Integrative Transcriptomic Analysis Reveals a Conserved Thermal-Sensitive Developmental Module in Tomato Sperm Cell Lineage

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Abstract

High night temperatures lower tomato (*Solanum lycopersicum*) yield by causing male sterility. The developing sperm cell lineage is highly sensitive to heat. Transcriptional heat responses are well characterized in vegetative tissues; however, their relationship to sperm cell development remains poorly understood. We propose that heat stress may contribute to sterility by disrupting developmental modules associated with sperm specification. We integrated two transcriptomic datasets. GSE131496 documents the response of tomato seedlings to negative temperature differentials, providing a reference set of heat-responsive genes but not a direct model of heat stress in reproductive tissues. GSE117185 contains transcriptomes from isolated sperm cell lineage stages. Using a shared Limma pipeline, we identified differentially expressed genes (adj.$P < 0.05$, $|\log FC| > 1$). We then analyzed the intersection of these gene sets and profiled their correlations. A set of 359 genes showed differential expression during both temperature stress and sperm cell development. Transcriptional responses to heat and sperm cell specification correlated positively (Pearson R = 0.321, $P < 0.0001$). Of these genes, 73% showed concordant regulation while 27% showed discordant regulation. Their expression patterns also differed by developmental stage. A heat-sensitive transcriptional module overlaps with the sperm cell developmental program. This overlap provides candidate genes for future studies on thermotolerant tomatoes and reproductive resilience. Since the heat-response data came from seedlings, these genes still need to be tested during heat-sensitive stages of male gametophyte development.

Keywords: *Solanum lycopersicum*, heat stress, sperm, negative temperature differentials, reproductive function.

Introduction

Rising temperatures and more frequent heatwaves lower crop yields and diminish agricultural output [1–3]. High temperatures affect tomato (*Solanum lycopersicum*) yield by disrupting the reproductive phase, which is less temperature tolerant than vegetative growth [4–6]. High night temperatures lower crop yield and are becoming more frequent with global warming [7, 8]. Fruit fails to develop correctly when night temperatures exceed day temperatures. This abnormal thermal cycle disrupts plant metabolism, unbalancing carbon allocation and hormone profiles.

Heat stress denatures proteins, generates reactive oxygen species, and changes membrane fluidity. Plants respond by activating Heat Shock Proteins and Heat Stress Transcription Factors through the Heat Shock Response [9, 10]. Plant defense activation inhibits growth and reproduction. How plants allocate resources between immediate survival and long-term fitness remains a primary question [11–15].

The male gametophyte (pollen) is the most sensitive reproductive component. Each step of pollen development is governed by precise transcriptional programs [16]. Research has

ISSN 2072-3857

consistently shown that this development process has limitations in yield security [17, 18]. Moderate heat stress that leaves the female pistil unaffected can cause complete male sterility [19, 20]. Heat stress during meiosis can lead to chromosomal defects. Stress during the microspore stage often results in tapetal dysfunction, failing to provide necessary nutrients [21–23]. However, the specific impact of heat on the final stages of sperm cell specification is less characterized. The sperm cells are the final product of pollen therefore their distinct transcriptome is required for double fertilization. Therefore, heat stress alters the expression of genes critical for sperm identity potentially by suppressing them or by altering their temporal expression, leading to failure in fertilization or inadequate fertilization [24–27]. However, this mechanism is not exclusive, as protein denaturation, disruption of the cell cycle, increased oxidative stress, impairment of translation, and subsequent alterations in hormonal balance may also contribute to reproductive failure. Hormones such as auxin (IAA), gibberellins (GA), and cytokinins serve as the integration hubs. For instance, auxin gradients drive tissue patterning but are also rapidly reshaped by temperature stress to modulate morphological plasticity [28–32].

We propose a novel perspective that the stress transcriptome induced by temperature fluctuations overlaps significantly with the developmental transcriptome of the sperm cell lineage. We hypothesize that a conserved thermal-sensitive developmental module exists. In this scenario, developmental regulators have retained stress-responsive elements in their promoters, or conversely, ancestral stress genes have been co-opted for developmental signaling. Identifying this overlap is crucial because it may highlight that the specific gene set that is at risk during heat waves, genes that are required for making sperm cells but are liable to be misrelated by the environment.

We used transcriptomics and a sperm cell lineage map to define a Temperature Stress Signature and a Sperm Cell Developmental Signature in tomato. We applied uniform statistical thresholds to identify the intersection of these signatures. Further analysis of this shared gene set revealed biological processes that link environmental and reproductive stress. This approach isolates the core regulatory network by filtering out housekeeping genes and markers specific to only one condition.

Materials and Methods

Dataset Acquisition and Pre-processing

We analyzed Agilent microarray data (NCBI GEO. GSE131496) from *Solanum lycopersicum* seedlings grown under Negative (25°C day/30°C night) and Positive (30°C day/25°C night) DIF regimes. We background-corrected raw signals and applied quantile normalization. To define a developmental signature, we used processed RNA-Seq FPKM values (GSE117185) from Sperm Cell (SC) and Leaf (control) samples. Leaf tissue was used only as a vegetative reference for identifying genes enriched in sperm cells. These details were obtained from the corresponding NCBI GEO records and metadata.

Differential Expression Analysis

We performed statistical analyses in R (v4.5.2). For microarray data (GSE131496), we used the Limma package to fit a linear model for each probe, comparing Negative and Positive DIF conditions with empirical Bayes smoothing. For RNA-Seq data (GSE117185), we calculated differential expression between Sperm Cells and Leaves using a linear model on log2-transformed FPKM values. We filtered both datasets using an adjusted P-value (FDR)<0.05 and an absolute log2 fold change>1. These genes were considered sperm-enriched rather than sperm-specific.

Correlation and Directionality Analysis

ISSN 2072-3857

We identified a "Shared Module" of significant DEGs from both comparisons and classified these genes into four groups. The groups were either concordantly (Up/Up, Down/Down) or discordantly (Up/Down, Down/Up) regulated. Pearson and Spearman correlation coefficients calculated on the log2 fold changes of these shared genes measured the global similarity of the transcriptional responses. The shared genes may also include general stress- or growth-related genes.

Results

Transcriptomic Response to Temperature Stress

We analyzed the GSE131496 dataset for transcriptional responses to temperature. Principal Component Analysis (PCA) separated Negative and Positive DIF samples, confirming the treatment induced a distinct transcriptional state (Figure 1). The first principal component explained most of this variance. We found 829 differentially expressed genes (adj.$P < 0.05$, |logFC|>1), which included both up- and downregulated transcripts (Figure 2). Upregulated genes showed higher expression under Negative DIF than under Positive DIF, whereas downregulated genes showed lower expression under Negative DIF. These groups therefore represent opposite transcriptional responses to the two temperature regimes. *Solyc06g072620* was one of the most downregulated genes, while *Solyc07g008240* was highly upregulated.

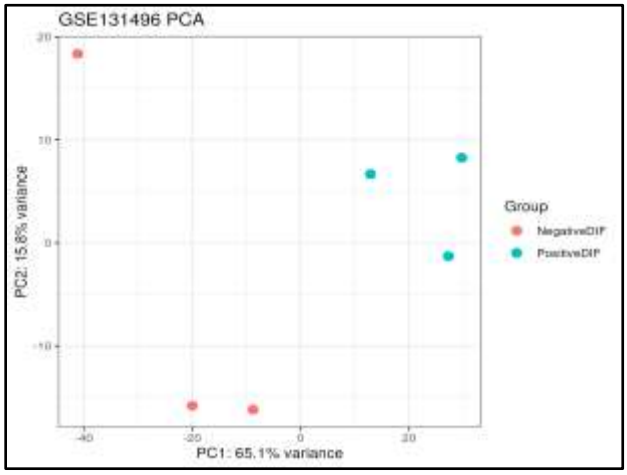


Figure 1. Principal Component Analysis (PCA) of between Negative and Positive DIF samples.

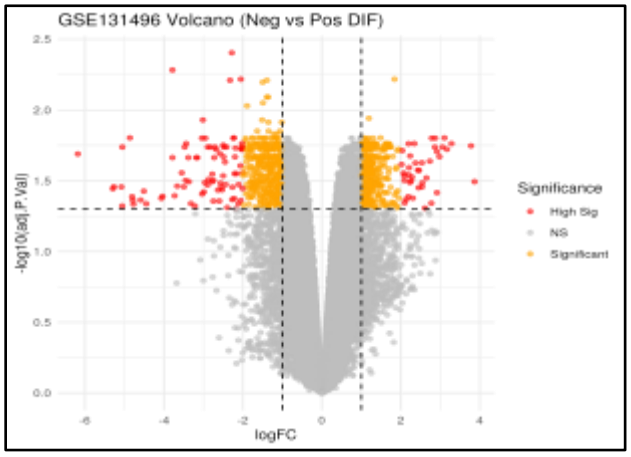


Figure 2. Red dots on the volcano plot show highly significant genes, whereas orange dots represent other significant differentially expressed genes under temperature stress.

Transcriptomic Definition of the Sperm Cell Lineage

PCA of the GSE117185 dataset separates sperm cells from vegetative leaf controls, showing a distinct transcriptomic profile associated with defining the transcriptomic reprogramming of gametogenesis (Figure 3). Comparing sperm cells and leaf tissue identified 19,676 differentially expressed genes, including the upregulated *Solyc06g075860* (logFC>10) and the downregulated, lineage-excluded transcript

Solyc03g097870 (logFC<-7) (Figure 4). Genes shared with the temperature-response dataset were therefore regarded as candidates, since some may also reflect a general cellular response to heat rather than a sperm-lineage-specific response.

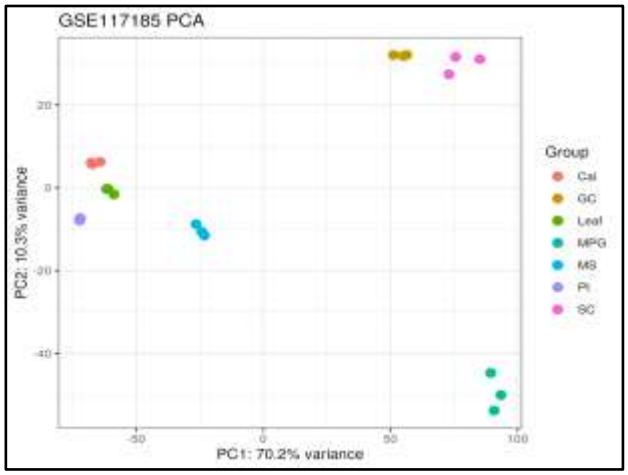


Figure 3. Principal Component Analysis (PCA) of the sampled cell types and stages in GSE117185, including sperm cells and leaf controls.

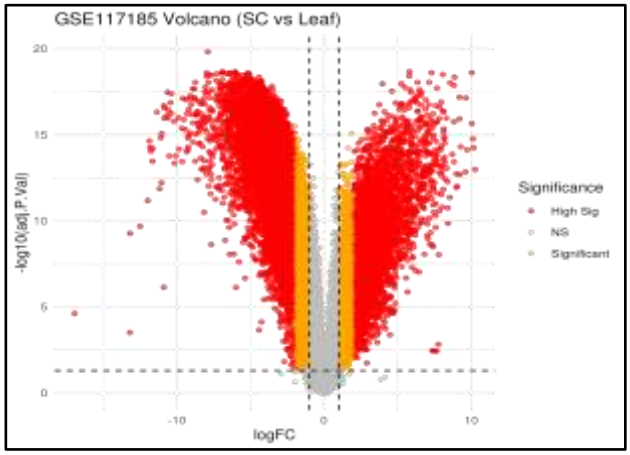


Figure 4. Gene expression differs significantly between sperm cells and leaf tissue, with red dots indicating highly significant genes and orange dots indicating other significant differentially expressed genes.

Identification of a Stress-Development Intersection

Intersecting gene lists from temperature stress and sperm development identified a 359-gene overlap. This shared module represents an overlap between environmental stress and reproductive development, distinct from the majority of genes unique to each process (Figure 5).

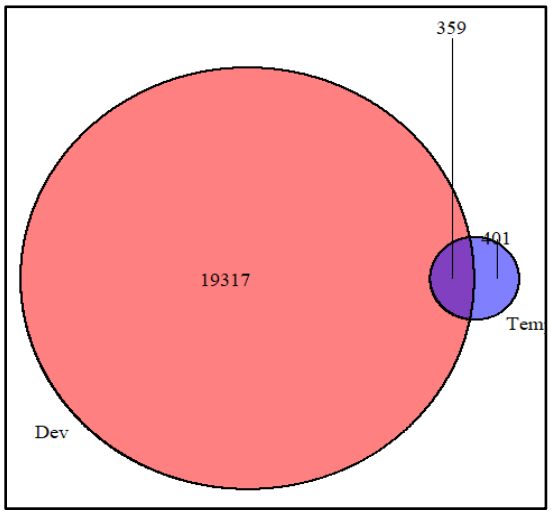


Figure 5. Venn Diagram showing the overlap of significant genes between Temperature Stress (GSE131496) and Sperm Cell Development (GSE117185).

Transcriptional Changes Are Positively Correlated

The log2 fold changes of shared genes correlated positively between temperature stress and sperm cell specificity (Pearson R = 0.321, $P < 0.001$). This positive correlation implies that the transcriptional program induced by high night temperatures mimics, to a partial extent, the transcriptional program of sperm differentiation, as visualized in the logFC-logFC plot, where the majority of genes fall into the concordant quadrants, Figure 6. Specifically, approximately 81 genes were found in the Up/Up quadrant (upregulated in both), and 193 genes were in the Down/Down quadrant (downregulated in both). In contrast, the discordant quadrants contained only about 84 and 20 genes, respectively. The Concordant

Up/Upset contains genes activated by both stress and development, including *Solyc06g073080* (Temp: 2.87, Dev: 3.52), *Solyc02g083640* (Temp: 1.49, Dev: 5.64), *Solyc11g012020* (Temp: 1.09, Dev: 7.40), *Solyc10g080950* (Temp: 1.07, Dev: 7.32), and *Solyc07g065210* (Temp: 1.60, Dev: 4.90). Conversely, the Concordant Down/Down set features strongly repressed genes including *Solyc03g097870* (Temp: -3.78, Dev: -7.90), *Solyc07g009380* (Temp: -4.59, Dev: -4.31), *Solyc04g007790* (Temp: -2.24, Dev: -6.97), *Solyc12g044330* (Temp: -1.55, Dev: -8.60), and *Solyc01g101060* (Temp: -1.64, Dev: -7.38). In the Discordant quadrants, genes such as *Solyc08g080640* (Temp: 2.53, Dev: -5.16) and *Solyc07g008240* (Temp: 1.84, Dev: -7.09) highlight the 'stress-high/development-low' pattern (Up/Down), while candidates like *Solyc04g080510* (Temp: -1.85, Dev: 5.51) and *Solyc02g087520* (Temp: -2.95, Dev: 2.45) illustrate the 'stress-low/development-high' profile (Down/Up).

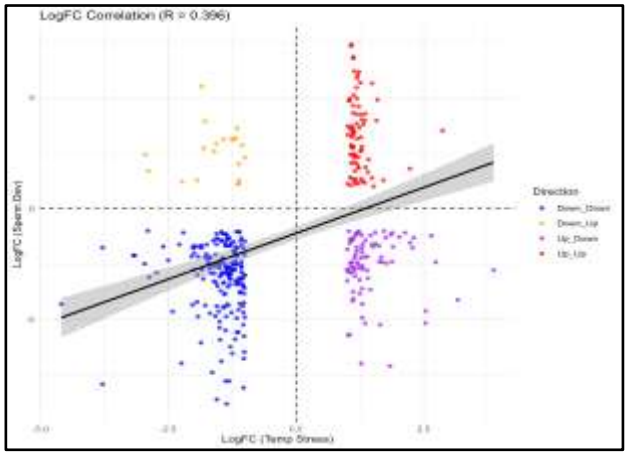


Figure 6. Scatter plot of log2 Fold Changes. The X-axis represents Temperature Stress, and the Y-axis represents Sperm Development. Points are colored by directionality quadrant.

Expression Dynamics of Concordant Candidates

Core candidate expression shows a binary, inversely correlated response to temperature stress. Genes activated under Negative DIF are suppressed under Positive DIF (Figure 7). As expected, in the developmental dataset, expression of these genes is highly tissue-specific, with distinct clusters of upregulated genes that sharply differentiate somatic tissues such as leaves and callus from reproductive stages like microspores, mature pollen grains, and sperm cells, thereby highlighting the specialized transcriptional programs driving male gametogenesis, suggesting a shared mechanism, Figure 8. These findings demonstrate that plant cell identity remains stable, yet gene expression adapts to thermal changes. Therefore, it suggests that these candidates are enriched in the sperm cell lineage compared to vegetative tissues.

Finally, to further examine the biological relevance of our concordance metric, we visualized the expression trajectories of the top 5 Concordant Up and top 5 Concordant Down genes across the sperm cell lineage (Figure 9). The Up/Up candidates show minimal to no expression in the vegetative (Leaf) and early microspore stages, followed by a sharp upregulation and peak expression mainly within the later stages of the male germline (Generative Cell, Mature Pollen, or Sperm Cell). Conversely, the Concordant Down/Down genes exhibit the opposite profile: high expression in the Leaf stage that is rapidly silenced upon entering the Microspore stage and remains suppressed throughout the remainder of the sperm cell lineage. These patterns indicate an association with male germline development but do not establish a direct heat-response mechanism in reproductive tissues. The heat-response data were obtained from seedlings, and the observed patterns may also depend on the duration of stress exposure.

ISSN 2072-3857

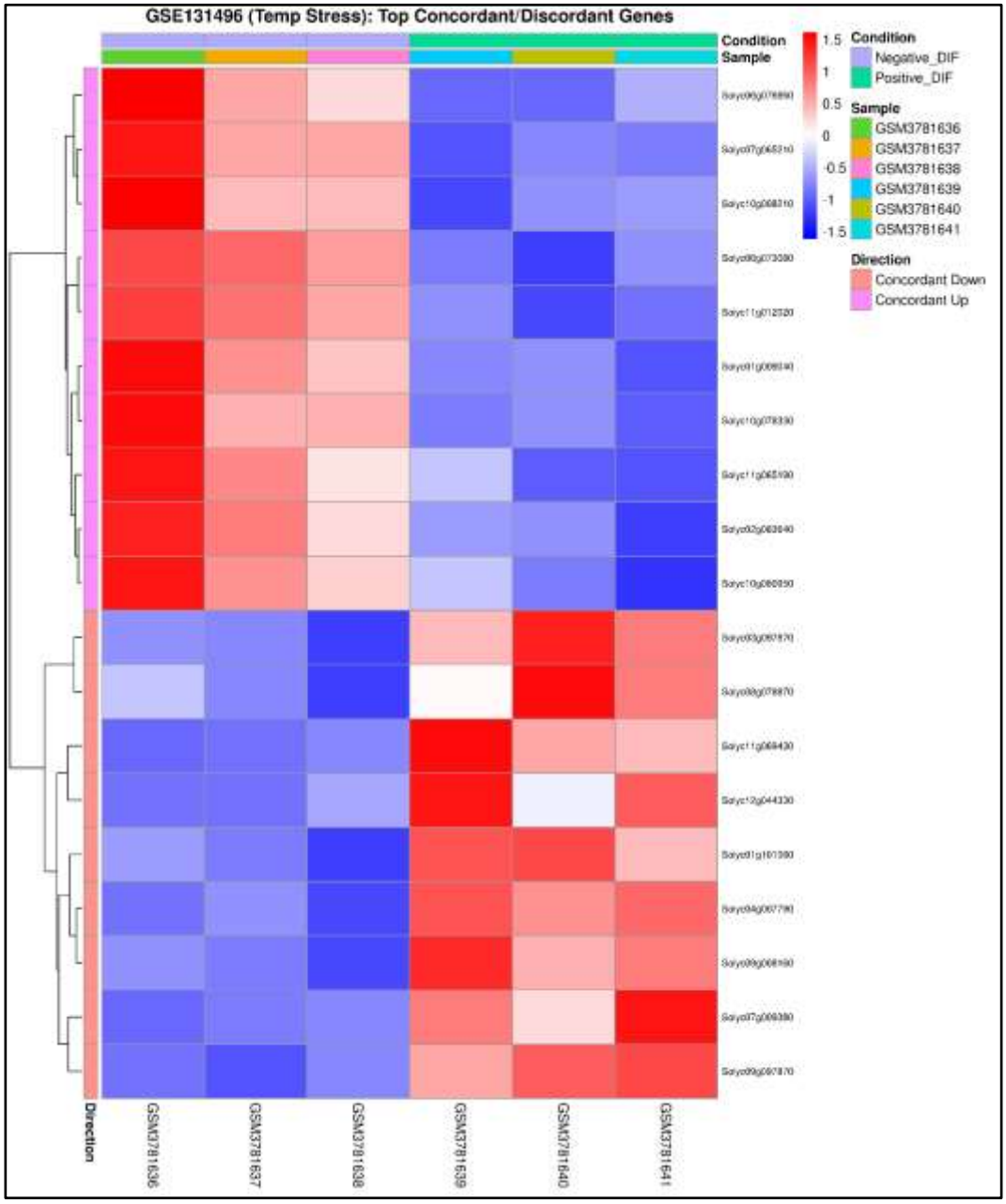


Figure 7. Heatmap of the top shared genes in the Temperature Stress dataset (GSE131496).

ISSN 2072-3857

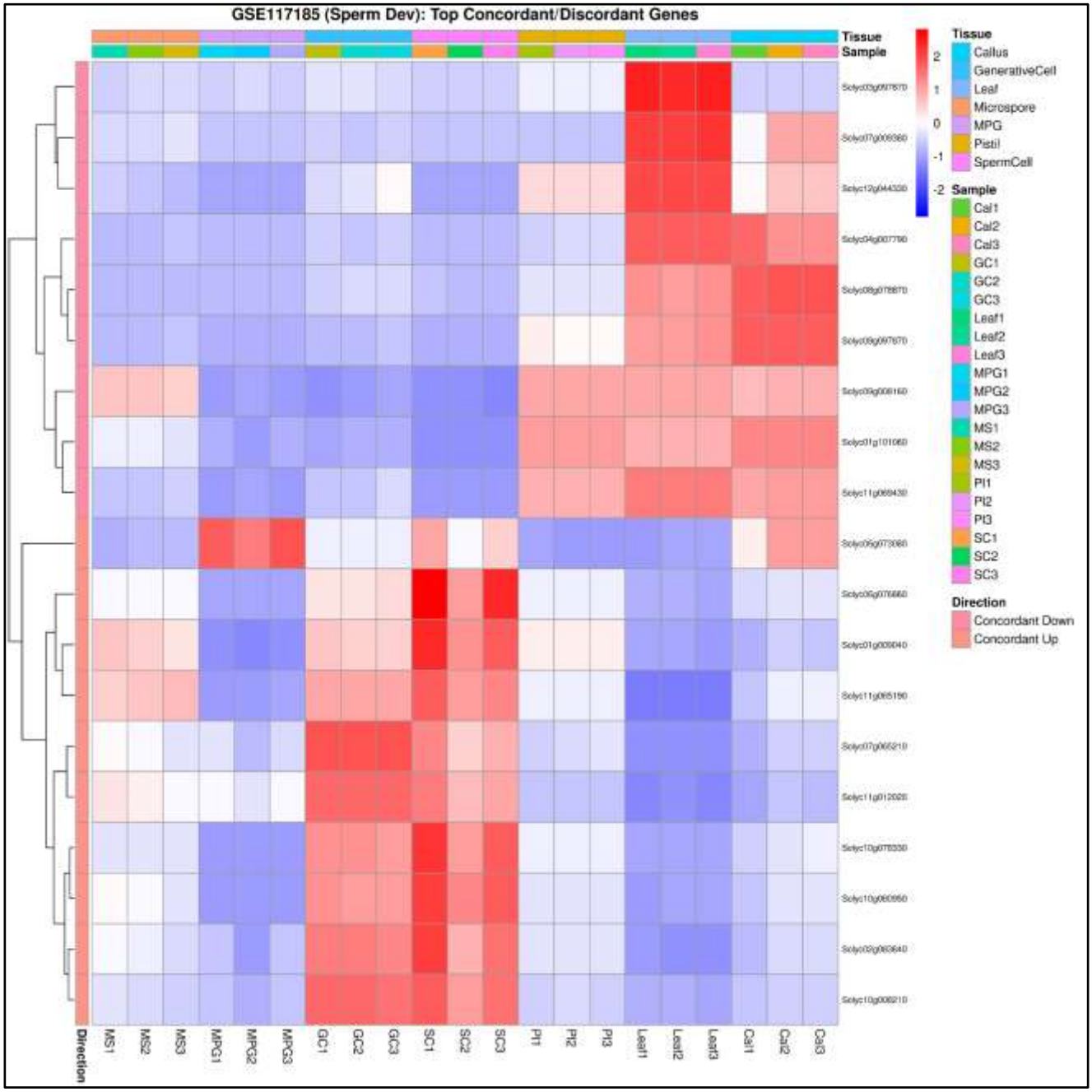


Figure 8. Heatmap of the top shared genes in the Sperm Development dataset (GSE117185). Genes were hierarchically clustered to show similarities in their expression patterns, while sample relationships and group separation were assessed separately by PCA.

ISSN 2072-3857

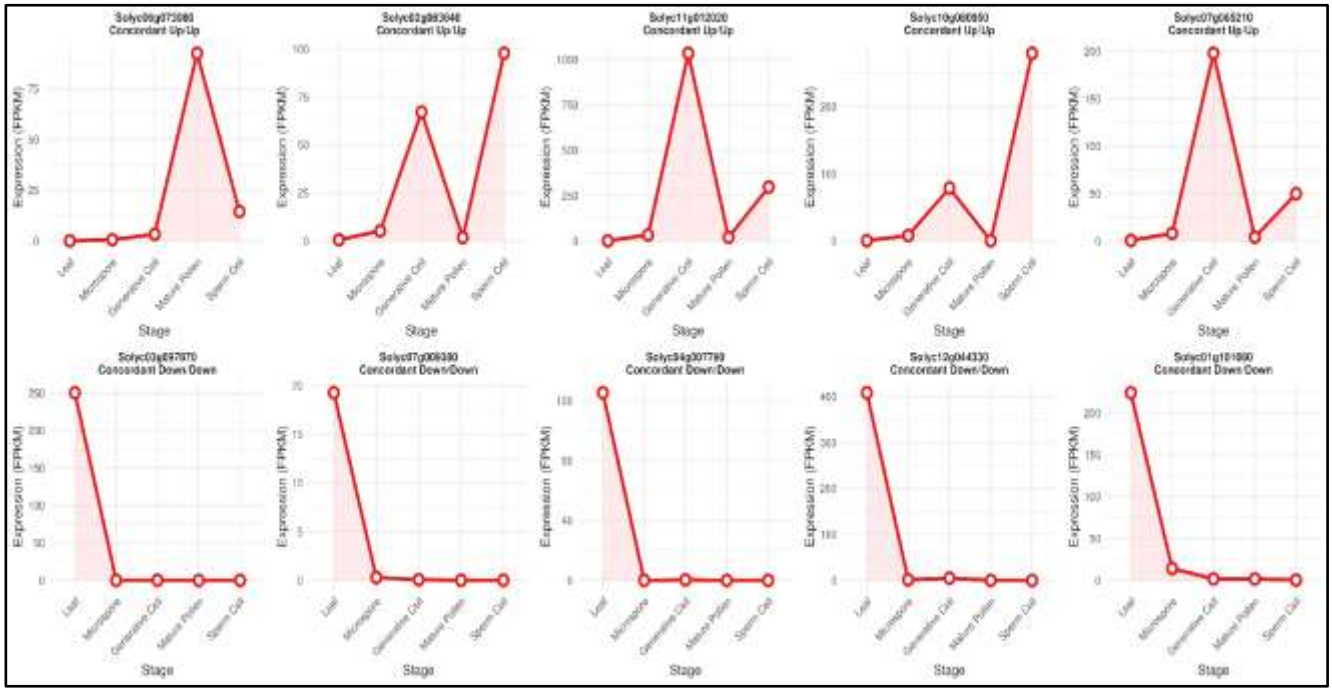


Figure 9. Expression profiles of the Top 5 Up/Up (red) and Top 5 Down/Down (blue) concordant genes across sperm cell development. Shaded areas represent expression magnitude. These profiles show developmental expression patterns but do not confirm that the heat response originates within the sperm cell lineage.

Discussion

The primary goal of this study was to identify the existence of a shared transcriptional expression pattern between heat stress and sperm cell development. Our findings show that there might be a potential nexus that exists, comprising 359 genes that serve as dual players in both systems. The positive correlation challenges the simple view that stress merely halts development. Instead, it suggests a more nuanced interaction where specific developmental modules, particularly those involving chloroplast reduction and hormonal signaling, are inherently temperature-sensitive [33, 34]. This co-option mechanism may explain why reproductive failure is the first symptom of heat stress, the very genes required to build a sperm cell are the ones being commandeered or suppressed for thermal adaptation, as shown similarly in previous studies in wheat and cereals [35–38]. The most striking finding is the behavior of the Concordant Up/Up gene cluster, where heat stress in vegetative seedlings induces the expression of genes otherwise strictly confined to the late stages of male gametogenesis (Generative Cell and Sperm Cell stages). This observation should be interpreted with caution in relation to the developmental check-point theory proposed by Müller and Rieu, who suggested that stress responses in the germline are distinct from vegetative tissues [39]. Therefore, the seedling data indicate a shared transcriptional pattern rather than a germline-specific heat-response mechanism. The activation of these genes in vegetative seedlings under heat stress suggests a conserved response pattern but does not prove that the same mechanism operates in the germline.

However, our data extends this by showing that the vegetative stress response mimics the

reproductive program. Candidates such as *Solyc06g073080* and *Solyc11g012020* show minimal expression in control vegetative tissues but are strongly induced by heat, mimicking their high expression profiles in the sperm lineage. We propose that high temperatures may trigger a differentiation-like signal. This is consistent with findings, who characterized the precise transcriptional reprogramming required for tomato sperm cell specification, the premature activation of these late-stage factors by environmental cues likely disrupts the chromatin landscape before the cell is competent for division [40]. Conversely, the Concordant Down/Down quadrant reveals a shared pattern of gene silencing. A Growth-Defense Trade-off that diverts energy to survival may explain why both heat stress and microspore development suppress housekeeping genes like *Solyc03g097870* and *Solyc12g044330* [11]. Tapetal dysfunction and sugar starvation make the microspore stage one of the most heat-sensitive stages of pollen development [23, 41, 42]. Heat stress may intensify the metabolic downregulation during gametogenesis, potentially reducing the energy available for pollen survival.

The 27% of discordantly regulated genes represent possible failure points. Heat upregulates genes like *Solyc08g080640* that show low expression during sperm specification. This altered expression may interfere with silencing mechanisms essential for germline commitment [40]. Therefore, these genes may provide targets for future studies aimed at uncouple stress tolerance from yield. Further functional analysis of heat-responsive promoter elements and developmental regulators is required to determine whether their modification could reduce heat-induced sperm cell failure and improve fruit set without altering the systemic stress response.

5. Conclusion

Heat stress disrupts tomato cell identity by activating a transcriptional module that mimics sperm differentiation. Isolating sperm-lineage genes from general stress responses yielded 359 thermotolerance breeding candidates with a shared positive transcriptional correlation, implying a common regulatory framework for crop improvement. The current study achieves with the following detailed insights:

1. Transcriptional responses to heat and sperm cell specification correlated positively (Pearson R = 0.321, $P < 0.0001$). Of these genes, 73% showed concordant regulation while 27% showed discordant regulation.
2. Their expression patterns also differed by developmental stage. A heat-sensitive transcriptional module is part of the sperm cell developmental program.
3. Heat stress activates a subset of these developmental genes, suggesting the pathway is inherently responsive to environmental signals.

Thus, this overlap provides candidate genes for breeding thermotolerant tomatoes by uncoupling the plant's stress response from its reproductive function.

References

[1] Saleem, A., Anwar, S., Nawaz, T. et al., 2025. Securing a sustainable future: the climate change threat to agriculture, food security, and sustainable development goals. *J. Umm Al-Qura Univ. Appl. Sci.* 11: 595–611.

[2] Verma, K.K., Song, X.P., Kumari, A. et al., 2025. Climate change adaptation: challenges for agricultural sustainability. *Plant Cell Environ.* 48: 2522–2533.

[3] Begna, T. and Wakweya, R.B., 2026. Mitigating climate change impacts on food

security via climate-smart agriculture. *Plant Stress*. 19: 101152.

[4] Ayenan, M.A.T., Danquah, A., Hanson, P. et al., 2019. Accelerating breeding for heat tolerance in tomato (*Solanum lycopersicum* L.): an integrated approach. *Agronomy*. 9: 720.

[5] Raja, V., Qadir, S.U., Alyemeni, M.N. et al., 2020. Impact of drought and heat stress individually and in combination on physio-biochemical parameters, antioxidant responses, and gene expression in *Solanum lycopersicum*. *3 Biotech*. 10: 208.

[6] Aldubai, A.A., Alsadon, A.A., Migdadi, H.H. et al., 2022. Response of tomato (*Solanum lycopersicum* L.) genotypes to heat stress using morphological and expression study. *Plants*. 11: 615.

[7] Ohtaka, K., Yoshida, A., Kakei, Y. et al., 2020. Difference between day and night temperatures affects stem elongation in tomato (*Solanum lycopersicum*) seedlings via regulation of gibberellin and auxin synthesis. *Front. Plant Sci.* 11: 577235.

[8] Felix Amuji, C., Beaumont, L.J. and Atwell, B.J., 2020. The effect of co-occurring heat and water stress on reproductive traits and yield of tomato (*Solanum lycopersicum*). *Hortic. J.* 89: 530–536.

[9] Peer, L.A., Dar, Z.A., Lone, A.A. et al., 2020. High temperature triggered plant responses from whole plant to cellular level. *Plant Physiol. Rep.* 25: 611–626.

[10] Khan, Q., Wang, Y., Xia, G. et al., 2024. Deleterious effects of heat stress on the tomato, its innate responses, and potential preventive strategies in the realm of emerging technologies. *Metabolites*. 14: 283.

[11] He, Z., Webster, S. and He, S.Y., 2022. Growth–defense trade-offs in plants. *Curr. Biol.* 32: R634–R639.

[12] Sestari, I. and Campos, M.L., 2022. Into a dilemma of plants: the antagonism between chemical defenses and growth. *Plant Mol. Biol.* 109: 469–482.

[13] Cunha, A.F.A., Rodrigues, P.H.D., Anghinoni, A.C. et al., 2023. Mechanical wounding impacts the growth versus defense balance in tomato (*Solanum lycopersicum*). *Plant Sci.* 329: 111601.

[14] Leibman-Markus, M., Schneider, A., Gupta, R. et al., 2023. Immunity priming uncouples the growth–defense trade-off in tomato. *Development*. 150: dev201158.

[15] Busche, M., Menon, S. and Brunkard, J.O., 2025. Decoding the growth–defense dialectic: TOR signaling and developmental genetics in maize. *J. Exp. Bot.* DOI: 10.1093/jxb/eraf358.

[16] Dai, S., Kai, W., Liang, B. et al., 2018. The functional analysis of SlNCED1 in tomato pollen development. *Cell Mol. Life Sci.* 75: 3457–3472.

[17] Pacini, E. and Dolferus, R., 2019. Pollen developmental arrest: maintaining pollen fertility in a world with a changing climate. *Front. Plant Sci.* 10: 679.

[18] Mehmood, M., Tanveer, N.A., Joyia, F.A. et al., 2025. Effect of high temperature on pollen grains and yield in economically important crops: a review. *Planta*. 261: 141.

[19] Peet, M.M., Sato, S. and Gardner, R.G., 1998. Comparing heat stress effects on male-fertile and male-sterile tomatoes. *Plant Cell Environ.* 21: 225–231.

[20] Peet, M.M., Willits, D.H. and Gardner, R., 1997. Response of ovule development and post-pollen production processes in male-sterile tomatoes to chronic, sub-acute high temperature stress. *J. Exp. Bot.* 48: 101–111.

[21] Schindfessel, C., De Storme, N., Trinh, H.K. et al., 2023. Asynapsis and meiotic restitution in tomato male meiosis induced by heat stress. *Front. Plant Sci.* 14: 1210092.

ISSN 2072-3857

[22] Yang, D., Wang, Z., Huang, X. et al., 2023. Molecular regulation of tomato male reproductive development. *aBIOTECH*. 4: 72–82.

[23] Lohani, N., Singh, M.B. and Bhalla, P.L., 2025. Deciphering the vulnerability of pollen to heat stress for securing crop yields in a warming climate. *Plant Cell Environ.* 48: 2549–2580.

[24] Bita, C.E., Zenoni, S., Vriezen, W.H. et al., 2011. Temperature stress differentially modulates transcription in meiotic anthers of heat-tolerant and heat-sensitive tomato plants. *BMC Genomics*. 12: 384.

[25] Solankey, S.S., Singh, R.K., Baranwal, D.K. et al., 2015. Genetic expression of tomato for heat and drought stress tolerance: an overview. *Int. J. Veg. Sci.* 21: 496–515.

[26] Fragkostefanakis, S., Mesihovic, A., Simm, S. et al., 2016. HsfA2 controls the activity of developmentally and stress-regulated heat stress protection mechanisms in tomato male reproductive tissues. *Plant Physiol.* 170: 2461–2477.

[27] Hoshikawa, K., Pham, D., Ezura, H. et al., 2021. Genetic and molecular mechanisms conferring heat stress tolerance in tomato plants. *Front. Plant Sci.* 12: 786688.

[28] Kojima, K., Tamura, Y., Nakano, M. et al., 2003. Distribution of indole-acetic acid, gibberellin and cytokinins in apoplast and symplast of parthenocarpic tomato fruits. *Plant Growth Regul.* 41: 99–104.

[29] Mariotti, L., Picciarelli, P., Lombardi, L. et al., 2011. Fruit-set and early fruit growth in tomato are associated with increases in indoleacetic acid, cytokinin, and bioactive gibberellin contents. *J. Plant Growth Regul.* 30: 405–415.

[30] Fleishon, S., Shani, E., Ori, N. et al., 2011. Negative reciprocal interactions between gibberellin and cytokinin in tomato. *New Phytol.* 190: 609–617.

[31] Ding, J., Chen, B., Xia, X. et al., 2013. Cytokinin-induced parthenocarpic fruit development in tomato is partly dependent on enhanced gibberellin and auxin biosynthesis. *PLoS One*. 8: e70080.

[32] Mignolli, F., Vidoz, M.L., Picciarelli, P. et al., 2019. Gibberellins modulate auxin responses during tomato (*Solanum lycopersicum* L.) fruit development. *Physiol. Plant.* 165: 768–779.

[33] Luo, S. and Kim, C., 2021. Current understanding of temperature stress-responsive chloroplast FtsH metalloproteases. *Int. J. Mol. Sci.* 22: 12106.

[34] Staacke, T., Mueller-Roeber, B. and Balazadeh, S., 2025. Stress resilience in plants: the complex interplay between heat stress memory and resetting. *New Phytol.* 245: 2402–2421.

[35] Barnabás, B., Jäger, K. and Fehér, A., 2008. The effect of drought and heat stress on reproductive processes in cereals. *Plant Cell Environ.* 31: 11–38.

[36] Driedonks, N., Rieu, I. and Vriezen, W.H., 2016. Breeding for plant heat tolerance at vegetative and reproductive stages. *Plant Reprod.* 29: 67–79.

[37] Ullah, A., Nadeem, F., Nawaz, A. et al., 2022. Heat stress effects on the reproductive physiology and yield of wheat. *J. Agron. Crop Sci.* 208: 1–17.

[38] Resentini, F., Orozco-Arroyo, G., Cucinotta, M. et al., 2023. The impact of heat stress in plant reproduction. *Front. Plant Sci.* 14: 1271644.

[39] Müller, F. and Rieu, I., 2016. Acclimation to high temperature during pollen development. *Plant Reprod.* 29: 107–118.

[40] Liu, L., Lu, Y., Wei, L. et al., 2018. Transcriptomics analyses reveal the molecular roadmap and long non-coding RNA landscape of sperm cell lineage development. *Plant J.* 96: 421–437.

ISSN 2072-3857

[41] Kumar, D., Singh, B.P. and Kumar, P., 2004. An overview of the factors affecting sugar content of potatoes. *Ann. Appl. Biol.* 145: 247–256.

[42] Kobylińska, A., Borek, S. and Posmyk, M.M., 2018. Melatonin redirects carbohydrates metabolism during sugar starvation in plant cells. *J. Pineal Res.* 64: e12466.

ISSN 2072-3857