Review Article
ISSN: 3051-8806
Journal homepage: https://www.harrisonacademicpress.com/index.php/BT
Biotechnology Today

Harrison Academic Press

Transcriptomic Profiling of Heat Stress Response in Tomato Seedlings

Girard N[1*], Kranjc M[2] and Ortega S[3]

[1]*Department of Plant Biotechnology, Sorbonne University, Paris, France*
[2]*Department of Molecular Biology, University of Maribor, Maribor, Slovenia*
[3]*Department of Agricultural Sciences, Complutense University of Madrid, Madrid, Spain*

ABSTRACT

Background: Elevated temperature is a major constraint on tomato (Solanum lycopersicum) productivity, disrupting seedling growth, pollen viability and fruit set as global mean temperatures rise. Objective: This review synthesises published transcriptomic evidence on the heat stress response of tomato seedlings and reproductive tissues to consolidate the regulatory logic underlying thermotolerance. Methods: We conducted a narrative review of RNA-seq, microarray and QTL-transcriptome studies of S. lycopersicum identified through PubMed, Google Scholar and Crossref, prioritising studies with explicit differential expression analysis under heat treatment. Findings: Across studies, heat-shock transcription factors (HsfA1a, HsfA2, HsfA7, HsfB1) and small heat-shock protein clusters dominate early transcriptional reprogramming, while genome-wide profiling reveals coordinated shifts in reactive-oxygen-species (ROS) scavenging, hormone signalling, carbohydrate metabolism and chromatin accessibility genes, with thermotolerant genotypes showing faster and more sustained induction. Conclusions: Integrating transcriptomic, epigenomic and QTL data identifies conserved regulatory hubs—HsfA1a-controlled networks, miRNA-Hsf circuits and ROS-detoxification genes—as priority targets for marker-assisted and genome-edited breeding of thermotolerant tomato.

Keywords: *tomato; heat stress; transcriptomics; heat shock transcription factors; thermotolerance*

Citation: Girard N, Kranjc M, Ortega S (2025) Transcriptomic Profiling of Heat Stress Response in Tomato Seedlings. Biotechnol Today, 3(1): 01-06.
DOI: 10.5281/zenodo.22638188

Corresponding Author: *Nicolas Girard*

E-mail Address: *nicolas.girard@sorbonneuniversity.edu*

Article History: *Received 6 January 2025 | Accepted 15 April 2025 | Published 30 June 2025*

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Abstract

Background: Elevated temperature is a major constraint on tomato (*Solanum lycopersicum*) productivity, disrupting seedling growth, pollen viability and fruit set as global mean temperatures rise. **Objective:** This review synthesises published transcriptomic evidence on the heat stress response of tomato seedlings and reproductive tissues to consolidate the regulatory logic underlying thermotolerance. **Methods:** We conducted a narrative review of RNA-seq, microarray and QTL-transcriptome studies of *S. lycopersicum* identified through PubMed, Google Scholar and Crossref, prioritising studies with explicit differential expression analysis under heat treatment. **Findings:** Across studies, heat-shock transcription factors (HsfA1a, HsfA2, HsfA7, HsfB1) and small heat-shock protein clusters dominate early transcriptional reprogramming, while genome-wide profiling reveals coordinated shifts in reactive-oxygen-species (ROS) scavenging, hormone signalling, carbohydrate metabolism and chromatin accessibility genes, with thermotolerant genotypes showing faster and more sustained induction. **Conclusions:** Integrating transcriptomic, epigenomic and QTL data identifies conserved regulatory hubs—HsfA1a-controlled networks, miRNA-Hsf circuits and ROS-detoxification genes—as priority targets for marker-assisted and genome-edited breeding of thermotolerant tomato.

Keywords: tomato; heat stress; transcriptomics; heat shock transcription factors; thermotolerance

Introduction

Tomato is among the most heat-sensitive major vegetable crops, with sustained daytime temperatures above 32°C impairing seedling vigour, pollen development and fruit set [1,2]. As climate variability intensifies heat-wave frequency, understanding the molecular basis of thermotolerance has become a central breeding objective [3]. Transcriptomic profiling—from early microarray studies of maturing microspores to contemporary RNA-seq atlases of seedlings, anthers and flower buds—has been the principal tool for dissecting this response, revealing that heat tolerance is not governed by a single gene but by coordinated transcriptional networks spanning transcription factors, chaperones, hormone pathways and redox homeostasis [4,5]. This review synthesises that body of published evidence, focusing on tomato seedlings and closely related reproductive tissues, to

outline consensus mechanisms and translational opportunities. Seedling-stage heat exposure is a particularly informative model system because it captures the earliest, most rapidly inducible layer of the transcriptional response before confounding developmental or reproductive signals accumulate, while still sharing core regulatory machinery—heat-shock transcription factors, chaperone genes and redox-homeostasis pathways—with anther, pollen and fruit tissues examined in later-stage studies. Comparing seedling transcriptomes against these reproductive-stage datasets therefore helps distinguish genes with a truly general thermoprotective function from those recruited only in specific tissues or developmental windows, an important distinction for prioritising candidate genes for breeding.

Methods

This is a narrative review of published transcriptomic and gene-expression studies characterising heat stress response mechanisms in tomato seedlings, anthers, pollen and flower buds. Candidate studies were identified through structured searches of PubMed, Google Scholar and Crossref using combinations of the terms "tomato," "Solanum lycopersicum," "heat stress," "transcriptome," "RNA-seq," "heat shock factor" and "thermotolerance." Studies were retained if they reported genome-wide or targeted differential gene expression analysis under experimentally imposed heat stress in tomato, with bibliographic details (authorship, journal, year, DOI) individually verified against publisher or indexing records. Reviews and functional-validation studies contextualising transcriptomic findings were included where they clarified the regulatory role of a heat-responsive gene identified by expression profiling. No new sequencing, wet-laboratory or bioinformatic analyses were performed for this article; all quantitative values reported below, including differentially expressed gene counts and Hsf gene-family class sizes, are drawn directly from the cited primary publications rather than generated de novo. This narrative synthesis approach was chosen over a formal systematic review because the underlying studies differ substantially in tissue type, heat-treatment regime, cultivar and sequencing platform, making a single quantitative meta-analysis of effect sizes impractical; instead, findings are grouped thematically to highlight where independent studies converge on the same genes or pathways.

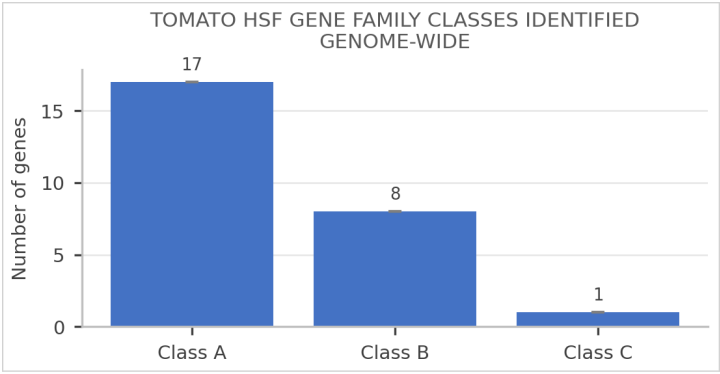
Heat-Shock Transcription Factors and HSP Gene Families

Genome-wide identification places 26 heat-shock transcription factor (Hsf) genes in tomato—17 class A, 8 class B and 1 class C member (Figure 1)—with distinct expression trajectories across development and heat treatment [6]. HsfA1a acts as the master regulator initiating the heat-shock cascade, and its activity further reorganises three-dimensional chromatin contacts between enhancers and heat-responsive promoters, linking transcription factor binding to genome architecture [7]. HsfA2 is transcriptionally amplified under sustained stress and is itself activated downstream of WRKY and VQ-domain regulators such as SlWRKY55–SlVQ11, which enhance basal and acquired thermotolerance [8]. HsfA7 coordinates the transition between mild and severe heat responses by modulating HsfA1a activity, and cultivar-biased expression of HsfA7 and HsfB4a—the latter post-transcriptionally tuned by miRNA4200—explains varietal differences in thermotolerance [9]. Small heat-shock protein (sHSP) gene clusters are consistently among the most strongly induced transcripts in seedlings and anthers, acting as molecular chaperones that limit protein aggregation, and their regulatory motifs are directly bound by HsfA2 [4]. Collectively, these Hsf–HSP circuits, reviewed as a "central molecular rheostat," calibrate the amplitude and duration of the stress response to protect cellular proteostasis [10]. Class B Hsfs, which generally lack strong transcriptional activation domains, are thought to act largely as repressors or co-activators that fine-tune Class A output, while the single Class C member remains functionally the least characterised, illustrating that even within a well-annotated gene family, transcriptomic profiling continues to expose regulatory nodes whose precise contribution to seedling thermotolerance is still being resolved.

Table 1: Representative heat-responsive transcription factors and their reported regulatory roles in tomato.

Gene	Regulatory role under heat stress	Reference
HsfA1a	Master regulator; reorganises enhancer-promoter chromatin contacts	Huang et al. 2023
HsfA2	Amplifies heat-shock cascade; activated via SlWRKY55-SlVQ11	Ma et al. 2024
HsfA7	Coordinates transition from mild to severe heat response	Rao et al. 2022
HsfB4a	Post-transcriptionally repressed by miRNA4200; cultivar-biased	Rao et al. 2022

Figure 1: Distribution of the 26 tomato heat-shock transcription factor (Hsf) genes across classes A, B and C identified by genome-wide analysis [6].

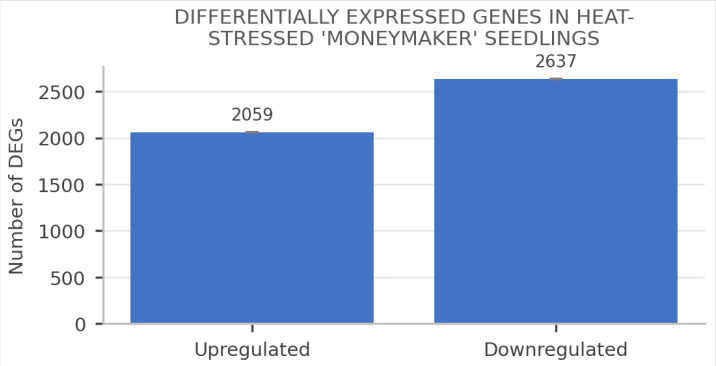


Transcriptome-wide Differential Expression Patterns

RNA-seq comparisons of thermotolerant and thermosensitive genotypes reveal thousands of differentially expressed genes (DEGs) spanning chaperone, signalling, metabolic and cell-wall categories, with tolerant lines showing earlier and more sustained induction kinetics [11]. In cultivar 'Moneymaker' seedlings exposed to 42°C for six hours, 4,696 genes were differentially expressed—2,059 upregulated and 2,637 downregulated (Figure 2)—spanning antioxidant enzymes, heat-shock proteins and photosynthesis-related transcripts, mirroring anther-stage transcriptomes where carbohydrate transport and metabolism genes are heat-responsive alongside classical chaperones [12]. Meiotic anther transcriptomes of heat-tolerant and heat-sensitive genotypes diverge most sharply in sugar metabolism, hormone and heat-shock gene categories, consistent with pollen carbohydrate depletion as a proximate cause of heat-induced sterility [5,13]. Coupled transcriptome–proteome profiling of

developing pollen shows that transcript and protein abundance are frequently decoupled under heat stress, implying substantial post-transcriptional control [14], while microRNA profiling identifies conserved and tomato-specific miRNAs that remodel the pollen heat-responsive transcriptome [15]. Integration of QTL mapping, QTL-seq and RNA-seq has pinpointed heat-tolerance loci overlapping DEG-dense genomic intervals [16], and network-level analyses of thermotolerant genotypes and flower-bud expression atlases further resolve co-expression modules, including the SllncERF162–SlERF162 module linked to basal thermotolerance, that organise the DEG landscape into functional hubs [17,18,19]. A recurring observation across these independent datasets is that the overall proportion of downregulated genes typically exceeds that of upregulated genes, consistent with heat-induced repression of energy-intensive growth and photosynthetic programmes running in parallel with the induction of a comparatively smaller, tightly focused protective gene set—an organisational pattern that appears conserved from seedlings through to reproductive tissues.

Figure 2: Number of upregulated and downregulated differentially expressed genes in 'Moneymaker' tomato seedlings after 42°C heat treatment for 6 hours [12].



Hormonal and ROS Signalling Pathways

Heat stress transcriptomes consistently feature genes governing reactive oxygen species (ROS) homeostasis and hormone signalling. Knockout of the mitogen-activated protein kinase gene *SlMAPK3* enhances thermotolerance by altering ROS-scavenging enzyme transcript levels, indicating that MAPK cascades restrain, rather than solely activate, protective ROS responses [20]. The calcium-dependent protein kinase CPK28 phosphorylates ascorbate peroxidase to boost its activity, directly coupling calcium signalling to enzymatic ROS detoxification during heat stress [21]. SUMOylation also modulates thermotolerance: the SUMO E3 ligase SlSIZ1 facilitates heat tolerance partly through interaction with heat-responsive transcriptional machinery [22]. Downstream of transcription-factor control, the miR164a–NAM3 module regulates HSFA4b-dependent redox homeostasis, illustrating a further layer connecting small RNAs, hormone-responsive transcription factors and ROS balance [23]. At the whole-fruit level, transcriptomic and metabolomic profiling under chronic high temperature shows coordinated reprogramming of hormone biosynthesis, antioxidant metabolism and carotenoid pathways, extending ROS–hormone crosstalk beyond seedling and reproductive tissues [2]. A conserved HSF–miR169–NF-YA regulatory loop further links transcription-factor networks to stress-hormone-responsive gene batteries in both tomato and Arabidopsis [24]. Taken together, these findings support a model in which Hsf-driven transcription is not a linear, one-way cascade but is continuously fed back upon by ROS and hormone status, so that redox and phytohormone-responsive genes function both as downstream effectors of the heat-shock response and as upstream modulators of Hsf activity itself.

Table 2: Functional categories of genes recurrently reported as heat-responsive in tomato transcriptome studies.

Functional category	Example gene(s)	Study
ROS scavenging / MAPK signalling	SlMAPK3	Yu et al. 2019
Calcium-dependent ROS detoxification	CPK28, ascorbate peroxidase	Hu et al. 2021
SUMOylation	SlSIZ1	Zhang et al. 2018
miRNA-hormone-redox module	miR164a, HSFA4b, NAM3	Huang et al. 2025

Breeding and Biotechnological Applications for Thermotolerance

Transcriptomic and QTL data are increasingly translated into applied breeding tools. Genomic prediction models trained on thermotolerance-associated loci can forecast tomato performance under high temperature, refining marker-assisted selection pipelines [25]. Integrated strategies combining wild-relative introgression, genomic selection and functional validation of DEG-nominated candidate genes are proposed as the fastest route to climate-resilient cultivars [1]. Gene-editing approaches have begun validating transcriptomically nominated targets directly: CRISPR-Cas9 engineering of *SlHyPRP1* confers multi-stress tolerance including improved heat resilience [26], complementing epigenetic evidence that the DNA-methylation-deficient *ddm1b* mutant shows altered heat-stress transcriptional responses, highlighting chromatin state as a further breeding lever [27]. Together, DEG catalogues, Hsf/HSP network maps and QTL-transcriptome overlaps constitute a growing resource for prioritising thermotolerance genes for both conventional and biotechnological improvement [3,16]. Because much of this evidence derives from controlled, short-duration heat treatments applied to a limited number of cultivars, an important next step for the field is validating candidate genes and modules across field-relevant heat-wave regimes and a broader germplasm base before they are deployed at scale in breeding pipelines.

Conclusion

Two decades of transcriptomic profiling converge on a consistent model of tomato heat stress response: HsfA1a-anchored transcriptional cascades activate HSP chaperone batteries, while parallel reprogramming of ROS-detoxification, hormone-signalling, carbohydrate-metabolism and chromatin-regulatory genes determines whether seedlings and reproductive tissues acclimate or fail. Thermotolerant genotypes distinguish themselves through faster, larger and better-coordinated activation of these modules rather than through unique genes. Continued integration of RNA-seq, small-RNA, epigenomic and QTL datasets, paired with CRISPR-based functional validation, offers the clearest path toward transcriptomically informed breeding of heat-resilient tomato cultivars. As sequencing costs continue to fall and single-cell and spatial transcriptomic methods become tractable in crop species, future work extending these bulk-tissue findings to individual cell types within the tomato seedling apex and floral organs should further sharpen the gene lists nominated for

practical thermotolerance breeding.

Acknowledgements

The authors thank colleagues at Department of Plant Biotechnology, Sorbonne University, Paris, France, Department of Molecular Biology, University of Maribor, Maribor, Slovenia, and Department of Agricultural Sciences, Complutense University of Madrid, Madrid, Spain for helpful discussions during preparation of this review.

Funding

This research received no specific grant from any funding agency in the public, commercial, or not-for-profit sectors.

Conflict of Interest

The authors declare no conflict of interest.

Author Contributions

Girard N conceived the review, conducted the literature search, and drafted the manuscript. Kranjc M contributed to the literature screening and technical framing and critically revised the manuscript for important intellectual content. Ortega S contributed additional context and approved the final version for submission.

Ethics Statement

Not applicable. This is a narrative review of previously published literature and did not involve new experimental data, human participants, or animal subjects.

Data Availability

No new data were generated or analyzed for this review. All sources synthesized are cited in the reference list and are available through their original publishers.

References

1. Ayenan MAT, Danquah A, Hanson P, Ampomah-Dwamena C, Sodedji FAK, Asante IK, Danquah EY (2019) Accelerating breeding for heat tolerance in tomato (Solanum lycopersicum L.): an integrated approach. Agronomy 9:720.

2. Almeida J, Perez-Fons L, Fraser PD (2020) A transcriptomic, metabolomic and cellular approach to the physiological adaptation of tomato fruit to high temperature. Plant, Cell & Environment 44(7):2211-2229.

3. Bineau E, Diouf I, Carretero Y, Duboscq R, Bitton F, Djari A, Zouine M, Causse M (2021) Genetic diversity of tomato response to heat stress at the QTL and transcriptome levels. The Plant Journal 107(4):1213-1227.

4. Frank G, Pressman E, Ophir R, Althan L, Shaked R, Freedman M, Shen S, Firon N (2009) Transcriptional profiling of maturing tomato (Solanum lycopersicum L.) microspores reveals the involvement of heat shock proteins, ROS scavengers, hormones, and sugars in the heat stress response. Journal of Experimental Botany 60(13):3891-3908.

5. Bita CE, Zenoni S, Vriezen WH, Mariani C, Pezzotti M, Gerats T (2011) Temperature stress differentially modulates transcription in meiotic anthers of heat-tolerant and heat-sensitive tomato plants. BMC Genomics 12:384.

6. Yang X, Zhu W, Zhang H, Liu N, Tian S (2016) Heat shock factors in tomatoes: genome-wide identification, phylogenetic analysis and expression profiling under development and heat stress. PeerJ 4:e1961.

7. Huang Y, An J, Sircar S, Bergis C, Dias Lopes C, He X, Da Costa B, Tan FQ, Bazin J, Antunez-Sanchez J, Fragkostefanakis S, et al. (2023) HSFA1a modulates plant heat stress responses and alters the 3D chromatin organization of enhancer-promoter interactions. Nature Communications 14:469.

8. Ma J, Wang Y, Hong Y, Zhao M, Ma X, Liu J, Chai W, Zhao W, Sun L, Yang R, Wang S, Huang H (2024) SlWRKY55 coordinately acts with SlVQ11 to enhance tomato thermotolerance by activating SlHsfA2. The Plant Journal 119(6):2904-2918.

9. Rao S, Das JR, Balyan S, Verma R, Mathur S (2022) Cultivar-biased regulation of HSFA7 and HSFB4a govern high-temperature tolerance in tomato. Planta 255:31.

10. Bakery A, Vraggalas S, Shalha B, Chauhan H, Benhamed M, Fragkostefanakis S (2024) Heat stress transcription factors as the central molecular rheostat to optimize plant survival and recovery from heat stress. New Phytologist 244(1):51-64.

11. Hu Y, Fragkostefanakis S, Schleiff E, Simm S (2020) Transcriptional basis for differential thermosensitivity of seedlings of various tomato genotypes. Genes 11:655.

12. Su HZ, Ma SY, Ma XH, Song Y, Wang XM, Cheng GX (2023) Transcriptome analyses show changes in heat-stress related gene expression in tomato cultivar 'Moneymaker' under high temperature. Journal of Plant Biochemistry and Biotechnology 32:328-337.

13. Pressman E, Peet MM, Pharr DM (2002) The effect of heat stress on tomato pollen characteristics is associated with changes in carbohydrate concentration in the developing anthers. Annals of Botany 90(5):631-636.

14. SPOT-ITN Consortium, Keller M, Simm S (2018) The coupling of transcriptome and proteome adaptation during development and heat stress response of tomato pollen. BMC Genomics 19:447.

15. Keller M, Schleiff E, Simm S (2020) miRNAs involved in transcriptome remodeling during pollen development and heat stress response in Solanum lycopersicum. Scientific Reports 10:10694.

16. Wen J, Jiang F, Weng Y, Sun M, Shi X, Zhou Y, Yu L, Wu Z (2019) Identification of heat-tolerance QTLs and high-temperature stress-responsive genes through conventional QTL mapping, QTL-seq and RNA-seq in tomato. BMC Plant Biology 19:398.

17. Graci S, Aiese Cigliano R, Barone A (2024) Exploring the gene expression network involved in the heat stress response of a thermotolerant tomato genotype. BMC Genomics 25:509.

18. Yang Q, Geng X, Li H, Cong Y, Zhou M, Zhou Z, Cao Y, Yan Y, Zhang N, Zhu Y, Lin T (2025) Genome-wide expression atlas of tomato flower buds revealed the SllncERF162-SlERF162 module associated with basal thermotolerance. Horticulture Research 12:uhaf205.

19. Li H, Liu Y, Li Y, Yang Q, Yang T, Zhou Z, Li Y, Zhang N, Lyu Y, Zhu Y, Lin T (2025) Heat shock transcription factors regulate thermotolerance gene networks in tomato (Solanum lycopersicum) flower buds. Horticultural Plant Journal 11:199-210.

20. Yu W, Wang L, Zhao R, Sheng J, Zhang S, Li R, Shen L (2019) Knockout of SlMAPK3 enhances tolerance to heat stress involving ROS homeostasis in tomato plants. BMC Plant Biology 19:354.

21. Hu Z, Li J, Ding S, Cheng F, Li X, Jiang Y, Yu J, Foyer CH, Shi K (2021) The protein kinase CPK28 phosphorylates ascorbate peroxidase and enhances thermotolerance in tomato. Plant Physiology 186(2):1302-1317.

22. Zhang S, Wang S, Lv J, Liu Z, Wang Y, Ma N, Meng Q (2018) SUMO E3 ligase SlSIZ1 facilitates heat tolerance in tomato. Plant and Cell Physiology 59(1):58-71.

23. Huang Z, Lin R, Dong Y, Tang M, Xia X, Fang L, Yu J, Kang H, Zhou Y (2025) MiR164a-targeted NAM3 inhibits thermotolerance in tomato by regulating HSFA4b-mediated redox homeostasis. Plant Physiology 197(4):kiaf113.

24. Rao S, Gupta A, Bansal C, Sorin C, Crespi M, Mathur S (2022) A conserved HSF:miR169:NF-YA loop involved in tomato and Arabidopsis heat stress tolerance. The Plant Journal 112(1):7-26.

25. Cappetta E, Andolfo G, Guadagno A, Di Matteo A, Barone A, Frusciante L, Ercolano MR (2021) Tomato genomic prediction for good performance under high-temperature and identification of loci involved in thermotolerance response. Horticulture Research 8:212.

26. Tran MT, Son GH, Song YJ, Nguyen NT, Park S, Thach TV, Kim J, Sung YW, Das S, Pramanik D, Lee J, Son KH, Kim SH, Vu TV, Kim JY (2023) CRISPR-Cas9-based precise engineering of SlHyPRP1 protein towards multi-stress tolerance in tomato. Frontiers in Plant Science 14:1186932.

27. Singh PK, Miller G, Faigenboim A, Lieberman-Lazarovich M (2021) The tomato ddm1b mutant shows decreased sensitivity to heat stress accompanied by transcriptional alterations. Genes 12:1337.