

Thesis of doctoral (PhD) dissertation

**INVESTIGATION OF THE MOLECULAR GENETIC
MECHANISMS OF PLANT STRESS MEMORY**

Dóra Farkas

PhD candidate

Supervisor:

Dr. Judit Dobránszki, Doctor of the Hungarian Academy of Sciences



**UNIVERSITY of
DEBRECEN**

**Kerpely Kálmán Doctoral School of Crop Production and Horticultural
Sciences**

Debrecen, 2026

1. The antecedents and the objectives of the doctoral dissertation

Global climate change and the increasing frequency of drought periods pose a critical challenge to agriculture and food security (BISBIS et al., 2018). Due to the limited adaptability of conventional cultivation technologies, the focus of plant biological research is shifting toward innovative, physical-based conditioning (priming) methods that exploit the natural physiological plasticity of plants to enhance resilience (SELEIMAN et al., 2021). Alongside its high economic importance, tomato (*Solanum lycopersicum* L.) is a key model organism in molecular plant physiology. Since drought stress limits productivity at all stages of ontogeny (ZHOU et al., 2019), it has become essential to develop methods to pre-condition the plant organism for expected stress impacts. One of the most defining paradigm shifts in plant biology is the recognition of somatic and transcriptomic memory, as well as cognitive processes (TREWAVAS, 2014). Plants are capable of storing and recalling environmental information at the cellular level through sophisticated epigenetic mechanisms, such as DNA methylation and histone modifications (GALLUSCI et al., 2023). Whole-genome methylation and transcriptomic analyses are capable of revealing how a transient environmental effect becomes a lasting physiological imprint (ZHANG et al., 2018).

Based on inheritance, we distinguish between meiotically inherited memory via sexual reproduction (LIU et al., 2022) and mitotic memory, the latter of which is maintained through clonal cell division (GARAI & SOPORY, 2023). Based on duration, a distinction is made between intra-, inter-, and transgenerational memory. While the transgenerational level is fixed by stable DNA methylation, intragenerational (somatic) responses are driven by small RNAs and transient, reversible DNA methylation and histone modifications (GALLUSCI et al., 2023). During transcriptomic memory, the plant maintains an altered gene expression pattern as a result of prior stress exposure, or exhibits a response to repeated stimuli that differs from its naive state (AVRAMOVA, 2015). Based on the temporal relationship of expression levels, transcriptional memory can be classified into two main types (OBERKOFER et al., 2021):

- Type 1 (sustained induction) memory: the altered gene expression extends temporally beyond the stimulus, and the intensity of gene expression does not return to the baseline, thereby maintaining a continuous state of molecular readiness (hysteresis) within the plant.
- Type 2 memory (modified re-induction): the intensity of gene expression returns to the baseline level between stimuli, but upon repeated stress exposure, the magnitude

or direction of the response significantly differs from the initial gene expression response to the same stimulus (AVRAMOVA, 2015; BALAZADEH, 2022).

A higher level of memory functions is associative memory, during which a plant links a neutral environmental stimulus with another stimulus and subsequently modifies its response reactions in a proactive manner solely under the influence of this neutral stimulus. This fundamentally differs from cross-tolerance, which is a general biochemical conditioning based on overlapping molecular signaling pathways (BHANDAWAT et al., 2020; GAGLIANO et al., 2016).

As a non-invasive physical stimulus, ultrasonic treatment is capable of influencing cellular signaling pathways through mechanical vibrations and cavitation phenomena, without any chemical load. The central hypothesis of this dissertation is that ultrasonic or drought conditioning can establish intragenerational memory. Based on this theoretical background, my work investigated the effects of ultrasound and drought treatments on plant transcription and epigenetic patterns along the following specific objectives. My aim was to:

- determine whether significant differences occur in the transcriptome and DNA methylation of the Micro Tom tomato variety depending on the applied stress types, by analyzing RNA-seq and WGBS data, and to identify stress-specific molecular patterns;
- investigate whether the treatments applied under controlled conditions trigger stable memory traces identifiable at the molecular level, or if they represent merely transient physiological reactions;
- clarify whether the joint application of the stress types results in intragenerational memory, and to determine how long the established memory persists within the life cycle of the individual plant;
- examine whether associative memory can be formed where a previously neutral stimulus becomes a predictor for another stimulus regarding the investigated target genes, and whether this association is stimulus-dependent.

2. Material and Methods

For our experiments, the Micro Tom variety of tomato (*Solanum lycopersicum* L.) was used. Seeds were sown into Jiffy-7[®] peat pellets saturated with a solution containing MS macro- and microelements (MURASHIGE & SKOOG, 1962) and 0.15% Previcur Energy[®] fungicide, and then grown in Veg-boxes inside a climate chamber (24 °C, 16/8-hour photoperiod, 89 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD, 65% RH). Three-week-old seedlings were maintained in a completely randomized design, and watering was provided twice a week with 15 ml of tap water.

A total of 168 plants were included in the experiment. During Treatment I, four main groups (42 individuals per group) were established: control (C), ultrasonic treatment (US), drought stress (D), and combined treatment (US+D) group. Drought stress was induced using 10 ml of a 20% PEG-6000 solution, while ultrasonic treatment was performed using an ultrasound generator (30 kHz, 120 W, 5-minute exposure, plant distance from the US head: 6 cm). In the combined group, the ultrasound treatment was immediately followed by PEG irrigation (Figure 1).

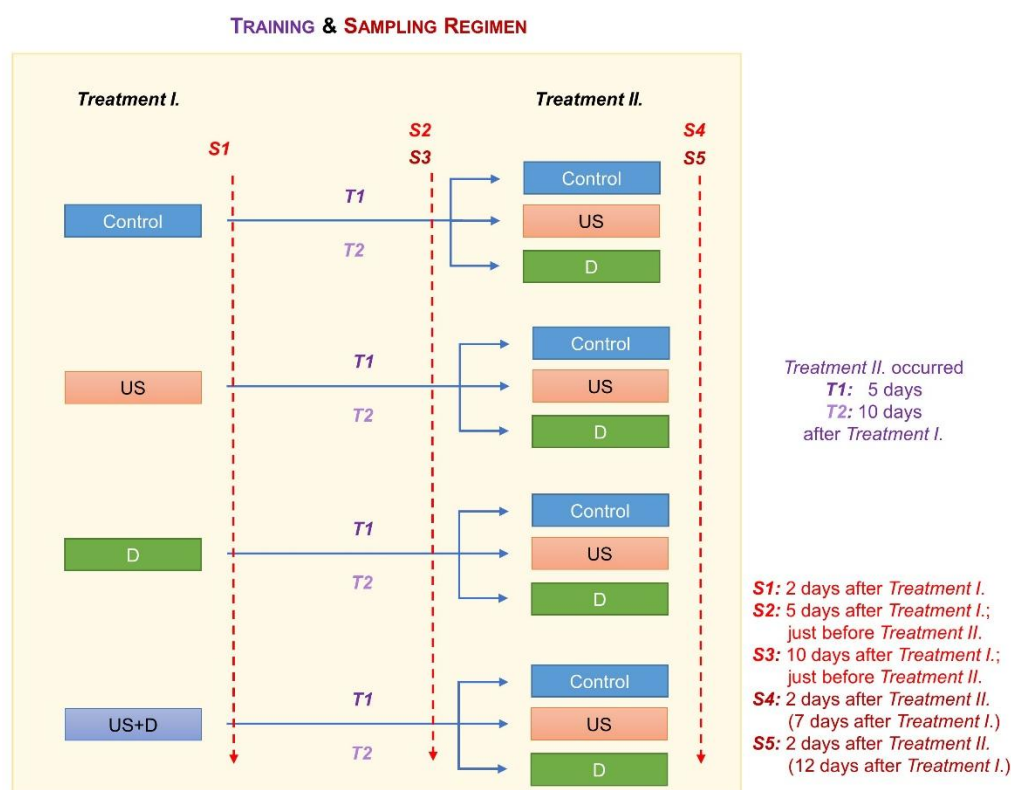


Figure 1 Schematic illustration of the treatment (T) and sampling (S) regimen (abbreviations: US - ultrasonic treatment; D - drought treatment; US+D - ultrasonic and drought treatment). (Source: FARKAS et al., 2025)

During Treatment II, on the 5th day (T1 experimental series) or 10th day (T2 experimental series) following the first stimulus, each main group was divided into 3 subgroups each (control, repeated US, repeated D) according to the schedule (Figure 1).

To monitor transcriptomic (RNA-seq) and DNA methylation (WGBS) changes, sampling was performed at five time points (3 biological replicates per time point): S1 (2 days after Treatment I); S2 and S3 (5 and 10 days after Treatment I, respectively, immediately prior to Treatment II); S4 and S5 (2 days after Treatment II of the T1 and T2 series, respectively).

Genomic DNA isolation (S1 samples, 2 replicates) was performed using the Macherey-Nagel Nucleospin[®] Plant II kit, while total RNA extraction (3 replicates) was conducted using the Zymo Quick-RNA[™] Plant Miniprep Kit. Quality control was validated with a NanoPhotometer[®] N50 instrument, and nucleic acid integrity was assessed on an Agilent Bioanalyzer 2100 system (using RNA 6000 Nano Kit). Only samples free of protein and salt contamination ($A_{260}/A_{280} \sim 1.8\text{--}2.0$; $A_{260}/A_{230} > 1.8$) and exhibiting excellent integrity (RIN > 7.0) were utilized for sequencing. mRNA library preparation (poly-A enrichment, fragmentation, cDNA library) and sequencing were performed by Novogene on an Illumina NovaSeq X Plus platform in paired-end (PE150) mode.

During bioinformatics processing, quality control of the raw data was performed using FastQC v0.12.1, and filtering was conducted using fastp v0.26.0 software. RNA-seq reads were aligned to the *S. lycopersicum* SL4.0 reference genome using the Hisat2 v2.1.1 algorithm, and gene-level expression was quantified using FeatureCounts v2.1.1 (ITAG4.0 annotation). Statistical analysis of differentially expressed genes (DEGs) was performed using the DESeq2 v1.44.0 package in the R environment ($|\log_2FC| > 0.58$; $p\text{-adj.} < 0.05$).

Alignment of WGBS data following bisulfite conversion was performed using Bismark v0.24.2 software (SL4.0 genome). After deduplication, methylation levels were extracted in CpG, CHG, and CHH contexts. Differentially methylated regions (DMRs) and differentially methylated genes (DMGs) were identified using the MethylKit v1.30.0 package ($\geq 10\times$ coverage, $P < 0.05$, 200 bp sliding window, $> 10\%$ methylation difference). Units containing a DMR within the gene body or the 3 kb upstream promoter region were considered DMGs, and annotation was performed using Genomation v1.36.0. Functional Gene Ontology (GO) enrichment analysis was conducted using the ClusterProfiler v4.12.6 package ($P < 0.05$), and visualization was performed using the ggplot2 v3.5.2 package in the R v4.4.1 environment.

For RT-qPCR analyses, cDNA synthesis was initiated from 200 ng of total RNA using the Reverse Transcriptase Core Kit (Eurogentec) and 2.5 μM random nonamer primers. For normalization, four reference genes were selected (SEC, ELO, GAPDH, UBI). Their expression

stability was evaluated using the comparative ΔC_t method (SILVER et al., 2006), as well as the geNorm (VANDESOMPELE et al., 2002), NormFinder (ANDERSEN et al., 2004), and BestKeeper (PFAFFL et al., 2004) algorithms via the RefFinder (XIE et al., 2012) software.

Table 1: Primer pairs for housekeeping/constitutive and target genes.

Gene description	Abbreviation	Forward and reverse primer sequences (5'–3')	Amplicon length (bp)
Exocyst complex component SEC3A	<i>SEC</i>	F – CTCCTCAGTGGACAATGCGT R – TCTTCCACAGCAGCACTGAC	208
Elongation factor 1-alpha	<i>ELO</i>	F – AAGAGGCCATCAGACAAGCC R – TGAGGCAACATAACCACGCT	267
Glyceraldehyde 3-phosphate dehydrogenase	<i>GAPDH</i>	F – ATTCCATGGGCACAGACTGG R – GGGAGCAAGGCAATTTGTGG	225
Ubiquitin-ribosomal protein eS31 fusion protein-like	<i>UBI</i>	F – CCACTCTCCATCTCGTGCTC R – GTGAGCCCACACTTACCACA	247
Protein auxin-regulated gene involved in organ size	<i>ARGOS</i>	F – GACATGGAATCATCAGAGGCA R – TGGCAATGGTGAAGCATCA	240
Protein EXORDIUM-like 5	<i>EX</i>	F – ACTCCCTCCGAGAACTATCTTC R – CAACGAAACAGTACTCCACCACT	241
Transcription factor MYB24-like	<i>MYB</i>	F – AGGCAGATGGAATTGTGTTGC R – CGTTGTCAGTTCTCCCTGGCA	206
Chlorophyllase-2	<i>CHL</i>	F – CAAATCCGTACTGCCGGAGA R – ACGAGGGATGTATTCGAGAACG	205
Probable aquaporin TIP3-2-like	<i>TIP</i>	F – TAGTGATAGCGTTGGCGCAT R – GCCATCAGTAGCAAGCCTCA	206

The target genes were selected based on the LFC values from the RNA-seq data. For two target genes, ultrasound served as the conditioned stimulus (CS) and drought as the unconditioned stimulus (UCS), whereas for the other two target genes, the roles were reversed. The groups receiving only the control after Treatment I ("US and C", "D and C", "US+D and C") served to monitor memory maintenance. Primers were designed using SnapGene v8.0 software, their properties were verified with the PCR Primer Stats tool, and specificity was validated via NCBI BLASTn (synthesis: Integrated DNA Technologies). The design criteria were as follows: melting temperature T_m : 56–62 °C; length: 18–25 bp; GC content: 40–60%; amplicon length: 150–250 bp (Table 1).

RT-qPCR reactions (2.5 μ l cDNA, 0.1 μ M primer concentration) were performed using the Takyon™ No Rox® SYBR MasterMix dTTP Blue (Eurogentec) kit on an AriaMx Real-Time PCR (Agilent) system. The amplification protocol consisted of the following steps: initial denaturation and enzyme activation (95 °C, 3 min), followed by 40 cycles (95 °C - 10 s; primer-

specific annealing: 52.5 °C - 20 s; elongation: 72 °C - 30 s). Measurements were conducted in 3 biological and 3 technical replicates.

Relative gene expression was determined using the $2^{-\Delta\Delta C_q}$ method. The correlation between RNA-seq and RT-qPCR data was examined using Pearson's correlation coefficient. Detailed statistical analysis was performed using IBM SPSS Statistics 25 software: the effects of treatment type and time point as main factors were determined by two-way analysis of variance (two-way ANOVA), while significant differences between groups were assessed using Tukey's B post-hoc test ($P < 0.05$). Graphs and significance markings were generated using GraphPad Prism 10.0.0 software.

3. Results

3.1. Global changes in the transcriptome profile and the priming effect

Multivariate statistical analysis of global gene expression patterns, based on the results of principal component analysis (PCA), showed a sharp molecular separation between the different treatment groups along the second principal component (PC2). Compared to the untreated absolute control (C), drought stress (D) and ultrasonic treatment (US) induced transcriptomic rearrangements in opposite directions within the plant tissues. Under the drought stress, the samples shifted toward the negative domain of the coordinate system, whereas ultrasonic stimulation shifted the global gene expression profile in the positive direction. This distinct variance provides indirect evidence that the two stimuli activate fundamentally different molecular pathways, i.e. calcium signals, and maybe phytohormone responses. Plants are therefore may be capable of distinguishing between these stimuli at the molecular level (GAGLIANO, 2014) (Figure 2).

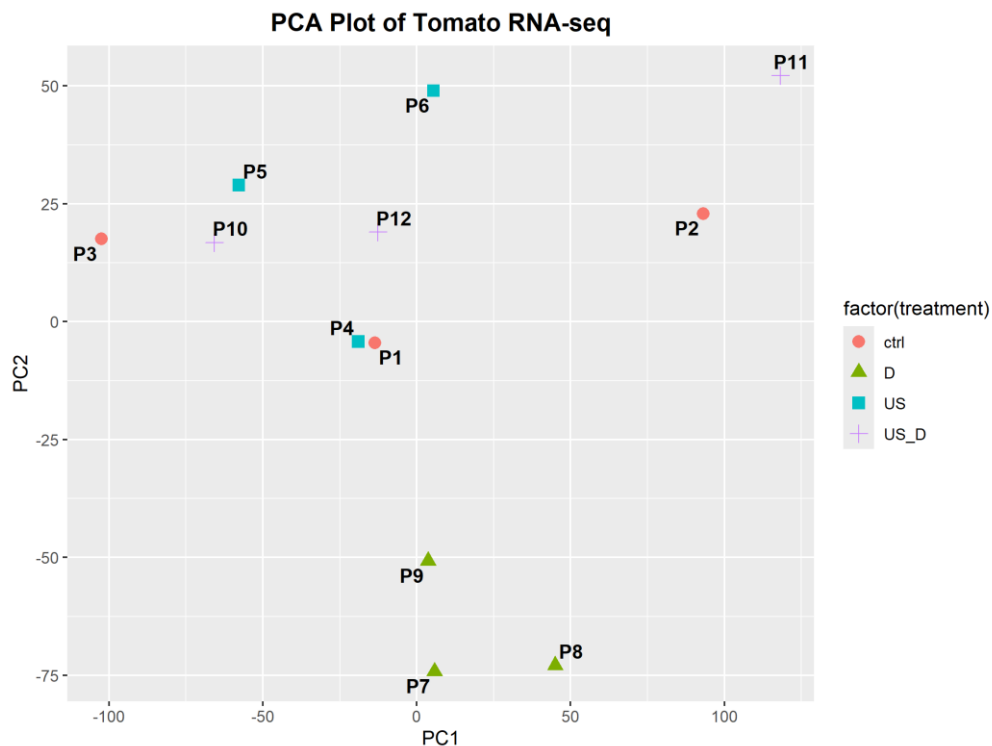


Figure 2 Principal component analysis (PCA) based on transcriptomic (RNA-seq) data of tomato *Solanum lycopersicum* L. cv. Micro Tom.

The position of the samples subjected to the combined treatment (US+D) along the PC2 axis is identifiable in the band between the control and the ultrasonic treatment. This observation is

of key biological significance, as it indicates that the ultrasonic treatment was capable of modifying or "overriding" the typical transcriptomic response induced by drought; that is, a substantial portion of the gene expression responses characteristic of drought was meaningfully altered. Here, the ultrasonic treatment acted as a type of priming (pre-conditioning) agent within the plant. Under the influence of the pre-treatment, the plant did not exhibit the typical, “panic-like” drought response, but instead assumed a modified state that shows greater similarity to the US-specific profile (MAUCH-MANI et al., 2017) (Figure 2).

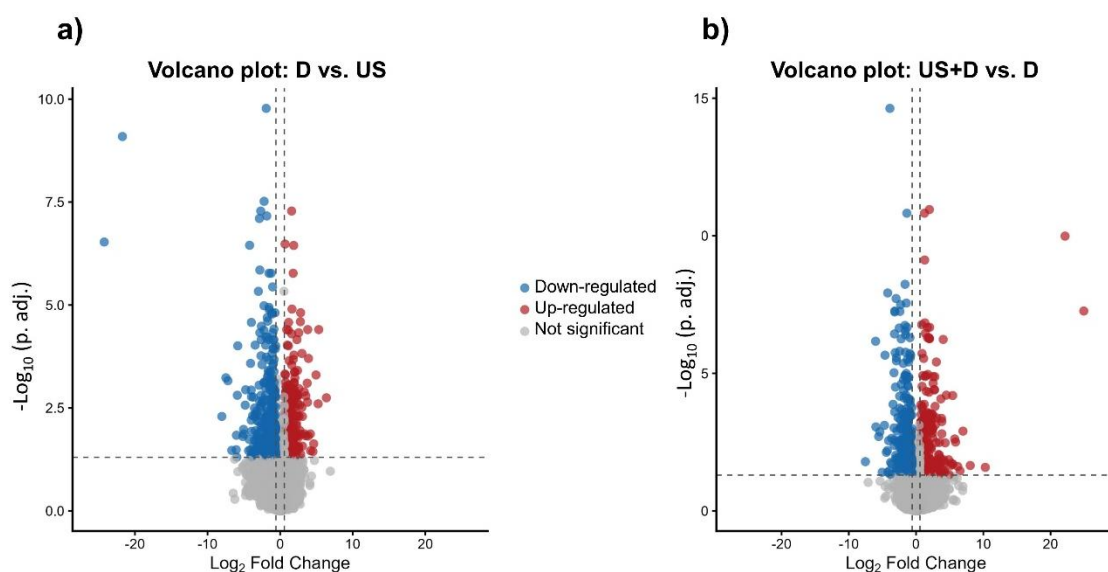


Figure 3 Statistical distribution of differentially expressed genes (DEGs). Volcano plots illustrate the magnitude of change in gene expression ($\log_2 \text{Fold Change}$) and its significance ($-\log_{10}$ adjusted p-value).

The extremely high gene expression change values ($|\log_2 \text{FC}| > 20$) on the volcano plots and the sharp shifts observed on the PCA confirm that ultrasound initiates an independent, specific transcriptome-remodeling process. The gene expression response in the opposite direction to drought, as shown on the heatmaps, verifies that plant molecular pathways are capable of qualitative separation of stimuli, which is the first prerequisite for the functional definition of learning (a change occurring as a result of interaction) (TREWAVAS, 2014; CALVO et al., 2020). Acting as a type of pre-conditioning agent, ultrasound mitigated the stress-specific transcriptome shift (HILKER & SCHMÜLLING, 2019) (Figure 3).

During the investigation of the global mRNA expression profile involving 34,075 genes, a significant magnitude of up- and down-regulation was identified compared to the control

Transcriptomic analysis revealed 86, 410, and 148 differentially expressed genes (DEGs) in response to the ultrasonic, drought, and combined treatments, respectively ($|\log_2FC| > 0.58$; adjusted $p\text{-adj.} < 0.05$). In the analysis of overlaps, we found 7 shared differentially expressed genes (DEGs) between the US+D and D treatments, 9 between the D and US treatments, and 40 between the US and US+D treatments. Only 4 genes were identified that responded with a significantly different expression level to all three treatments, which supports the high degree of stimulus-specificity of the experimental treatments and the reliability of the obtained data, that is in line with previous transcriptomic studies (DOBRÁNSZKI et al., 2019; TEIXEIRA DA SILVA et al., 2020).

3.2. Genome-wide DNA methylation responses as the epigenetic basis of memory

Similar to the mRNA expression profile, both applied stimuli altered the global DNA methylation of the tomato plants. In the global cytosine DNA methylation analysis encompassing both the promoter and coding regions of the 34,075 genes, a total of 211 differentially methylated genes (DMGs) were identified compared to the untreated control, considering all treatments and sequence contexts. These epigenetic modifications serve as stable cellular carriers of stored information, representing methylation memory traces. Twenty-five DMGs proved to be completely identical across the comparison of all three treatment groups.

In parallel with the transcriptomic changes, the analysis of genome-wide methylation profiles highlighted that the methylation landscape exhibits a characteristic distribution along the gene structure across all three sequence contexts. The level of DNA methylation is highest within the gene body, while a marked local decrease is observed around the transcription start sites (TSS) and transcription termination sites (TTS). In the CpG, CHG, and CHH contexts, 122, 86, and 46 DMGs were affected, respectively. Based on the asymmetry of the volcano plots, the most intense epigenetic remodeling occurred within the CpG context, indicating that drought stress triggers systemic hyper- and hypomethylation processes that impact fundamental metabolic pathways.

The profile shifts of the contexts confirmed the non-additive nature of the treatments. The significant variance observed in the direct comparison between ultrasound and drought (US vs. D) within the CHG context proves that the two stimuli leave behind completely different epigenetic fingerprints. This supports the finding that the plant is capable of making a qualitative distinction between mechanical vibration and osmotic stress at the methylome level

as well. The combined treatment (US+D) resulted in a unique methylation pattern entirely distinct from the separate treatments, especially at the more plastic CHG and CHH levels, showing clearly visible local differences within the gene body area. This indicates that the co-occurrence of ultrasound and drought is not merely the mathematical summation of the two effects, but triggers a complex epigenetic retuning. The unique methylation sites observed in the CHH context foreshadow the fine-tuning role of *de novo* methylation processes in the establishment of stress memory.

No direct linear correlation was found between the RNA-seq and WGBS data - meaning gene-level transcriptional and genome-wide DNA methylation changes - during the stress response reactions. This result can be explained by the fact that other cooperating molecular and epigenetic mechanisms also play a role in the establishment of plant memory, which collectively influence the transcriptomic response (DOBRÁNSZKI et al., 2025; GALLUSCI et al., 2023). Based on the literature, other epigenetic mechanisms in response to drought, such as specific histone methylation, histone acetylation, and histone phosphorylation patterns (GUARINO et al., 2022), as well as non-coding RNAs, including microRNAs (GELAW et al., 2021), have already been linked to stress memory. For this reason, during the subsequent direct memory investigations, we relied on the stable and validatable expression results obtained from RNA sequencing and took transcriptional memory into account.

3.3. Selection of Target Genes and Validation of Transcriptional Data

Plant transcriptional memory is based on modified transcriptome-level response reactions. Certain responding genes are expressed at a specific level under the influence of an initial stimulus. Following the cessation of the stimulus, they either maintain the altered gene expression level for a certain period (Type 1 transcriptional memory: sustained induction), or return to the baseline status after the stimulus ceases, and if the plant subsequently receives the same stimulus, the examined gene exhibits a significantly different transcriptional response compared to the reaction given to the initial stimulus (Type 2 transcriptional memory: modified re-induction) (OBERKOFER et al., 2021). For the detailed investigation of transcriptional memory and associative memory, 4 specific, stress-representative target genes suitable for tracking memory traces were selected based on the omics data:

- Drought-specific markers: the up-regulated aquaporin TIP3-2-like (TIP) gene and the down-regulated MYB24-like (MYB) transcription factor.

- Ultrasound-specific markers: the up-regulated EXORDIUM-like 5 (EX) protein and the down-regulated ARGOS gene.

Since ultrasound had no effect on the expression of drought-specific genes, and drought did not influence ultrasound-specific genes either, we concluded that the two stimuli are indeed independent of each other. A prerequisite for accurate RT-qPCR measurements is the selection of reference (housekeeping) genes that are stably expressed under the specific experimental conditions. Because different mathematical algorithms weight gene expression variances differently, the stability of four potential reference genes (UBI, ELO, SEC, GAPDH) was evaluated through an integrated software approach.

Based on the BestKeeper algorithm, UBI proved to be the most stable reference gene, as it exhibited the lowest standard deviation ($SD = 1.05$) and coefficient of variation ($CV = 5.21\%$). In contrast, GAPDH showed the highest fluctuation, making it unsuitable for normalization. The results from the geNorm, NormFinder, and Delta Ct methods confirmed this ranking. Based on the comprehensive RefFinder index calculated from the geometric mean of the ranking scores of the different algorithms, UBI (ranking score: 1) was the most suitable reference gene for the analyses; therefore, the UBI gene was utilized as the internal control in our subsequent mRNA expression studies.

To verify the reliability of the results, the expression data obtained from mRNA sequencing were validated using RT-qPCR measurements. The expression patterns of the target genes selected for analysis (ARGOS, CHL, EX, MYB, TIP) showed directional changes in the same direction as was seen in the RNA-seq data regarding all treatments. When comparing the logarithmic fold change (LFC) values determined by the two technologies, a highly strong and significant positive Pearson correlation was observed ($r = 0.881$; $R^2 = 0.7761$; $P < 0.0001$), which confirms the tight alignment of the data points with the regression line. The homogeneous groups determined based on Tukey's B test clearly demonstrated the significant differences between the individual treatments. This high degree of data consistency and the success of the validation process allowed us to perform the relative quantification of the target genes and the analysis of transcriptional memory in additional plant samples with high confidence, using the UBI reference gene.

3.4. Temporal Dynamics of Transcriptional Memory

Based on the changes in the expression intensity of the target genes, we investigated the duration of somatic memory retention on days 2 (S1), 5 (S2), and 10 (S3) compared to the

absolute control group. Based on Pearson's correlation, a significant relationship was demonstrated between the 2-day (mRNA-seq and RT-qPCR data) and the 5-day RT-qPCR data ($r = 0.757$ and $r = 0.748$, respectively). A slightly lower ($r = 0.647$) but still highly significant correlation was found when comparing the 5- and 10-day RT-qPCR data, which statistically confirms the presence of transcriptional memory.

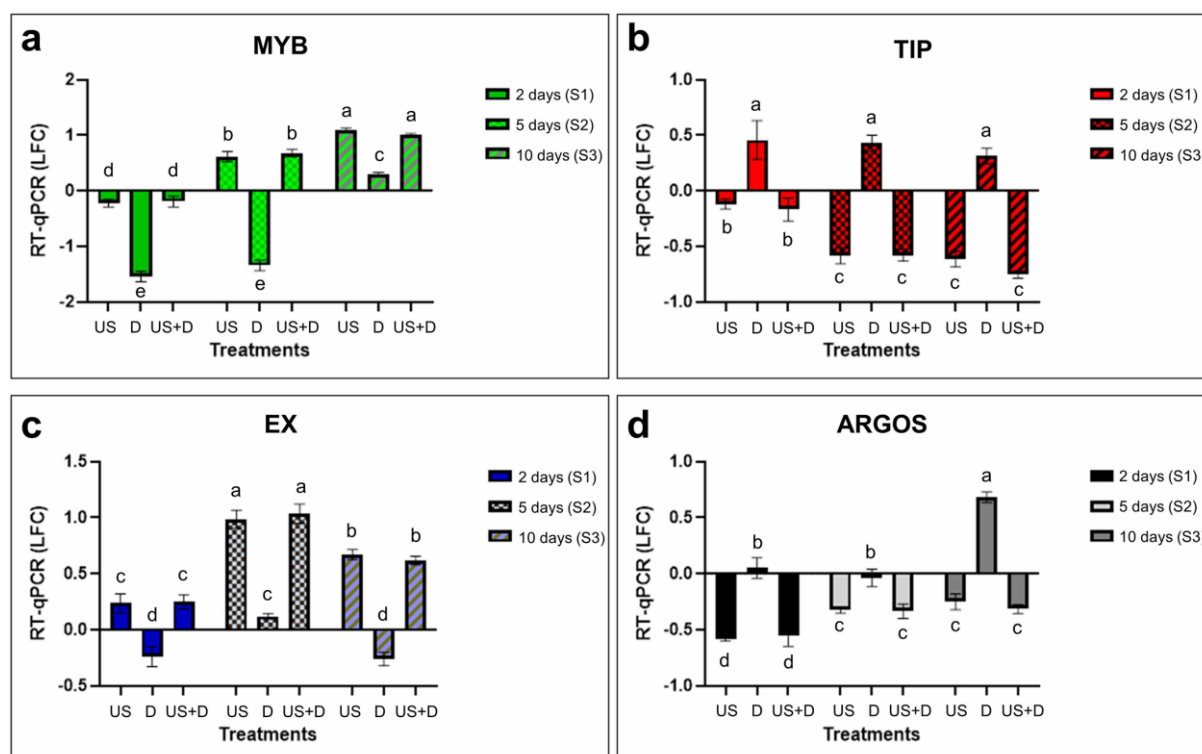


Figure 4 Memory maintenance on the 5th or 10th day following the stress stimulus. Differential expression log₂ fold change (LFC) values of the target genes estimated by RT-qPCR on days 2 (S1), 5 (S2), and 10 (S3).

For the MYB transcription factor, no significant difference was observed between the transcriptional response to the initial stimulus (D, S1) and the gene expression intensity measured on the 5th day (D, S2), suggesting that the plants stably retained the memory for 5 days (Figure 4). Since the duration of gene expression extended beyond the initial stimulus and the LFC values deviated from the baseline, hysteresis developed in the process, proving Type 1 (or sustained induction) memory. In contrast, after 10 days, the measured expression values (D, S3) significantly differed from the previous measurements, indicating that the transcriptional memory faded between the 5th and 10th days. More precisely, on the 7th day, the expression intensity of MYB was still differentially expressed compared to the absolute control group (S4), but to a lesser extent; therefore, the memory was still partially maintained.

This is further supported by the observation that when the plants were re-treated on the 5th day, no significant difference was found between the values measured on the 7th day (S4) for the "D and D" and "D and C" treatment groups; that is, because the memory persisted, repeated exposure to drought stress did not trigger an additional reaction. However, when the repeated exposure to the initial stimulus occurred on the 10th day (S3) - in contrast to all previous measurements of MYB expression intensity - a positive LFC value was observed on the 12th day (S5). This corroborates our earlier assumption that the pure maintenance of memory lasted for 7–10 days, as the repeated stimulus on the 10th day yielded significantly different responses on the 12th day. The up-regulation of the MYB gene observed on the 12th day is presumably driven by the differing physiological age of the plants and the associated developmental characteristics (Figure 5).

The TIP aquaporin gene also showed signs of Type 1 transcriptional memory, but in contrast to the sustainability of MYB, the induction of TIP remained completely unchanged not only for 5 but for 10 days (no significant difference was observed among the LFC values of the D treatment group measured at time points S1, S2, or S3). On the 12th day, however, TIP became significantly down-regulated, indicating that the memory of drought did not persist for 12 days (Figure 4). When the D treatment was repeated on the 5th day, TIP was still up-regulated on the 7th day (S4), but to a lesser extent, which may be a sign of habituation or familiarization. However, since the memory was maintained only for 10 days, a significant up-regulation of TIP was observed on the 12th day (S5) compared to the value measured on the 2nd day. This indicates that on the 10th day, the plants responded more sensitively to the repeated drought stimulus than before; that is, a sensitization response reaction developed. The intensity of expression was significantly higher on the 12th day (S5) than when applied to younger, 3-week-old plants (Figure 5).

The results of the expression intensity of EX in the ultrasonic (US) treatment group show that the magnitude of up-regulation increased from day 2 to day 5. At the same time, on the 10th day (S3), the EX target gene was still up-regulated, though to a lesser extent compared to the values measured at time points S1 and S2. This indicates that the gene expression response to US occurred with a temporal delay, but the sustained effect was still observable after 10 days, suggesting a sustained induction (Type 1 transcriptional memory) of this target gene (Figure 4).

On the 7th day (S4), there was no excessive reaction to the repeated stimulus (US and US), as no significant up-regulation occurred in the EX target gene; therefore, the plants may have learned and remembered to ignore the two stimuli, silencing the intensity of their response (familiarization). On the 12th day, however, a change occurred in the direction of the reaction

to US, as the expression intensity of EX became down-regulated, suggesting that the memory of the stimulus was completely erased by the 10th day (Figure 4). This is supported by the fact that the repeated US treatment on the 10th day caused an up-regulation of the EX gene on the 12th day (US and US, S5) that did not differ significantly from the LFC values measured on day 2. In this case - in contrast to TIP - the age of the plant presumably did not influence the response intensity (Figure 5).

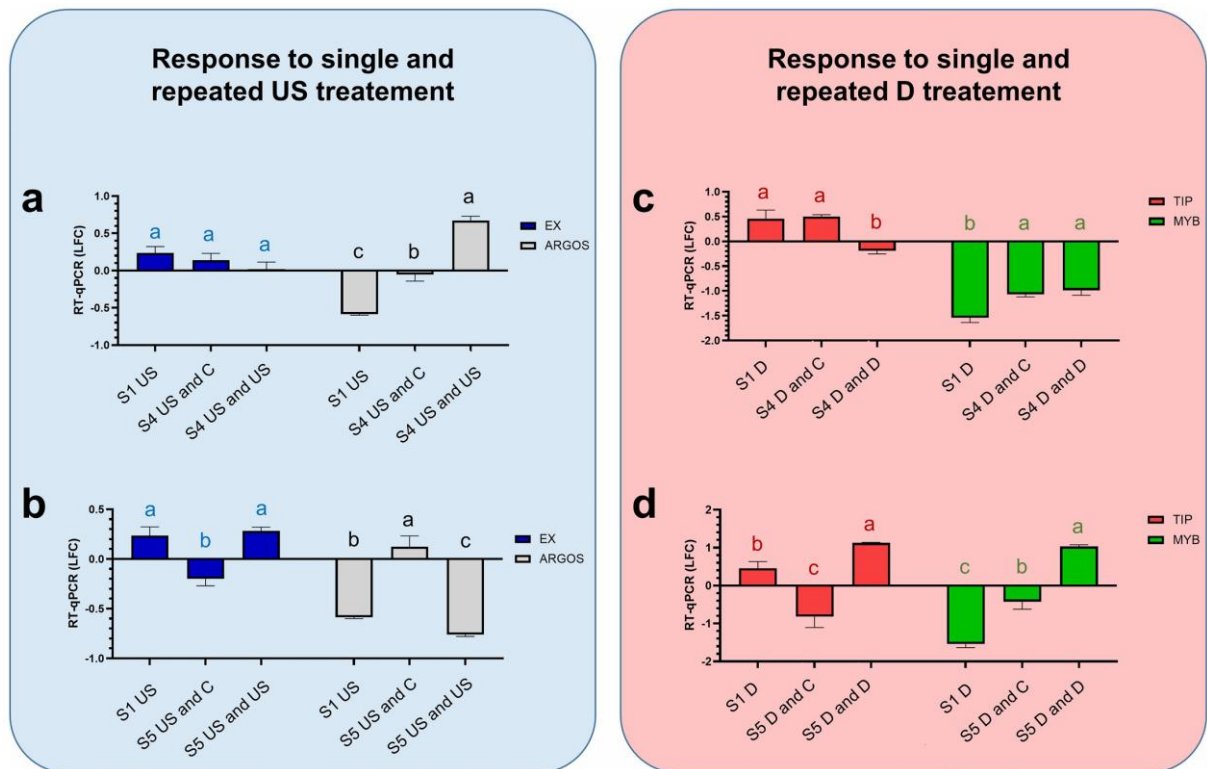


Figure 5 Effect of single and repeated stress exposure on the expression intensity of target genes at two time points. Differential expression (LFC values) of target genes determined by RT-qPCR on days 2 (S1), 7 (S4), and 12 (S5) under the influence of different treatments (ultrasound and drought stress). All LFC values are relative to the absolute control group (C at S1; 'C and C' at S4 and S5).

Regarding ARGOS, under the US treatment, the LFC values measured at time points S2 and S3 did not differ significantly from each other, but they were significantly different from the value measured at S1. This result indicates that for ARGOS, a case of sustained induction persists for 10 days in response to the US treatment (Figure 4). If the repeated US stimulus fell within this 10-day time interval, the intensity of the response changed in both direction and strength (S4). However, on the 12th day, the LFC value measured in response to the US treatment significantly differed from previous measurements, suggesting that the memory was erased by the 10th day. The repeated US stimulus on the 10th day triggered a response by the

12th day similar to that observed at S1, meaning a renewed down-regulation of ARGOS. The expression behavior of ARGOS in response to the repeated US effect indicates Type 2 transcriptional memory (modified re-induction; -/+) (BALAZADEH, 2022; OBERKOFER et al., 2021) (Figure 5).

In some cases, the maintenance of memory may inhibit the regeneration process or slow down plant development; at other times, however, storing previously acquired information is beneficial to maximize individual fitness in times of need. Studying the temporal aspects of memory, DING and co-workers (2012) reported that prior exposure to unfavorable stimuli provided plants with the opportunity to remember this experience through increased transcript levels of two genes for a short period (5 days), and after 7 days, this memory was erased. This supports our findings indicating that plants are capable of remembering past events at the transcriptomic level for a short duration (7–10 days).

The physiological age at which plants are exposed to a stimulus can determine the establishment of memory and the duration of its maintenance. To minimize the costs of future stress responses by reallocating resources between defense and growth, investing in memory maintenance can be beneficial for young plants (HOUT et al., 2014). While long-term memory lasting several months or years is known in woody plants to "handle" herbivore damage from the previous year (NYKÄNEN & KORICHEVA, 2004), annual plants primarily invest in the establishment of short-term memory prior to flowering, thereby minimizing their energetic costs to ensure successful reproduction (HILKER et al., 2016). In our experimental setup, the ARGOS and EX genes remembered the ultrasonic stimulus for 10 days, while for drought, the decreased expression of MYB lasted for 7 days, and the increased expression of TIP persisted for 10 days.

3.5. Associative Transcriptional Memory

Cross-acclimation is based on shared signaling pathways that can be activated by different types of stress exposures. However, to rigorously exclude the possibility of cross-priming, the target genes were selected to display distinct expression patterns in response to the two signals (US and D): based on mRNA sequencing (S1), they reacted exclusively to one stimulus and not at all to the other. Association was assumed if, after the combined training (US+D treatment), the conditioned stimulus (CS) triggered the same gene expression response as that observed under the influence of the other, unconditioned stimulus (UCS), meaning a clear conditioned

response (CR) was detected. Among the four investigated target genes, three - TIP, MYB, and EX - clearly demonstrated the associative learning capability of the plants on the 7th day (S4).

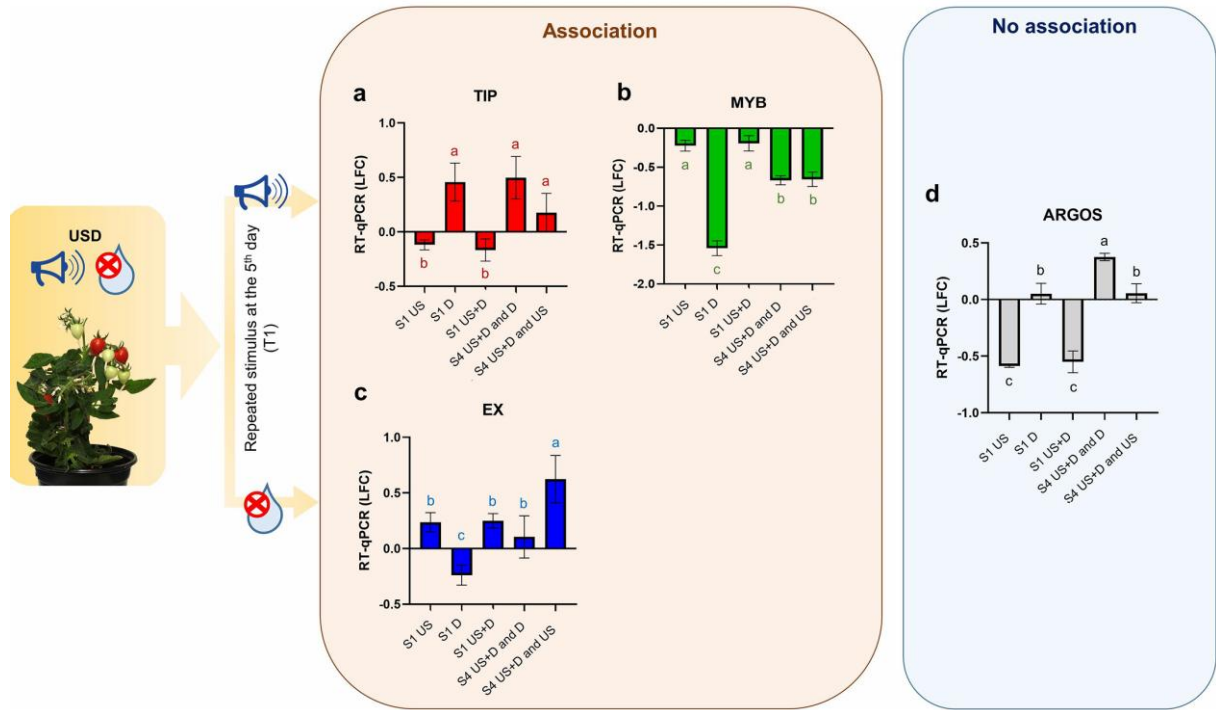


Figure 6 Changes in the expression intensity of target genes in response to repeated stimulation following combined training (conditioning). Differential expression log₂ fold change (LFC) values of the target genes estimated by RT-qPCR on days 2 (S1, relative to the absolute control - C), 5 (S2), and 7 (S4). The S2 and S4 values are relative to their own control group (US+D and C - the value measured 7 days after the first application of the combined ultrasound and drought stress).

The expression of TIP was significantly up-regulated under the influence of drought (D) at time point S1, whereas ultrasound alone triggered no response (neutral stimulus) (Figure 4). Following the combined training (US+D) and subsequent exposure of the plants to the initially neutral stimulus, ultrasound (CS), ultrasound alone triggered a significant up-regulation of TIP on the 7th day (S4). The achieved expression value did not differ significantly from either the LFC value of the pure D treatment measured at S1 or the LFC value of the "US+D and D" treatment (repetition of drought after combined training) measured at S4. Therefore, this stimulus successfully triggered the conditioned response (CR). Although there was a numerical difference between the expression intensity values, the two groups ("US+D and D" and "US+D and US") did not differ statistically significantly from each other. This observation proves that, due to the combined training, the plants were capable of remembering the association between the two stimuli and provided a corresponding proactive response at the transcriptomic level,

up-regulating TIP following the application of the conditioned stimulus (CS) and ultrasound on the 5th day (Figure 6).

Following the exact same logic, ultrasound successfully served as a conditioned stimulus (CS) for the MYB gene as well. Based on the molecular data, ultrasound had no effect on the expression of the MYB gene at time point S1, whereas drought triggered an intensive down-regulation of this target gene (Figure 4). After conditioning (US+D) - similarly to TIP - ultrasound (US) alone triggered the conditioned response (CR). The existence of associative memory is clearly proven, as statistically completely the same expression intensity was measured (no significant difference) on the 7th day (S4) when the conditioned plants received either drought treatment ("US+D and D") or ultrasonic treatment ("US+D and US") on the 5th day (Figure 6).

In the reversed stimulus association for the EX gene, drought (D) served as the neutral signal (CS) and ultrasound (US) functioned as the unconditioned stimulus (UCS), since the US signal caused a significant up-regulation of EX (Figure 4). The expression intensities of EX originating from the "US+D and US" and "US+D and D" treatments - where either D or US was applied on the 5th day to the plants trained with US+D - significantly differed from each other on the 7th day (S4). Presumably, this difference is attributable to the delayed response given to ultrasound, as EX was inherently overexpressed on the 5th day (S2) compared to the results measured on the 2nd day (S1). Regardless, on the 7th day (S4), the drought treatment of plants trained with US+D ("US+D and D") caused a significant up-regulation of EX, which clearly indicates that drought successfully triggered the conditioned response (CR), verifying the formation of the association (Figure 6).

In contrast, regarding ARGOS, although the maintenance of somatic transcriptional short-term memory was successfully demonstrated for the US and US+D treatments (Figures 4 and 5), we found no evidence for the formation of an association between the two stimuli. Based on this hypothesis, we should have observed that by the 7th day (S4) following conditioning, drought (CS) triggers the conditioned response (CR) (the down-regulation of ARGOS); however, the results showed expression levels with completely different magnitudes and directions, meaning that the formation of an association cannot be assumed in this case.

4. New Scientific Results of the Dissertation

As a result of molecular investigations conducted on tomato (*Solanum lycopersicum* L. cv. Micro Tom), the following new scientific findings have been recorded in the field of plant stress memory:

1. Through the integrated analysis of RNA-seq and WGBS data, I verified that the transcriptomic and DNA methylation responses of the Micro Tom tomato variety exhibit significant, stress-specific differences. I successfully revealed the unique molecular patterns proving that the applied stimuli do not merely trigger a general stress response, but induce well-distinguishable stress-specific transcriptomic and DNA methylation changes. Furthermore, I demonstrated that there is no direct correlation between transcriptomic and DNA methylation changes.
2. I confirmed the existence of a molecular-level "buffering effect" through which ultrasonic pre-treatment is capable of modifying the response given to subsequent drought stress. My results proved that this process mitigates the stress-specific DNA-methylation and transcriptome shift, which directly supports the functional priming (pre-conditioning) role of ultrasound.
3. Using transcriptomic analyses, I verified the existence of plant memory at the molecular (transcriptomic) level, proving that the applied treatments did not induce merely transient reactions, but triggered short-term, intragenerational memory.
4. By analyzing the temporal course of the process, I demonstrated the dynamics of somatic transcriptional memory and determined that the persistence of memory for the investigated marker genes is restricted to a 7–10 day time window. In parallel, I distinguished two types of memory: sustained induction (Type 1; MYB, TIP, EX) and modified re-induction (Type 2; ARGOS) memory.
5. Through short-term conditioning, I proved the establishment of plant associative memory, revealing that following a single training period, the neutral stimulus alone is capable of triggering the specific gene expression response characteristic of the unconditioned stimulus regarding the expression of given genes. My results also supported that this associative process develops in a stimulus-dependent manner.
6. I identified molecular habituation as an adaptive strategy, given that repeated stress occurring within the memory time window (10 days) triggered a more moderate gene expression response for the TIP gene, thereby enabling the avoidance of unnecessary energy

loss. In contrast, I verified that following the fading of the transcriptomic memory (day 10), a form of molecular sensitization can occur, during which the repeated stimulus can induce an extreme degree of gene expression response. This duality suggests that the prior learning process modified the responsiveness of the plant, where the nature of the response varied as a function of the time elapsed since the first stimulus.

5. Future Applications and Perspectives

Understanding the molecular mechanisms and transcriptional response reactions revealed during this research provides an opportunity to consciously influence plant stress memory processes, establishing the following results and recommendations applicable in agricultural practice:

1. The verified priming effect of ultrasonic treatment offers the possibility to develop a non-invasive and chemical-free technology. Ultrasonic treatment can be applied to mitigate the physiological damage caused by drought stress, thereby improving plant survival rates and yield stability during drought periods.
2. The proof of associative learning enables the design of predictive defense strategies, where an easily controllable stimulus (e.g., specific vibration or ultrasound) can activate the internal defense mechanisms of plants prior to the occurrence of the actual, perhaps lethal stress event (e.g., drought).
3. Based on the determined 7–10 day transcriptional memory interval, the timing of stress management protocols can be optimized. In agricultural practice, this provides a framework for planning repeated treatments or irrigation cycles more effectively, avoiding plant habituation or, conversely, exploiting the benefits of sensitization.
4. Uncovering the relationship between transcriptional memory and DNA methylation patterns can contribute to the selection of more resilient varieties possessing "stress memory." The identified marker genes (e.g., TIP, EX) can serve as suitable tools to monitor plant "trainability" and stress tolerance at the molecular level.
5. Exploiting plant memory can reduce the reliance on fertilizers and plant conditioning agents, as the activation of plant memory can naturally improve the environmental adaptation of the crop.
6. The identification of molecular habituation holds significant practical relevance, as it demonstrates that pre-conditioning plants can prevent the unnecessary energy loss and metabolic exhaustion caused by repeated stress exposure. This insight paves the way for precision plant conditioning technologies, where targeted fine-tuning of environmental responsiveness can achieve more stable yields and enhanced stress tolerance in field cultivation.

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7. Publications in the Subject of the Dissertation



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Subject:

PhD Publication List

Candidate: Dóra Farkas

Doctoral School: Kálmán Kerpely Doctoral School

MTMT ID: 10086787

List of publications related to the dissertation

Foreign language scientific articles in international journals (5)

1. **Farkas, D.**, Dobránszki, J.: Quantifying Intergenerational Plasticity in Tomato: Temporal Divergence as a Cost-Effective Survival Strategy Against Drought Following Parental Ultrasound Priming.
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In: I. Magyar Agrártudományi Doktoranduszok Szimpóziuma. Szerk.: Hajdú Péter, Doktoranduszok Országos Szövetsége, Debrecen, 86, 2023. ISBN: 9786156457189

20. Tólas, L., Kiss, A., **Farkas, D.**, Deák, A. G., Szemán-Nagy, G.: Az Aspergillus Fumigatus tapadási és növekedési dinamikájának hosszútávú videomikroszkópos vizsgálata.

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In: Libro Resumen XVI Convención Científica Internacional UNICA 2024. Szerk.: C. Anisia Ruiz Gutiérrez, Editorial Universitaria Ciego de Ávila, Ciego de Ávila, Kuba, 73-74, 2024.

Total IF of journals (all publications): 57,2

Total IF of journals (publications related to the dissertation): 27

The Candidate's publication data submitted to the Tudóstér have been validated by DEENK on the basis of the Journal Citation Report (Impact Factor) database.

16 September, 2026

