance. Most of the combined form of Hsp 70 essentially functions in both normal and stressed condition. Hsp 70 play important role in the expression of tress responsive genes under unfavorable environmental condition like heat and drought stress. Hsp 70 genes associated with heat and drought tolerance have been identified in many plant species. The Arabidopsis genome contains at least 18 genes encoding members of the Hsp70 family, of which 14 belong to the *Dna-K* subfamily and four to the Hsp110/SSE subfamily.

2.2. Hsp 60 family: Hsp 60 family is also known as chaperonins. Most of the chaperonins are found in the plastids and mitochondria of prokaryotes. They are important in assisting plastid proteins such as Rubisco.

2.3. Hsp 90 family: HSP 90 is completely different from other classes of molecular chaperons. Hsp90 is one of the major species of molecular chaperones that requires ATP for its functions. Most of Hsp 90 chaperons are involved in the high molecular weight protein folding. They also play vital role in the signal transduction, cell-cycle control protein trafficking and protein degradation. Additionally, it might also play a role in morphological evolution and stress adaptation in Drosophila and Arabidopsis.

2.4. Hsp100 family: This is member of large AAA *ATPase* super family having diverse range of function in various cellular activities. They were first described as components of the two-subunit bacterial *Clp* protease system. Hsp 100 molecular chaperons have been reported in many plant species like Arabidopsis, soybean, tobacco, rice, maize, Lima bean and wheat. They are generally involved in protein disaggregation and/or protein degradation. The major role of these molecular chaperons is to recovery of cell stress.

2.5. Small HSP families: Small HSPs family includes low molecular weight chaperons. They are highly diverse than normal chaperon families. They are synthesized in both prokaryotic and eukaryotic cells in response to high temperature and other environmental stresses (Koo, et al., 2015). Some of the members of small HSP chaperons are express during developmental stage of the plant.

3. HSP network

Most of the heat sock proteins are able to establish highly regulated network that regulates proteostasis system. These networks play crucial role in stress signaling and protein quality control. Studies at molecular level revealed that abiotic threats like drought and heat stress causes protein unfolding that expose hydrophobic residues and triggering protein aggregation. The small heat sock proteins (sHSPs) works as primary responders by formation of oligogenic complexes that facilitates binding with partially unfolded proteins in ATP-independent manner to prevent irreversible aggregation (Basha, et al., 2013; Koo, et al., 2015). These substrates are later transferred to ATP-dependent molecular chaperons like Hsp70. The HSp70 in cooperation with co-chaperons (HSp40) stimulates mechanism like ATP hydrolysis, stabilizing client binding, whereas nucleotide exchange factor promotes substrate release for establishment of refolding cycles.

Similarly, other classes of molecular chaperons like Hsp60 i.e. chaperonin complexes like GroEL/GroES facilitates isolated folding chamber for more complex proteins, while another chaperons Hsp90 provide fine turn maturation of signaling proteins in association co-chaperons like p23 and Hop. When plants are under adverse environmental conditions, stress sensing is sharply regulated by heat sock transcriptional factors (HSFs). The misfolded proteins due to stress allowing HSF termination, phosphorylation and binding to heat sock elements in DNA that rapidly upregulating the genes associated with HSPs. Under normal

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environmental conditions, these factors are remaining inactive state with Hsp70 and Hsp90. Further, the damaged proteins that are unable to refold may be directed to proteasome for degradation. Thus, the multilayered network ensures robust balance between protein repair and removal system. Such type of repair and removal system maintains cellular homeostasis under adverse environmental situations.

4. Mechanism of action

Molecular chaperons are essential for establishment of cellular safeguard in the plants under diverse environmental conditions. These chaperons function as safeguard cellular proteostasis in the plant tissues when exposed to unfavourable environmental situation like extreme heat, drought, salinity and oxidative stress (Bosl, et al., 2006). Primarily, these molecular chaperons (HSPs) prevents misfolding and aggregation of the proteins then protecting functional proteins and establishment of sustainable cellular mechanism under adverse climatic conditions.

Most of the cellular proteins maintain stable tertiary structures under normal physiological conditions. When plant subjected to stressed conditions like extreme temperature, dehydration of plant tissues takes place and breaks weak covalent bands and causing unfolding of the protein. These unfolding of the proteins expose hydrophobic amino acid residues. In most of the cases, exposed regions have tendency to develop non-specific interactions that leads protein aggregation and cellular toxicity. During protein aggregation and cellular toxicity, most of the high molecular weight heat sock proteins rapidly accumulated in response to stress and binds with hydrophobic surfaces to shield unfolded proteins and maintaining their solubility (Banerjee and Roychoudhury, 2018).

Additionally, small heat sock proteins (sHSPs) facilitate first line of defense by formation of large oligomeric assemblies having ability to unfold proteins in ATP-independent manners (Koo, et al., 2015). Later, ATP-independent chaperons like Hsp70 and Hsp90 facilitates protein refolding mechanism. Further, HHSp70 associated with co-chaperons like Hsp40 and release state driven ATP hydrolysis attempts correct protein folding (Ding, et al., 1998). In some cases where refolding requires compartmental isolation, chaperonins like Hsp60 strengthen protected folding chamber for polypeptide establishment to achieve native confirmation. During protein refolding, heat sock proteins are involved in intracellular protein trafficking and ensuring proper targeting of newly synthesized proteins essential for particular cellular organelles. Thus, the coordinated mechanism ensures selective protein quality control and preventing toxic aggregation that allows plants to survive under fluctuating environmental stresses.

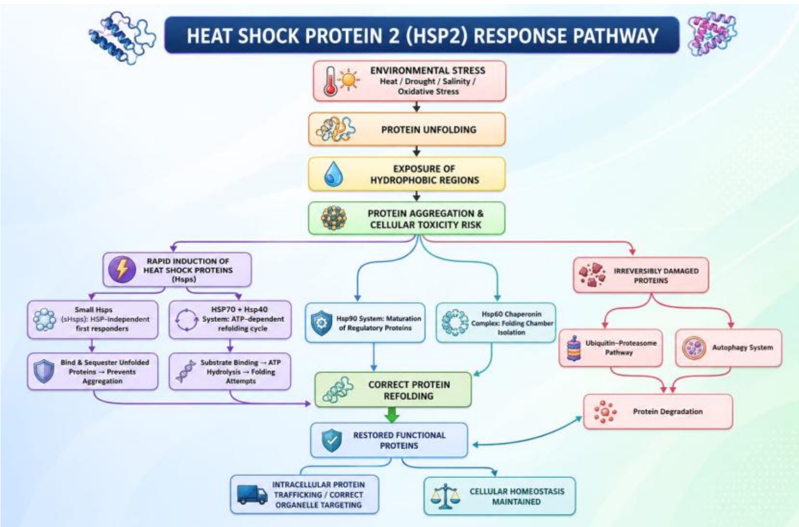

Figure-1: Mechanism of action of HSPs in plants under stressed condition

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5. Integration of molecular chaperones with stress signaling

Heat sock proteins are not involved in the protein folding mechanism but play central role in the development of stress signaling networks. Expression and integration of the molecular chaperons (HSPs) with cellular mechanism enabling the rapid response under stressed condition for the development of adaptation. Under unfavourable environmental conditions like drought, extreme heat, and salinity, protein misfolding acts as inter-cellular signals that interlinked with proteotoxic stress to enable transcriptional reprogramming. Furthermore, the heat sock transcriptional factors (HFSs) family plays key role in association with cellular mechanism. Under non-stressed situation, these heat sock transcriptional factors (HSFs) remain inactive by physical association with high molecular weight heat sock protein family Hsp70 and Hsp90 (Banerjee and Roychoudhury, 2018). When stress induces under unfavourable environmental conditions that would accelerates protein unfolding, then these misfolding proteins binds with high molecular weight heat sock proteins like Hsp70 and Hsp90 and quickly releases heat sock transcriptional factors (Ding, et al., 1998). After releasing heat sock transcriptional factors, these factors undergoes post-transcriptional modification like phosphorylation and tightly binds with heat sock elements (HSEs) near to promoter region and rapidly initiating the transcription of heat sock protein genes.

Additionally, heat sock proteins interact with redox signaling and hormonal pathways like reactive oxygen species (ROS), Abscisic acid (ABA) and calcium dependent signaling. Moreover, these molecular chaperons regulate stability of key signaling chaperons and ensuring their proper propagation. Therefore, heat sock proteins works as stress sensors and effectors for strategic interaction between stress responsive gene regulation and protein quality control and enabling plant survival under extreme heat, drought and salinity stress.

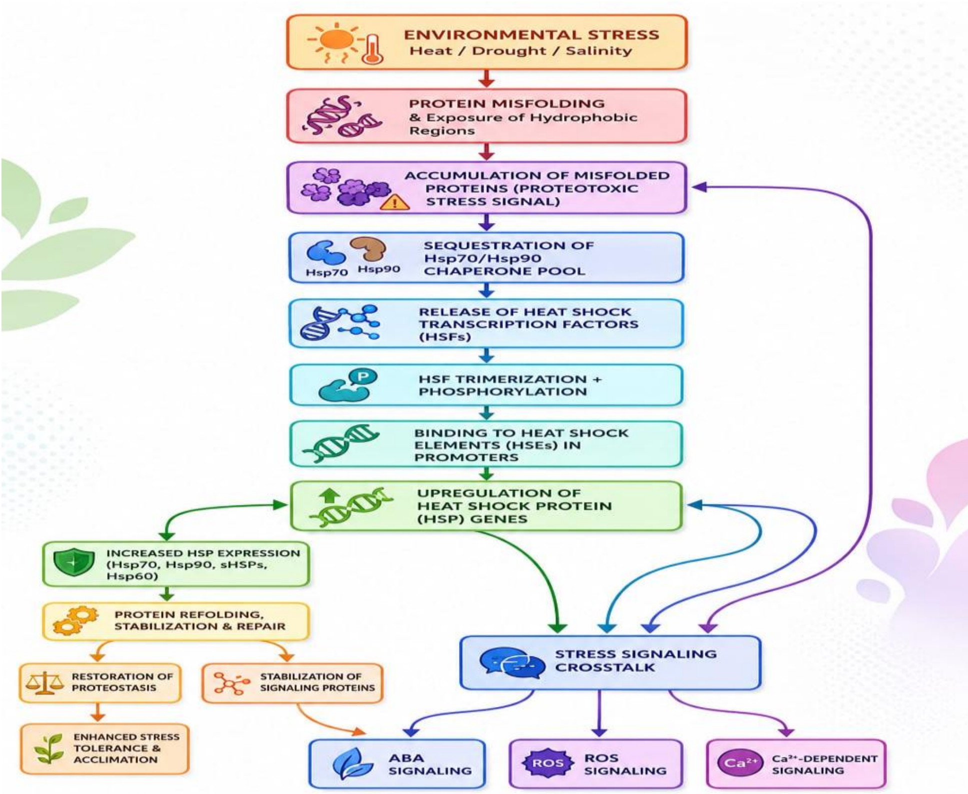

Figure 2: Integration of molecular chaperones with stress signaling in plants

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CONCLUSION

Globally, plants are challenged by biotic and abiotic stress including insects, pests, diseases, intense light, high and low temperature, drought, salinity and heavy metals. The extreme of climatic condition significantly degrades cellular proteins and result as aggregation and dysfunction. Prevention of cellular proteins and retaining its proper function is very essential for the plants under stressed condition. Molecular chaperons often called heat-sock proteins perform significantly in sustaining the cellular protein integrity by preventing it from dysfunction and degradation. The diverse classes of heat-sock proteins plays crucial role in the development of sustainability at cellular protein level through folding of misfolded proteins and disaggregation of aggregated misfolded proteins. These molecular chaperons are also play important role in degradation of unwanted non-native proteins to accelerate the desirable proteins motifs. In several case studies, it has been observed that most of the heat-sock proteins expressed under abiotic stress. The expression of heat-sock proteins under abiotic stress encodes for the responsive genes which trigger cellular network to combat with effect of stresses. Some heat-sock proteins are transcribed continuously in all cells or tissues under specific developmental control.

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