

A Review of Heat Shock Proteins Research on Bemisia tabaci

Shunxiao Liu^{1,2*}, Kui Wang¹, Vlasenko Volodymyr^{2#}

¹Department of Plant Protection, Henan Institute of Science and Technology, Xinxiang, China ²Department of Plant Protection, Sumy National Agrarian University, Sumy, Ukraine Email: lshx_07@163.com, *vlasenkova@ukr.net

How to cite this paper: Liu, S.X., Wang, K. and Volodymyr, V. (2022) A Review of Heat Shock Proteins Research on Bemisia tabaci. Agricultural Sciences, 13, 393-403. https://doi.org/10.4236/as.2022.133027

Received: February 5, 2022 Accepted: March 12, 2022 Published: March 15, 2022

Copyright © 2022 by author(s) and Scientific Research Publishing Inc. This work is licensed under the Creative Commons Attribution International License (CC BY 4.0).

http://creativecommons.org/licenses/by/4.0/ **Open Access**

Abstract

Bemisia tabaci (Gennadius) (Homoptera: Aleyrodidae) is the most destructive invasive pests in agricultural production and has a high tolerance to heat. Heat shock proteins play an essential role in life activities such as growth and development, reproduction and diapause of *B. tabaci*. At the same time, they are also crucial in resisting adverse environments and in adaptive evolution. The expression of heat shock protein in *B. tabaci* is not only related to temperature, but also to the tolerance of the environment. After receiving external stimuli, the expression level can be increased or decreased to maintain the stability of cells in vivo. This paper reviews the classification, biological characteristics, biological functions, and research status of HSPs in recent years. This mini-review will provide helpful information related to the use of heat shock proteins to study the occurrence and damage of B. tabaci. This has important theoretical and practical significance for revealing Hsps in explaining the population expansion mechanism of B. tabaci invasion and predicting population dynamics.

Keywords

Bemisia tabaci, Heat Shock Proteins, Molecular Chaperone, Heat Shock Transcriptional Factor, Stress

1. Introduction

B. tabaci was first reported in 1889 when it was found on tobacco in Greece and was named Aleyrodes tabaci [1]. B. tabaci belongs to Hemiptera, Aleyrodidae. It is a tiny, herbivorous piercing-sucking pest concentrated in tropical and subtropical regions [2] [3]. B. tabaci is a species complex containing more than 30 *First author. *Corresponding author.

cryptic species [4] [5]. Among the various biotypes of *B. tabaci*, it spreads worldwide through trade activities such as the transportation of poinsettia or other flower seedlings [6] [7]. *B. tabaci* has become an essential worldwide pest due to its sizeable feeding amount, broad host range, strong viability, large egg production, rapid development, and easy to develop drug resistance, with high ecological adaptability and thermotolerance [8] [9].

Heat shock proteins (HSPs) are anti-stress proteins when organisms are under the pressure of adverse environmental conditions for a certain period [10] [11]. HSPs can be used as molecular chaperones to transfer intracellular nascent peptide chains and recognize denatured proteins, and it is an essential mechanism for organisms to cope with adverse environments [12] [13] [14] [15].

In 1962, Ritossa [16] first discovered that a brief heat shock could induce the formation of new bulges in the salivary gland chromosomes of *Drosophila* melanogaster larvae, which is called heat shock response (HSR). After that, many studies have proved that heat shock proteins have the function of conferring heat resistance to organisms [17] [18] [19] [20]. Until 1974, Tissiéres *et al.* [21] used SDS-PAGE and autoradiography to confirm that the substance predicted by Ritossa at that time was a group of particular proteins and named these proteins as HSP. Furthermore, *whiteflies* can utilize heat shock proteins (HSPs) (encoded by Hsp genes) and other stress-related genes to overcome thermal stress [22]. When *B. tabaci* is exposed to harsh environments to a sub-lethal level, heat shock proteins will increase or decrease protein expression to supplement cellular toughness. This paper reviews the different types, characteristics and gene expression of HSP in *B. tabaci*, in order to illustrate the progress of HSP in *B. tabaci* [23].

2. Classification of Heat Shock Proteins

In recent years, with the rapid development of biological science and technology and the improvement of sequencing efficiency and accuracy, the research on HSPs has made significant progress. At present, we divide heat shock proteins into five families: Hsp90, Hsp70, Hsp60, small-molecule heat shock proteins, and ubiquitin according to their molecular weight and homology similarity [20] [24] [25] [26]. Within the HSPs, Hsp70s are the most studied group [27]. There are many reports on Hsp90 and Hsp70 of *B. tabaci* [28]. Salvucci *et al.* [22] found that Hsp70 and Hsp90 were the major polypeptides synthesized by *whiteflies* in response to heat stress. Wang *et al.* [29] observations highlighted the molecular evolutionary properties and the response mechanism to temperature assaults of Hsp genes in *whitefly*.

2.1. Hsp90

Hsp90 exists in various types of cytoplasm under normal or stress conditions. Its primary function is to bind to denatured proteins as a molecular chaperone and

participate in the regulation and maintenance of the conformation and role of various proteins in cells so that cells can usually survive under a stress environment [30] [31] [32]. Hsp90 can also interact with signal transduction proteins, promote the binding of steroid hormone receptors and protein kinases to form complexes, and regulate kinase phosphorylation activity [31] [33] [34] [35]. The interaction between environmental stress and Hsp90 of *B. tabaci* and the analysis of the molecular mechanism has practical significance for further understanding the resistance mechanism of *B. tabaci* to achieve the control effect [30] [36]. Kinene [37] investigated the variability of the HSP90 gene in the *B. tabaci* species complex and found evidence of recombination in the coding region of the HSP90 gene in the *B. tabaci* species complex.

2.2. Hsp70

The Hsp70 family is a class of highly conserved heat shock proteins. Its main functions are: involved in protein folding and unfolding, protein translocation, and multimeric complex translocation. It has weak ATPase activity when combined with ATP [38] [39]. When *B. tabaci* is under high-temperature stress, a large amount of Hsp70 is synthesized in the body to protect it from or reduce high-temperature damage [40] [41]. Differences in heat shock proteins (HSPs), especially Hsp70, which plays a vital role in heat tolerance, might cause the observed differences between females and males of *B. tabaci* [36] [42].

2.3. Hsp60

Hsp60 usually exists in the cytoplasm and mitochondria. Hsp60 is not only involved in the folding and assembly of proteins encoded by nuclear genes after entering mitochondria, but also in the folding, assembly and transport of proteins encoded by mitochondria themselves [43]. Under stress conditions, Hsp60 binds to ATP first, causing its own conformational change, so that it can bind proteins for maintenance and repair [44]. Wang *et al.* [29] employed comprehensive genomics approaches to identify one Hsp60 in the Middle East Asia Minor 1 *whitefly* genome.

2.4. Small Heat Shock Proteins

Small heat shock proteins exist in highly ordered oligomers in organisms. Because they have different biological functions in different environments, they are usually in two states of dissociation and aggregation. Their main parts are: participating in protein folding, unfolding, and assembling multimeric complexes [25] [45] [46]. Improving diapause and cold tolerance for most insects is vital for their safe overwintering. Small heat shock proteins have an essential contribution to enhancing diapause and cold tolerance of insects [47] [48] [49]. Small heat shock proteins (sHSPs) are probably the most diverse in structure and function among the various superfamilies of stress proteins, and they play essential roles in different biological processes. Bai *et al.* [50] confirmed that the sHSP genes of *B. tabaci* had shown differential expression changes under thermal stress.

2.5. Ubiquitin

Ubiquitin is a protein found in eukaryotic cells either free or covalently joined to a variety of cytoplasmic and nuclear proteins [51]. Its physiological function is to participate in protein degradation [52]. Xia *et al.* [53] found that ubiquitin-proteasome system might help the *whitefly* to counteract the negative influence from TYLCV through degrading the virus directly or activating immune response.

3. Characteristics of Heat Shock Proteins

Heat shock proteins were initially considered unique proteins expressed by organisms in response to increased temperature. Still, studies have found that a class of heat shock genes is also significantly expressed in unstimulated cells or produced in specific cell cycle stages [48] [54]. Meanwhile, studies have shown that many heat shock proteins exist in mitochondria and chloroplasts. Therefore, heat shock protein genes are a multigene superfamily in which not all members are regulated by heat shock [55] [56] [57]. Subsequent studies have shown that organisms may induce the synthesis of such stress proteins under stressful environmental conditions such as high temperature, salinity, drought, and osmosis, which function as molecular chaperones in cells and participate in folding new peptide chains, protein assembly, and transport [58] [59].

The growth and development of insects are very complex, they go through different developmental stages, and insects in different developmental stages also have significant differences in their morphology [60]. Heat shock proteins can improve the tolerance of organisms to adverse environments and protect organisms or cells from minor damage in subsequent lethal stress [61]. Organisms can often acquire heat tolerance under higher temperature stress after treating sub-lethal high temperatures [17]. Jinn *et al.* [62] [63] showed that the expression of HSPs is related to heat resistance, but also the thermal stability of different kinds of HSPs can substitute for each other. Heat shock proteins (HSPs) as molecular chaperones to assist in the refolding, stabilization, intracellular transport, and degradation of proteins to prevent the accumulation of damaged proteins and maintain the stability of the intracellular environment [11] [56] [64].

4. Heat Shock Protein Gene

Studies have found that the heat tolerance of organisms is closely related to the structure and expression of their Hsp genes [37] [65] [66]. The regulation of heat shock gene expression includes selective transcription and alternative translation; the former is the main one [62]. Studies have shown that heat shock proteins are not directly involved in protecting their intracellular environment in these organisms, but bind to the heat shock element (HSE) through heat shock

transcriptional factor (HSF), to form transcription complexes and promote the expression of heat shock protein genes [67] [68].

In organisms, the structure and function of HSF have less variation in evolution and have extensive homology. It is a protein that is ubiquitous in eukaryotic cells. We divided them into four types according to their different functions, including Hsf1, Hsf2, Hsf3, and Hsf4 [69]. Hsf1 is considered a major regulator of cellular heat shock protein expression. It is highly conserved in yeast, drosophila, and vertebrates, and the other three HSFs cannot replace Hsf1 [70] [71] [72] [73]. Hsf2 is resistant to heat-stimulating signals and is generally more sensitive to signals representing growth, development, and differentiation [74]. Hsf3 is a bird-specific heat-shock regulator [68] [75]. Hsf4 only exists in the human body, does not activate the transcription process, and plays an important role in cataract occurrence. Hsf4 can inhibit the expression of heat shock genes under certain conditions [76]. The molecular mechanism of heat tolerance in females of *B. tabaci* MEAM1 cryptic species compared with males shows that the differential expression of multiple genes regulates the heat tolerance of females [77] [78] [79].

5. Conclusion

With the continuous development of sequencing technology and the continuous reduction of sequencing costs, we will identify more heat shock protein genes of *B. tabaci*. Identifying these sequences will reveal the evolution of heat shock proteins in *B. tabaci*. The research on the function of heat shock proteins in *B. tabaci* must also be related to the physiology, growth, and development of *B. tabaci* to understand the different roles in the physiology and evolution of *B. tabaci*. Studying the properties and expression levels of HSP genes in B. tabaci is helpful to clarify the mechanism of *B. tabaci* diapause induction. In terms of biological control, we can use the expression mechanism of heat shock protein-related genes to regulate the timing of diapause in *B. tabaci*.

In conclusion, it is of great significance to study the heat shock protein of *B. tabaci*, which is helpful to understand the relationship between the growth and development of *B. tabaci* and various influencing factors (such as temperature, pathogen invasion, pesticides, *et al.*), to provide new ideas for the comprehensive control of *B. tabaci*, and better carry out plant protection and quarantine work.

Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

References

- [1] Gennadius, P. (1889) Disease of Tobacco Plantations in the Trikonia. The Aleurodid of Tobacco. *Elliniko Georgia*, **5**, 1-3.
- [2] Mound, L.A. and Halsey, S.H. (1978) Whitefly of the World: A Systematic Cata-

logue of the Aleyrodidae (Hemiptera) with Host Plant and Natural Enemy Data. British Museum (Natural History), London and John Wiley and Sons, Chichester. https://doi.org/10.5962/bhl.title.118687

- [3] Brown, J.K., Frohlich, D.R. and Rosell, R.C. (1995) The Sweetpotato or Silverleaf Whiteflies: Biotypes of *Bemisia tabaci* or a Species Complex. *Annual Review of Entomology*, 40, 511-534. <u>https://doi.org/10.1146/annurev.en.40.010195.002455</u>
- [4] De Barro, P.J., Liu, S.S., Boykin, L.M. and Dinsdale, A.B. (2011) *Bemisia tabaci*: A Statement of Species Status. *Annual Review of Entomology*, 56, 1-19. https://doi.org/10.1146/annurev-ento-112408-085504
- [5] Wang, H.L., Lei, T., Xia, W.Q., Cameron, S.L., Liu, Y.Q., et al. (2019) Insight into the Microbial World of *Bemisia tabaci* Cryptic Species Complex and Its Relationships with Its Host. *Scientific Reports*, 9, Article No. 6568. <u>https://doi.org/10.1038/s41598-019-42793-8</u>
- [6] Oliveira, M.R.V., Henneberry, T.J. and Anderson, P. (2001) History, Current Status, and Collaborative Research Projects for *Bemisia tabaci. Crop Protection*, 20, 709-723. <u>https://doi.org/10.1016/S0261-2194(01)00108-9</u>
- [7] Dinsdale, A., Cook, L., Riginos, C., Buckley, Y.M. and De Barro, P. (2010) Refined Global Analysis of *Bemisia tabaci* (Hemiptera: Sternorrhyncha: Aleyrodoidea: Aleyrodidae) Mitochondrial Cytochrome Oxidase 1 to Identify Species-Level Genetic Boundaries. *Annals of the Entomological Society of America*, **103**, 196-208. <u>https://doi.org/10.1603/AN09061</u>
- [8] De Barro, P.J., Liebregts, W. and Carver, M. (1998) Distribution and Identity of Biotypes of *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) in Member Countries of the Secretariat of the Pacific Community. *Australian Journal of Entomology*, 37, 214-218. <u>https://doi.org/10.1111/j.1440-6055.1998.tb01574.x</u>
- [9] Hu, J., De Barro, P.J., Zhao, H., Wang, J., Nardi, F. and Liu, S.S. (2011) An Extensive Field Survey Combined with a Phylogenetic Analysis Reveals Rapid and Widespread Invasion of Two Alien Whiteflies in China. *PLoS ONE*, 6, e16061. https://doi.org/10.1371/journal.pone.0016061
- [10] Lindquist, S. (1986) The Heat-Shock Response. Annual Review of Biochemistry, 55, 1151-1191. <u>https://doi.org/10.1146/annurev.bi.55.070186.005443</u>
- [11] Zhao, L. and Jones, W.A. (2012) Expression of Heat Shock Protein Genes in Insect Stress Responses. *Invertebrate Survival Journal*, 9, 93-101.
- [12] Lindguist, S. and Craig, E.A. (1988) The Heat Shock Proteins. Annual Review of Genetics, 22, 631-677. <u>https://doi.org/10.1146/annurev.ge.22.120188.003215</u>
- Yost, H.J., Peterson, R.B. and Lindquist, S. (1990) RNA Metabolism: Strategies for Regulation in the Heat Shock Response. *Trends in Genetics*, 6, 223-227. https://doi.org/10.1016/0168-9525(90)90183-7
- [14] Feder, M.E. and Hofmann, G.E. (1999) Heat-Shock Proteins, Molecular Chaperones, and the Stress Response: Evolutionary and Ecological Physiology. *Annual Review of Physiology*, **61**, 243-282. <u>https://doi.org/10.1146/annurev.physiol.61.1.243</u>
- [15] Nusayr, T. (2020) The Role of Heat-Shock Proteins, in Vector-Virus Transmission. *Applied Plant Virology*, 19, 249-254. <u>https://doi.org/10.1016/B978-0-12-818654-1.00019-0</u>
- [16] Ritossa, F.M. (1962) A New Puffing Pattern Induced by Temperature Shock and DNP in Drosophila. *Experientia*, 18, 571-573. <u>https://doi.org/10.1007/BF02172188</u>
- [17] Moseley, P.L. (1997) Heat Shock Proteins and Heat Adaptation of the Whole Organism. *Journal of Applied Physiology*, 83, 1413-1417.

https://doi.org/10.1152/jappl.1997.83.5.1413

- [18] Lin, H., Head, M. and Blank, M. (1998) Myc-Mediated Transactivation of HSP70 Expression Following Exposure to Magnetic Fields. *Journal of Cell Biochemistry*, 69, 181-188.
 <u>https://doi.org/10.1002/(SICI)1097-4644(19980501)69:2%3C181::AID-JCB8%3E3.0.</u> CO;2-O
- [19] Ekengren, S., Tryselius, Y., Dushay, M.S., Liu, G., Steiner, H. and Hultmark, D. (2001) A Humoral Stress Response in Drosophila. *Current Biology*, 11, 714-718. https://doi.org/10.1016/S0960-9822(01)00452-3
- [20] Sørensen, J.G., Kristensen, T.N. and Loeschcke, V. (2003) The Evolutionary and Ecological Role of Heat Shock Proteins. *Ecology Letters*, 6, 1025-1037. <u>https://doi.org/10.1046/j.1461-0248.2003.00528.x</u>
- [21] Tissiéres, A., Mitchell, H.K. and Tracy, U.M. (1974) Protein Synthesis in Salivary Glands of Drosophila Melanogaster: Relation to Chromosome Puffs. *Journal of Molecular Biology*, 84, 389-392. https://doi.org/10.1016/0022-2836(74)90447-1
- [22] Salvucci, M.E., Stecher, D.S. and Henneberry, T.J. (2000) Heat Shock Proteins in Whiteflies, an Insect that Accumulates Sorbitol in Response to Heat Stress. *Journal* of Thermal Biology, 25, 363-371. <u>https://doi.org/10.1016/S0306-4565(99)00108-4</u>
- [23] Mahadav, A., Kontsedalov, S., Czosnek, H. and Ghanim, M. (2009) Thermotolerance and Gene Expression Following Heat Stress in the Whitefly *Bemisia tabaci* B and Q Biotypes. *Insect Biochemistry and Molecular Biology*, **39**, 668-676. https://doi.org/10.1016/j.ibmb.2009.08.002
- [24] Morimoto, R.I. (1993) Cell in Stress: Transcriptional Activation of Heat Shock Genes. Science, 259, 1409-1410. <u>https://doi.org/10.1126/science.8451637</u>
- [25] Kim, K.K., Kim, R. and Kim, S. (1998) Crystal Structure of a Small Heat-Shock Protein. *Nature*, **394**, 595-599. <u>https://doi.org/10.1038/29106</u>
- [26] Buchanan, B.B., Gruissem, W. and Jones R. (2000) Biochemistry and Molecular Biology of Plants. American Society of Plant Biologists, Rockville, Maryland, 983-987.
- [27] Kregel, K.C. (2002) Invited Review: Heat Shock Proteins: Modifying Factors in Physiological Stress Responses and Acquired Thermotolerance. *Journal of Applied Physiology*, **92**, 2177-2186. <u>https://doi.org/10.1152/japplphysiol.01267.2001</u>
- [28] Elbaz, M., Weiser, M. and Morin, S. (2011) Asymmetry in Thermal Tolerance Trade-Offs between the B and Q Sibling Species of *Bemisia tabaci* (Hemiptera: Aleyrodidae). *Journal of Evolutionary Biology*, 24, 1099-1109. https://doi.org/10.1111/j.1420-9101.2011.02241.x
- [29] Wang, X.R., Wang, C., Ban, F.X., Zhu, D.T., Liu, S.S. and Wang X.W. (2019) Genome-Wide Identification and Characterization of HSP Gene Superfamily in Whitefly (*Bemisia tabaci*) and Expression Profiling Analysis under Temperature Stress. *Insect Science*, 26, 44-57. <u>https://doi.org/10.1111/1744-7917.12505</u>
- [30] Yonehara, M., Minami, Y., Kawata, Y., Nagai, J. and Yahara, I. (1996) Heat-Induced Chaperone Activity of HSP90. *Journal of Biological Chemistry*, 271, 2641-2645. <u>https://doi.org/10.1074/jbc.271.5.2641</u>
- [31] Picard, D. (2002) Heat-Shock Protein 90, a Chaperone for Folding and Regulation. *Cellular and Molecular Life Sciences*, 59, 1640-1648. <u>https://doi.org/10.1007/PL00012491</u>
- [32] Zuehlke, A. and Johnson, J.L. (2010) Hsp90 and Co-Chaperones Twist the Functions of Diverse Client Proteins. *Biopolymers*, 93, 211-217. <u>https://doi.org/10.1002/bip.21292</u>

- [33] Christine, Q., Todd, A.S. and Susan, L. (2002) Hsp90 as a Capacitor of Phenotypic Variation. *Nature*, 417, 618-624. https://doi.org/10.1038/nature749
- [34] Rutherford, S.L. and Zuker, C.S. (1994) Protein Folding and the Regulation of Signaling Pathways. *Cell*, **79**, 1129-1132. <u>https://doi.org/10.1016/0092-8674(94)90003-5</u>
- [35] Prodromou, C., Roe, S.M., O'Brien, R., Ladbury, J.E., Piper, P.W. and Pearl, L.H. (1997) Identification and Structural Characterization of the ATP/ADP-Binding Site in the Hsp90 Molecular Chaperone. *Cell*, **90**, 65-75. https://doi.org/10.1016/S0092-8674(00)80314-1
- [36] Lü, Z.C. and Wan, F.H. (2011) Using Double-Stranded RNA to Explore the Role of Heat Shock Protein Genes in Heat Tolerance in *Bemisia tabaci* (Gennadius). *Journal* of Experimental Biology, 214, 764-769. <u>https://doi.org/10.1242/jeb.047415</u>
- [37] Kinene, T., De Marchi, B.R., Alicai, T., Luboobi, L.S., Omongo, C.A., Savill, A. and Boykin, L.M. (2019) Recombination Detected in the Heat Shock Protein 90 (HSP90) of the *Bemisia tabaci* Species Complex. *BioRxiv*. https://doi.org/10.1101/655233
- [38] Guy, C.L. and Li, Q.B. (1998) The Organization and Evolution of the Spinach Stress 70 Molecular Chaperone Gene Family. *The Plant Cell*, **10**, 539-556. <u>https://doi.org/10.1105/tpc.10.4.539</u>
- [39] Wegele, H., Muller, L. and Buchner, J. (2004) Hsp70 and Hsp90—A Relay Team for Protein Folding. *Reviews of Physiology, Biochemistry and Pharmacology*, 151, 1-44.
- [40] Wolfe, G.R., Hendrix, D.L. and Salvucci, M.E. (1998) A Thermoprotective Role for Sorbitol in the Silverleaf Whitefly, *Bemisia argentifolii. Journal of Insect Physiology*, 44, 597-603. <u>https://doi.org/10.1016/S0022-1910(98)00035-3</u>
- [41] Bai, J., Wang, Y.C., Liu, Y.C., Chang, Y.W., Liu, X.N., Gong, W.R. and Du, Y.Z. (2021) Isolation of Two New Genes Encoding Heat Shock Protein 70 in *Bemisia tabaci* and Analysis during Thermal Stress. *International Journal of Biological Macromolecules: Part A*, **193**, 933-940. https://doi.org/10.1016/j.ijbiomac.2021.10.186
- [42] Yu, H. and Wan, F.H. (2009) Cloning and Expression of Heat Shock Protein Genes in Two Whitefly Species in Response to Thermal Stress. *Journal of Applied Entomology*, 133, 602-614. <u>https://doi.org/10.1111/j.1439-0418.2009.01403.x</u>
- [43] Horwich, A.L. and Willison, K.R. (1993) Protein Folding in the Cell: Functions of Two Families of Molecular Chaperone, Hsp60 and TF55-TCP1. In: Ellis, R.J., Laskey, R.A. and Lorimer, G.H., Eds., *Molecular Chaperones*, Springer, Dordrecht, 57-70. <u>https://doi.org/10.1007/978-94-011-2108-8_8</u>
- [44] King, A.M. and Macrae, T.H. (2015) Insect Heat Shock Proteins during Stress and Diapause. *Annual Review of Entomology*, **60**, 59-75. https://doi.org/10.1146/annurev-ento-011613-162107
- [45] Nakamoto, H. and Vígh, L. (2007) The Small Heat Shock Proteins and Their Clients. *Cellular and Molecular Life Sciences*, 64, 294-306. <u>https://doi.org/10.1007/s00018-006-6321-2</u>
- [46] Garrido, C., Paul, C., Seigneuric, R. and Kampinga, H.H. (2012) The Small Heat Shock Proteins Family: The Long-Forgotten Chaperones. *International Journal of Biochemistry & Cell Biology*, 44, 1588-1592. https://doi.org/10.1016/j.biocel.2012.02.022
- [47] Evgen'ev, M.B., Zatsepina, O.G., Garbuz, D., Lerman, D.N., Velikodvorskaya, V., Zelentsova, E. and Feder, M.E. (2004) Evolution and Arrangement of the Hsp70 Gene Cluster in Two Closely Related Species of the Virilis Group of Drosophila. *Chromo-soma*, **113**, 223-232. <u>https://doi.org/10.1007/s00412-004-0312-6</u>
- [48] Rinehart, J.P., Li, A., Yocum, G.D., Robich, R.M., Hayward, S.A. and Denlinger,

D.L. (2007) Up-Regulation of Heat Shock Proteins is Essential for Cold Survival during Insect Diapause. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 11130-11137. https://doi.org/10.1073/pnas.0703538104

- [49] Clark, M.S. and Worland, M.R. (2008) How Insects Survive the Cold: Molecular Mechanisms—A Review. *Journal of Comparative Physiology B, Biochemical, Systemic and Environmental Physiology*, **178**, 917-933. https://doi.org/10.1007/s00360-008-0286-4
- [50] Bai, J., Liu, X.N., Lu, M.X. and Du, Y.Z. (2019) Characterization of Genes Encoding Small Heat Shock Proteins from *Bemisia tabaci* and Expression under Thermal Stress. *PeerJ*, 7, e6992. <u>https://doi.org/10.7717/peerj.6992</u>
- [51] Finley, D. and Varshavsky, A. (1985) The Ubiquitin System: Functions and Mechanisms. *Trends in Biochemical Sciences*, **10**, 343-347. https://doi.org/10.1016/0968-0004(85)90108-2
- [52] Hoeller, D., Hecker, C.M. and Dikic, I. (2006) Ubiquitin and Ubiquitin-Like Proteins in Cancer Pathogenesis. *Nature Reviews Cancer*, 6, 776-788. https://doi.org/10.1038/nrc1994
- [53] Xia, W.Q., Liang, Y., Liu, Y.Q., Liu, S.S. and Wang, X.W. (2017) Effects of Ubiquitin-Proteasome System on Tomato Yellow Leaf Curl Virus in Whitefly (Hemiptera: Aleyrodidae). *Acta Entomologica Sinica*, **60**, 1411-1419.
- [54] Xiao, N., Pan, L.L., Zhang, C.R., Shan, H.W. and Liu, S.S. (2016) Differential Tolerance Capacity to Unfavourable Low and High Temperatures between Two Invasive Whiteflies. *Scientific Reports*, 6, Article No. 24306. https://doi.org/10.1038/srep24306
- [55] Hartman, D.J., Dougan, D., Hoogenraad, N.J. and Høj, P.B. (1992) Heat Shock Proteins of Barley Mitochondria and Chloroplasts Identification of Organellar Hsp10 and 12: Putative Chaperonin 10 Homologues. *FEBS Letters*, **305**, 147-150. <u>https://doi.org/10.1016/0014-5793(92)80883-1</u>
- [56] Wang, W.X., Vinocur, B., Shoseyov, O. and Altman, A. (2004) Role of Plant Heat-Shock Proteins and Molecular Chaperones in the Abiotic Stress Response. *Trends in Plant Science*, 9, 244-252. <u>https://doi.org/10.1016/j.tplants.2004.03.006</u>
- [57] Al-Whaibi, M.H. (2011) Plant Heat-Shock Proteins: A Mini Review. Journal of King Saud University-Science, 23, 139-150.
 <u>https://doi.org/10.1016/j.jksus.2010.06.022</u>
- [58] Mogk, A., Deuerling, E., Vorderwülbecke, S., Vierling, E. and Bukau, B. (2003) Small Heat Shock Proteins, ClpB and the DnaK System Form a Functional Triade in Reversing Protein Aggregation. *Molecular Microbiology*, **50**, 585-595. https://doi.org/10.1046/j.1365-2958.2003.03710.x
- [59] Sangster, T.A. and Queitsch, C. (2005) The HSP90 Chaperone Complex, an Emerging Force in Plant Development and Phenotypic Plasticity. *Current Opinion in Plant Biology*, 8, 86-92. <u>https://doi.org/10.1016/j.pbi.2004.11.012</u>
- [60] Jiang, R., Qi, L.D., Du, Y.Z. and Li, Y.X. (2017) Thermotolerance and Heat-Shock Protein Gene Expression Patterns in *Bemisia tabaci* (Hemiptera: Aleyrodidae) Mediterranean in Relation to Developmental Stage. *Journal of Economic Entomology*, 110, 2190-2198. https://doi.org/10.1093/jee/tox224
- [61] Jacques, R. (2003) Evolution of Heat Shock Protein and Immunity. *Developmental and Comparative Immunology*, 27, 449-464. https://doi.org/10.1016/S0145-305X(02)00160-X

- [62] Jinn, T.L., Yeh, Y.C., Chen, Y.M. and Lin, C.Y. (1989) Stabilization of Soluble Proteins in Vitro by Heat Shock Proteins-Enriched Ammonium Sulfate Faction from Soybean Seedlings. *Plant Cell Physiology*, **30**, 463-469. https://doi.org/10.1093/oxfordjournals.pcp.a077764
- [63] Jinn, T.L., Wu, S.H., Yeh, K.W., Hsieh, M.H., Yeh, Y.C., Chen, Y.M. and Lin, C.Y. (1993) Immunological Kinship of Class I Low Molecular Weight Heat Shock Proteins and Thermostabilization of Soluble Proteins in Vitro among Plants. *Plant & Cell Physiology*, 34, 1055-1062.
- [64] Becker, J. and Craig, E.A. (1994) Heat-Shock Proteins as Molecular Chaperones. *European Journal of Biochemistry*, 219, 11-23. https://doi.org/10.1111/j.1432-1033.1994.tb19910.x
- [65] Coleman, J.S., Heckathorn, S.A. and Hallberg, R.L. (1995) Heat-Shock Proteins and Thermotolerance: Linking Molecular and Ecological Perspectives. *Trends in Ecology and Evolution*, **10**, 305-306. <u>https://doi.org/10.1016/S0169-5347(00)89112-0</u>
- [66] Hoffmann, A.A., Sørensen, J.G. and Loeschcke, V. (2003) Adaptation of Drosophila to Temperature Extremes: Bringing Together Quantitative and Molecular Approaches. *Journal of Thermal Biology*, 28, 175-216. <u>https://doi.org/10.1016/S0306-4565(02)00057-8</u>
- [67] Wu, C. (1995) Heat Shock Transcription Factors: Structure and Regulation. Annual Review of Cell and Developmental Biology, 11, 441-469. <u>https://doi.org/10.1146/annurev.cb.11.110195.002301</u>
- [68] Pirkkala, L., Nykanen, P. and Sistonen, L. (2001) Roles of the Heat Shock Transcription Factors in Regulation of the Heat Shock Response and Beyond. *The FASEB Journal*, 15, 1118-1131. <u>https://doi.org/10.1096/fj00-0294rev</u>
- [69] Snoeckx, L.H., Cornelussen, R.N., Van Nieuwenhoven, F.A., Reneman, R.S. and Der Vusse, G.J. (2001) Heat Shock Proteins and Cardiovascular Pathophysiology. *Physiological Reviews*, 81, 1461-1497. <u>https://doi.org/10.1152/physrev.2001.81.4.1461</u>
- [70] Salda, L.D. and Romanucci, M. (2012) The Role of Heat Shock Proteins in Mammary Neoplasms: A Brief Review. *Journal of Cancer Therapy*, 3, 755-767. <u>https://doi.org/10.4236/jct.2012.325095</u>
- [71] Mcmillan, D.R., Xiao, X.Z., Shao, L., Graves, K. and Benjamin, I.J. (1998) Targeted Disruption of Heat Shock Transcription Factor 1 Abolishes Thermotolerance and Protection against Heat-Inducible Apoptosis. *Journal of Biological Chemistry*, 273, 7523-7528. <u>https://doi.org/10.1074/jbc.273.13.7523</u>
- [72] Xiao, X.Z., Zuo, X.X., Davis, A.A., Mcmillan, D.R., Curry, B.B., Richardson, J.A. and Benjamin, I.J. (1999) HSF1 Is Required for Extra-Embryonic Development, Postnatal Growth and Protection during Inflammatory Response in Mice. *The EMBO Journal*, 18, 5943-5952. <u>https://doi.org/10.1093/emboj/18.21.5943</u>
- [73] Wiederrecht, G., Seto, D. and Parker, C.S. (1988) Isolation of the Gene Encoding the S. Cerevisiae Heat Shock Transcription Factor. *Cell*, 54, 841-853. https://doi.org/10.1016/S0092-8674(88)91197-X
- [74] Mathew, A., Mathur, S.K. and Morimoto, R.I. (1998) Heat Shock Response and Protein Degradation: Regulation of HSf2 by the Ubiquitin-Proteasome Pathway. *Molecular and cellular biology*, 18, 5091-5098. https://doi.org/10.1128/MCB.18.9.5091
- [75] Nakai, A., Kawazoe, Y., Tanabe, M., Nagata, K. and Morimoto, R.I. (1995) The DNA-Binding Properties of Two Heat Shock Factors, HSF1 and HSF3, Are Induced in the Avian Erythroblast Cell Line HD6. *Molecular and Cellular Biology*, 15,

5268-5278. https://doi.org/10.1128/MCB.15.10.5268

- [76] Morimoto, R.I. (1998) Regulation of the Heat Shock Transcriptional Response: Cross Talk between a Family of Heat Shock Factors, Molecular Chaperones, and Negative Regulators. *Genes Development*, **12**, 3788-3796. https://doi.org/10.1101/gad.12.24.3788
- [77] Lü, Z.C. and Wan, F.H. (2008) Differential Gene Expression in Whitefly (*Bemisia tabaci*) B-Biotype Females and Males under Heat-Shock Condition. *Comparative Biochemistry and Physiology Part D*, **3**, 257-262. https://doi.org/10.1016/j.cbd.2008.06.003
- [78] Díaz, f., Orobio, R.F. and Chavarriaga, P. (2015) Differential Expression Patterns among Heat-Shock Protein Genes and Thermal Responses in the Whitefly *Bemisia tabaci* (MEAM 1). *Journal of Thermal Biology*, **52**, 199-207. <u>https://doi.org/10.1016/j.jtherbio.2015.07.004</u>
- [79] Cui, X.H., Wan, F.H., Xie, M. and Liu, T.X. (2008) Effects of Heat Shock on Survival and Reproduction of Two Whitefly Species, *Trialeurodes vaporariorum* and *Bemisia tabaci* Biotype B. *Journal of Insect Science*, 8, Article No. 24. https://doi.org/10.1673/031.008.2401