



Comparative transcriptomic analysis of drought stress response in *Solanum lycopersicum* and *Solanum tuberosum*

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Abstract

Drought stress is a major abiotic factor that limits crop productivity and threatens global food security. Tomato (*Solanum lycopersicum*) and potato (*Solanum tuberosum*) are economically important Solanaceae crops that exhibit distinct responses to water deficit conditions. This study compared drought-induced transcriptomic changes in both species using publicly available RNA-seq datasets. An integrated bioinformatics pipeline consisting of FastQC, Trim Galore, HISAT2, featureCounts, and DESeq2 was employed for quality assessment, read alignment, gene quantification, and differential gene expression analysis. Principal component analysis demonstrated clear separation between drought-treated and control samples in both species, indicating substantial transcriptomic alterations under drought stress. Sample-to-sample distance analysis further confirmed strong clustering consistency among biological replicates. Differential expression analysis identified numerous significantly regulated genes in both species, as revealed by MA and volcano plots. Potato exhibited broader fold-change distributions and more extensive differential expression patterns than tomato, suggesting a larger-scale transcriptional response to drought. Heatmap analysis of the top 50 differentially expressed genes clearly distinguished drought-treated samples from controls and revealed coordinated expression patterns associated with water deficit. Dispersion estimates and p-value distributions supported the reliability and statistical robustness of the RNA-seq datasets. The results demonstrate that drought stress induces substantial transcriptomic reprogramming in both tomato and potato while revealing differences in the magnitude of their molecular responses. These findings provide insights into drought-responsive regulatory mechanisms in Solanaceae crops and offer valuable resources for future studies on drought adaptation and crop improvement.

Keywords: comparative transcriptome, differential gene expression, drought-stress, *Solanum lycopersicum* (tomato), *Solanum tuberosum* (potato)

1. Introduction

Drought stress is considered one of the most severe environmental constraints affecting plant growth, agricultural productivity, and global food security. The increasing frequency of extreme climate events, prolonged dry seasons, and irregular precipitation patterns associated with global climate change have significantly intensified drought-related agricultural losses worldwide. Water deficit conditions adversely influence numerous physiological and biochemical processes in plants, including photosynthesis, respiration, nutrient transport, stomatal conductance, cellular homeostasis, and biomass accumulation. As a consequence, drought stress can substantially reduce crop yield and quality, particularly in economically important food crops (Nicolas et al., 2022).

Plants have evolved highly complex adaptive mechanisms to cope with drought stress at physiological, biochemical, cellular, and molecular levels. Under water-deficit conditions, plants activate diverse stress-responsive pathways to maintain cellular integrity and improve survival. These mechanisms include

osmotic adjustment, stomatal regulation, accumulation of osmoprotectants, reactive oxygen species (ROS) scavenging, hormonal signaling, and activation of stress-responsive transcription factors. Among various hormonal pathways, abscisic acid (ABA) signaling plays a central role in mediating drought responses through regulation of stomatal closure, stress-induced gene expression, and water conservation mechanisms (He et al., 2024).

At the molecular level, drought stress induces extensive transcriptomic reprogramming involving numerous genes associated with signal transduction, transcriptional regulation, antioxidant activity, osmoprotection, secondary metabolite biosynthesis, and cellular defense systems. Several transcription factor families, including DREB, MYB, NAC, WRKY, and bZIP, have been reported to contribute significantly to drought adaptation in plants by regulating downstream stress-responsive genes (Shinozaki & Yamaguchi-Shinozaki, 2007). In addition, drought stress often leads to metabolic alterations associated with carbohydrate metabolism, amino acid biosynthesis, lipid metabolism, and antioxidant defense pathways, reflecting the broad impact of water limitation on plant cellular processes.

The rapid development of next-generation sequencing (NGS) technologies has revolutionized transcriptomic studies in plant stress biology. Among these technologies, RNA sequencing (RNA-seq) has become one of the most powerful approaches for investigating genome-wide gene expression changes under various environmental conditions. Compared with conventional gene expression analysis methods such as microarrays, RNA-seq offers higher sensitivity, broader dynamic range, and improved capability for identifying novel transcripts and low-abundance genes (Wang et al., 2009). RNA-seq-based transcriptomic analysis enables comprehensive identification of differentially expressed genes (DEGs), biological pathways, and molecular networks associated with abiotic stress adaptation.

Within the Solanaceae family, tomato (*Solanum lycopersicum*) and potato (*Solanum tuberosum*) are among the most economically important horticultural crops worldwide. Tomato is widely cultivated as both a fresh-market and processed vegetable crop, whereas potato serves as one of the major staple food crops globally. Despite belonging to the same plant family, these species exhibit distinct physiological characteristics and adaptive responses to environmental stress. Tomato is generally regarded as moderately tolerant to drought stress due to its relatively flexible physiological adaptation mechanisms, whereas potato is often considered highly susceptible to water deficit because of its shallow root system, high transpiration rate, and substantial water requirements during tuber development (Aliche et al., 2021).

Previous transcriptomic studies have demonstrated that drought stress significantly alters gene expression patterns in both tomato and potato. In tomato, drought-responsive genes are frequently associated with ABA signaling, antioxidant enzymes, transcription factors, osmolyte biosynthesis, and stress-responsive proteins (Murtaza et al., 2025). Similarly, drought stress in potato has been reported to influence genes involved in carbohydrate metabolism, flavonoid biosynthesis, lipid transfer proteins, heat shock proteins, and cellular protective mechanisms (Aliche et al., 2021). However, comparative transcriptomic investigations evaluating drought-responsive expression patterns between tomato and potato using standardized analytical pipelines remain relatively limited.

Comparative transcriptomic analysis is particularly valuable because it enables identification of conserved and species-specific stress response mechanisms among related plant species. Understanding these transcriptional differences may provide insight into distinct adaptation strategies and potentially contribute to the development of drought-resilient crop varieties. Moreover, the increasing availability of publicly accessible RNA-seq datasets in repositories such as the NCBI Sequence Read Archive (SRA) provides important opportunities for reanalysis and comparative studies using integrated bioinformatics workflows.

Bioinformatics tools such as FastQC, Trim Galore, HISAT2, featureCounts, and DESeq2 have become widely adopted for RNA-seq data analysis due to their reliability and computational efficiency. FastQC enables evaluation of sequencing quality and adapter contamination, while Trim Galore performs adapter trimming and low-quality sequence removal. HISAT2 provides efficient splice-aware alignment of sequencing reads against reference genomes, featureCounts performs accurate gene-level quantification, and DESeq2 enables robust statistical identification of differentially expressed genes through normalization and dispersion modeling (Love et al., 2014).

Therefore, the present study aimed to perform a comparative transcriptomic analysis of drought stress responses in potato and tomato using publicly available RNA-seq datasets. An integrated bioinformatics workflow involving quality assessment, read preprocessing, genome alignment, gene quantification, and differential expression analysis was employed to characterize drought-responsive transcriptional alterations. In addition, principal component analysis (PCA), sample clustering, volcano plots, MA plots, and heatmap analyses were conducted to evaluate transcriptomic variation between control and drought-treated samples. This study is expected to provide insight into species-specific drought response mechanisms in Solanaceae crops and contribute to a broader understanding of plant abiotic stress adaptation.

2. Materials and Methods

2.1. RNA-seq Dataset Collection

Publicly available RNA-seq datasets associated with drought stress treatments in *Solanum lycopersicum* and *Solanum tuberosum* were obtained from the NCBI Sequence Read Archive (SRA). For tomato, three biological replicates representing control conditions (SRR11539290, SRR11539291, and SRR11539292) and three drought-treated samples (SRR11539296, SRR11539297, and SRR11539298) were analyzed. For potato, three control samples (SRR25425104, SRR25425105, and SRR25425106) and three drought-treated samples (SRR25425101, SRR25425102, and SRR25425103) were included in the analysis.

2.2. Quality Control and Read Preprocessing

Raw sequencing reads were subjected to quality assessment using FastQC to evaluate sequence quality, GC content, sequence duplication levels, and adapter contamination. Adapter trimming and removal of low-quality bases were subsequently performed using Trim Galore. For paired-end datasets, paired-end trimming mode was applied, whereas single-end trimming was used for single-end datasets. Following trimming, FastQC analysis was repeated to confirm improvements in read quality and removal of adapter sequences.

2.3. Reference Genome Preparation and Read Alignment

Reference genome sequences and annotation files for *S. lycopersicum* and *S. tuberosum* were obtained from publicly available genome repositories. HISAT2 was employed for transcriptome alignment due to its efficient splice-aware mapping capability. Clean reads from each sample were independently aligned against their respective reference genomes. The resulting alignment files were generated in BAM format for downstream analysis.

2.4. Gene Quantification

Gene-level read quantification was performed using featureCounts. Corresponding genome annotation files in GTF/GFF format were used to assign aligned reads to annotated genomic features. For paired-end datasets, fragments were counted as single fragments to avoid double-counting paired reads. The resulting count matrices were subsequently used for differential expression analysis.

2.5. Differential Expression Analysis

Differential gene expression analysis was conducted using the DESeq2 package. Raw count matrices and sample metadata describing experimental conditions were used as input. Genes exhibiting adjusted p-values (padj) below 0.05 and absolute log2 fold change values greater than 1 were considered significantly differentially expressed.

2.6. Data Visualization and Clustering Analysis

Principal component analysis (PCA) was performed to evaluate overall transcriptomic variation and sample clustering patterns. Sample-to-sample distance heatmaps were generated to assess biological replicate consistency and treatment-based clustering. Volcano plots were constructed to visualize significantly upregulated and downregulated genes under drought stress conditions. MA plots were generated to examine expression fold-change distributions relative to normalized expression levels. Additionally, heatmap analysis was performed using the top 50 significantly differentially expressed genes for each species. Normalized count data were log2-transformed prior to clustering analysis. Hierarchical clustering was conducted using Euclidean distance metrics and complete linkage methods to evaluate expression pattern similarities among samples.

3. Results

3.1. Transcriptomic Variation and Clustering Patterns Under Drought Stress

Principal component analysis (PCA) was conducted to evaluate overall transcriptomic variation between drought-treated and control samples in both potato and tomato. In potato, PC1 explained 61% of the total variance, whereas PC2 accounted for an additional 15% of the variance (Figure 1). Samples exposed to drought stress were clearly separated from control samples along the first principal component, indicating that water deficit substantially altered global gene expression patterns. Biological replicates belonging to the same treatment group clustered closely together, suggesting high consistency among replicates and limited technical variation within the dataset. The distinct grouping observed between drought-treated and control samples indicates that treatment effects represented the major source of transcriptional variation.

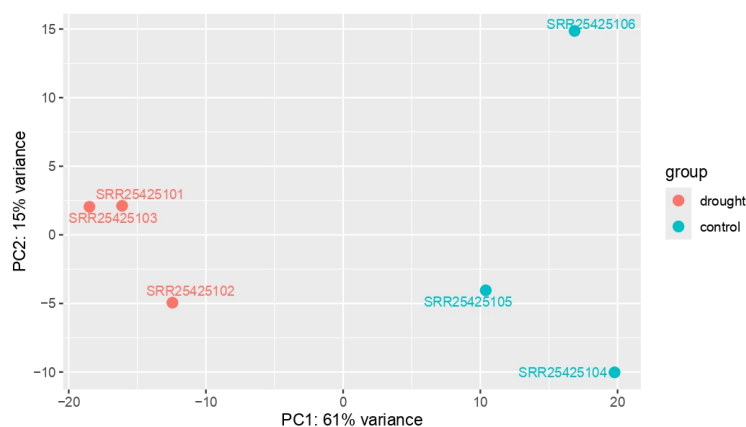


Figure 1. Principal component analysis (PCA) of transcriptomic profiles under drought stress conditions in potato.

A comparable separation pattern was observed in tomato (Figure 2). PC1 explained 71% of the total variance and PC2 contributed 13%, demonstrating that most transcriptomic variability could be attributed to treatment differences. Drought-treated samples formed a cluster distinct from the control group, with minimal overlap between treatments. The stronger variance explained by PC1 in tomato suggests that drought stress exerted a pronounced influence on overall transcriptomic organization. The PCA results collectively demonstrate that drought treatment induced substantial changes in gene expression profiles in both species and provided a clear basis for subsequent differential expression analysis.



Figure 2. Principal component analysis (PCA) of transcriptomic profiles under drought stress conditions in tomato.

The clustering patterns identified through PCA were further supported by sample-to-sample distance heatmaps (Figure 3). In potato, two major clusters corresponding to drought-treated and control samples were clearly observed. Samples within the same treatment exhibited shorter distances from one another than from samples belonging to the opposite treatment group, indicating strong within-group similarity. Similar clustering behavior was detected in tomato, where biological replicates consistently grouped according to treatment conditions. The concordance between PCA and distance-based clustering analyses confirms the reliability of the experimental design and demonstrates that drought treatment generated reproducible transcriptomic responses across biological replicates.

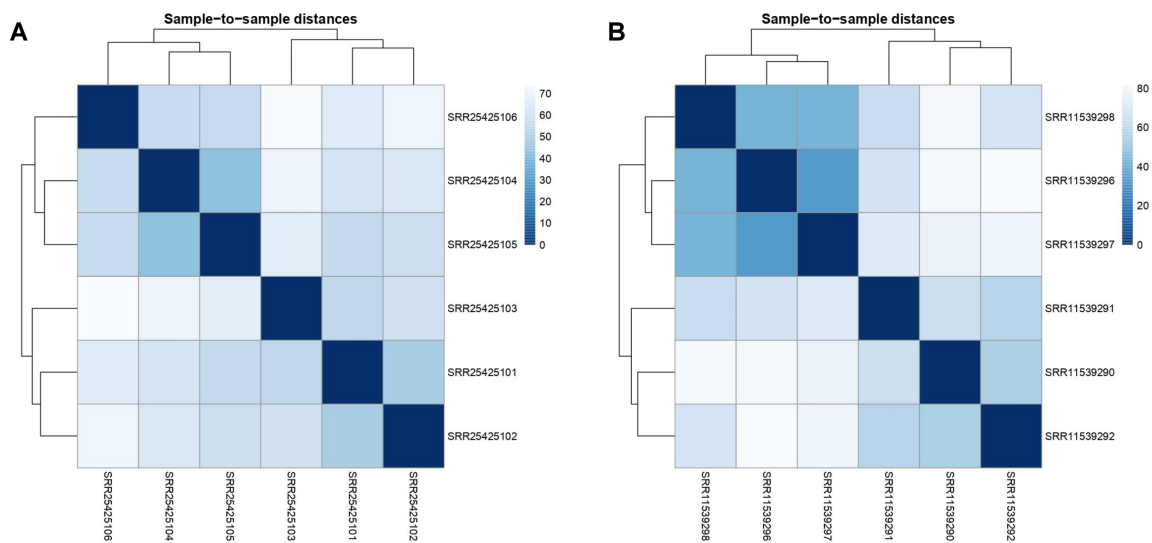


Figure 3. Sample-to-sample distance heatmaps of RNA-seq samples in response to drought stress: (A) potato, (B) tomato.

3.2. Quality Assessment of RNA-seq and Differential Expression Analysis

The quality and statistical reliability of the RNA-seq datasets were evaluated using DESeq2 dispersion estimates (Figure 4). In both species, dispersion values decreased as normalized gene expression levels increased, producing the characteristic trend commonly observed in RNA-seq experiments. The fitted dispersion curves closely followed the distribution of gene-wise estimates, indicating that the statistical model adequately captured the underlying variance structure of the datasets. Final dispersion estimates remained distributed around the fitted trend line, suggesting that variance stabilization and normalization procedures were successfully implemented prior to differential expression analysis.

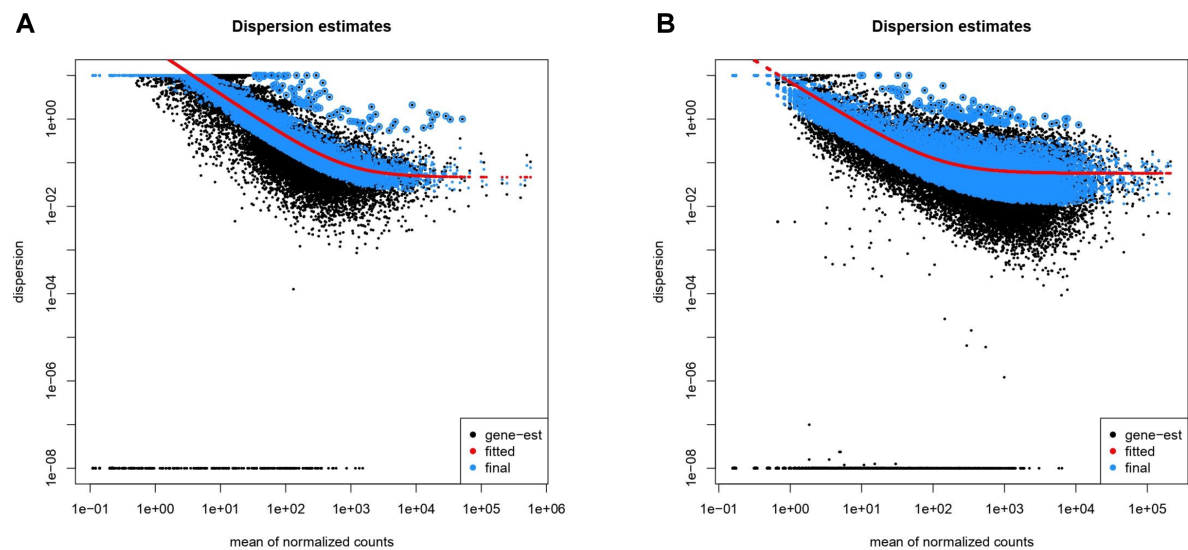


Figure 4. Dispersion estimate plots generated by DESeq2 for differential expression analysis: (A) potato, (B) tomato.

Additional quality assessment was performed through examination of p-value distributions (Figure 5). Both potato and tomato datasets displayed a pronounced enrichment of low p-values near zero, indicating the presence of numerous genes responding significantly to drought stress. Beyond the initial enrichment peak, p-values were distributed relatively uniformly across the remaining range, suggesting appropriate calibration of the statistical model. The observed distributions are consistent with well-performing differential expression analyses and indicate that the datasets contain biologically meaningful transcriptional signals suitable for downstream investigation. Together, the dispersion estimates and p-value histograms demonstrate that the RNA-seq datasets possessed appropriate statistical properties for differential expression analysis. The absence of irregular distribution patterns or excessive variance inflation provides confidence in the robustness of the identified drought-responsive genes and supports the validity of subsequent transcriptomic comparisons between treatment groups.

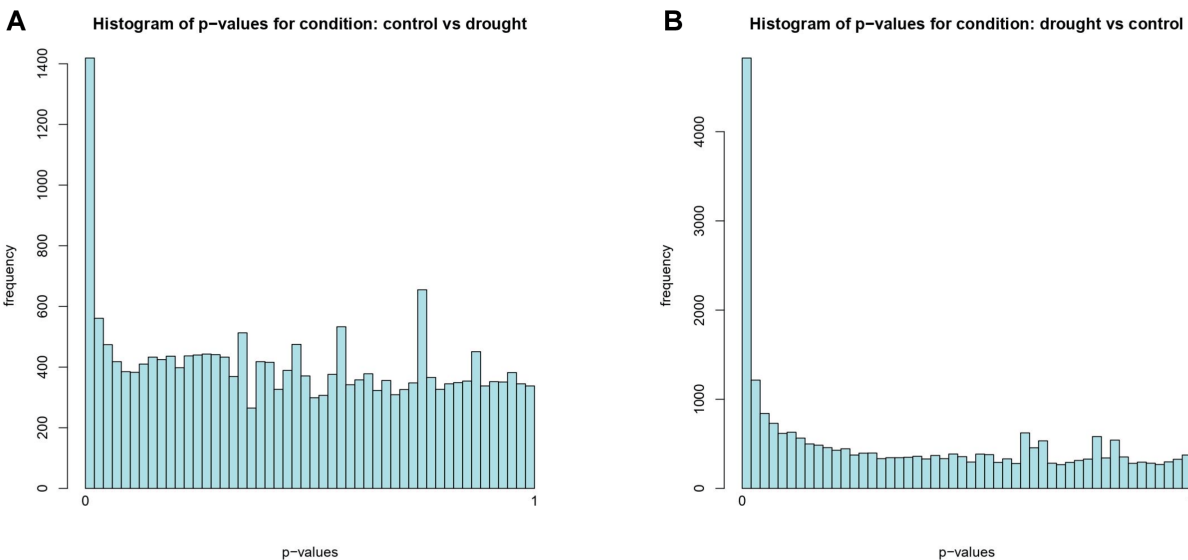


Figure 5. Histogram distribution of p-values obtained from differential expression analysis: (A) potato, (B) tomato.

3.3. Genome-Wide Differential Expression Responses to Drought Stress

Genome-wide differential expression patterns were examined using MA plots and volcano plots generated from DESeq2 results. MA plots revealed substantial transcriptional responses to drought stress in both species (Figure 6). In tomato, the majority of genes were concentrated around a log₂ fold-change value of zero, indicating relatively stable expression across treatment conditions for a large proportion of the transcriptome. Most data points were distributed symmetrically around the central axis, while a subset of genes showed significant positive or negative fold-change values. Differentially expressed genes were detected across a broad range of normalized expression levels, demonstrating that drought-responsive transcriptional changes occurred in both moderately and highly expressed genes. Several transcripts exhibited marked expression shifts despite moderate abundance levels, indicating that drought-induced regulation was not limited to the most abundant transcripts. The overall distribution pattern suggests that drought treatment affected multiple components of the tomato transcriptome while maintaining expression stability for a substantial proportion of genes.

Potato exhibited a broader distribution of fold-change values compared with tomato. Numerous genes displayed strong positive or negative expression changes, resulting in a wider spread of data points around the central axis. Differentially expressed genes were observed across nearly the entire range of normalized counts, indicating extensive transcriptional adjustments under drought conditions. Several transcripts demonstrated large fold-change magnitudes at moderate and high expression levels, reflecting substantial expression differences between drought-treated and control samples. The wider dispersion of points in the potato MA plot indicates a greater degree of transcriptional variability relative to tomato. In addition, the presence of genes with exceptionally high positive and negative fold-change values suggests that drought stress triggered pronounced regulation of specific transcriptional targets. These patterns collectively illustrate a more extensive transcriptomic response in potato and highlight substantial differences in the magnitude of drought-induced gene expression changes between the two species.

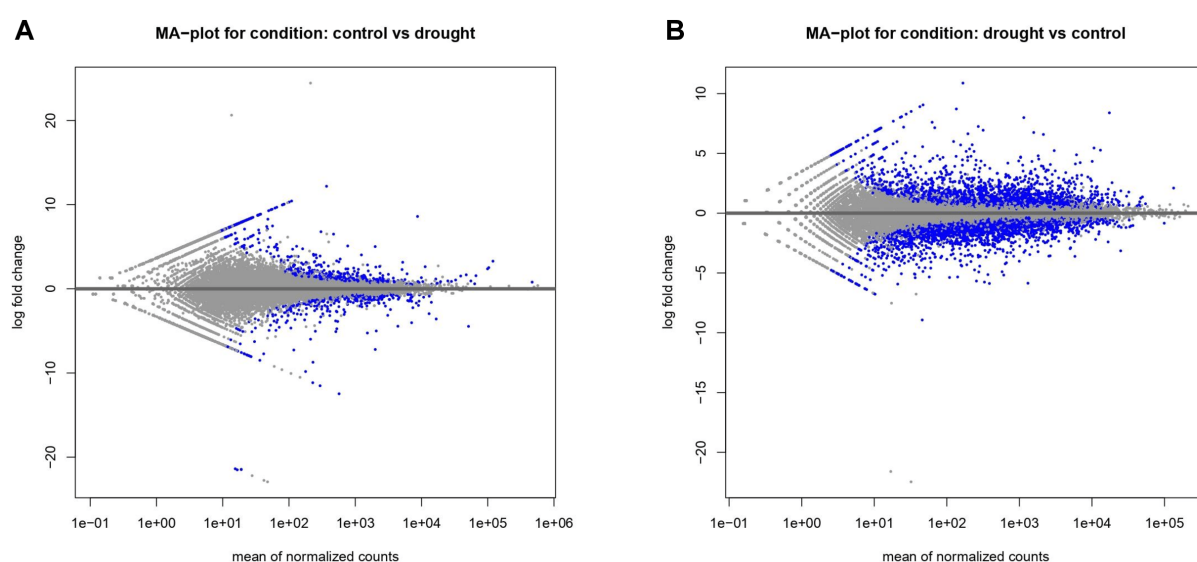


Figure 6. MA plots of differential gene expression under drought stress conditions: (A) potato, (B) tomato.

Volcano plots further illustrated the magnitude and significance of drought-induced transcriptional changes (Figure 7). In both species, significant genes were distributed on both sides of the plot, indicating the simultaneous occurrence of gene activation and repression under drought conditions. Tomato displayed numerous significantly regulated genes with moderate fold-change values. Potato showed a broader distri-

bution of significant genes and a larger number of transcripts exhibiting substantial fold-change magnitudes. These patterns indicate that drought stress triggered extensive transcriptomic remodeling in both species, with potato displaying a comparatively larger transcriptional response under the analyzed experimental conditions.

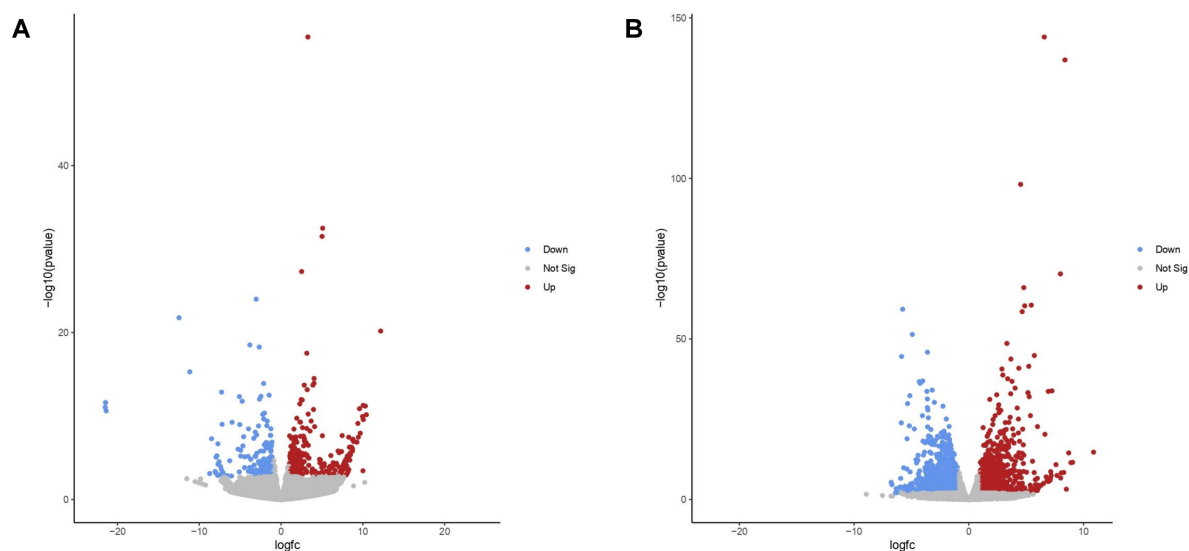


Figure 7. Volcano plots of differentially expressed genes (DEGs) under drought stress: (A) potato, (B) tomato.

3.4. Heatmap Analysis of Differentially Expressed Genes

To investigate expression dynamics among the most responsive transcripts, heatmaps were generated using the top 50 differentially expressed genes identified in each species (Figure 8). Hierarchical clustering revealed clear separation between drought-treated and control samples in both potato and tomato, indicating that these genes effectively captured treatment-associated transcriptional variation. Samples belonging to the same treatment consistently clustered together, further supporting the reproducibility of the RNA-seq datasets and the reliability of the differential expression results.

In potato, several gene clusters exhibited strong upregulation under drought conditions while remaining weakly expressed in control samples. Additional clusters displayed the opposite pattern, with higher expression levels observed in controls and reduced expression following drought treatment. The presence of multiple oppositely regulated gene groups indicates coordinated activation and repression of distinct transcriptional programs in response to water deficit. The observed expression patterns suggest extensive reorganization of gene regulatory networks associated with drought adaptation.

Tomato also displayed distinct drought-responsive expression signatures, although the overall contrast between treatment groups appeared less pronounced than that observed in potato. Multiple genes showed consistent increases or decreases in expression across drought-treated samples, indicating coordinated regulation despite moderate expression amplitudes. The clustering structure revealed stable expression patterns among biological replicates and highlighted a subset of genes strongly associated with drought exposure. These results demonstrate that drought stress induced reproducible and treatment-specific transcriptional responses in both species while revealing differences in the magnitude of gene expression reprogramming between tomato and potato.

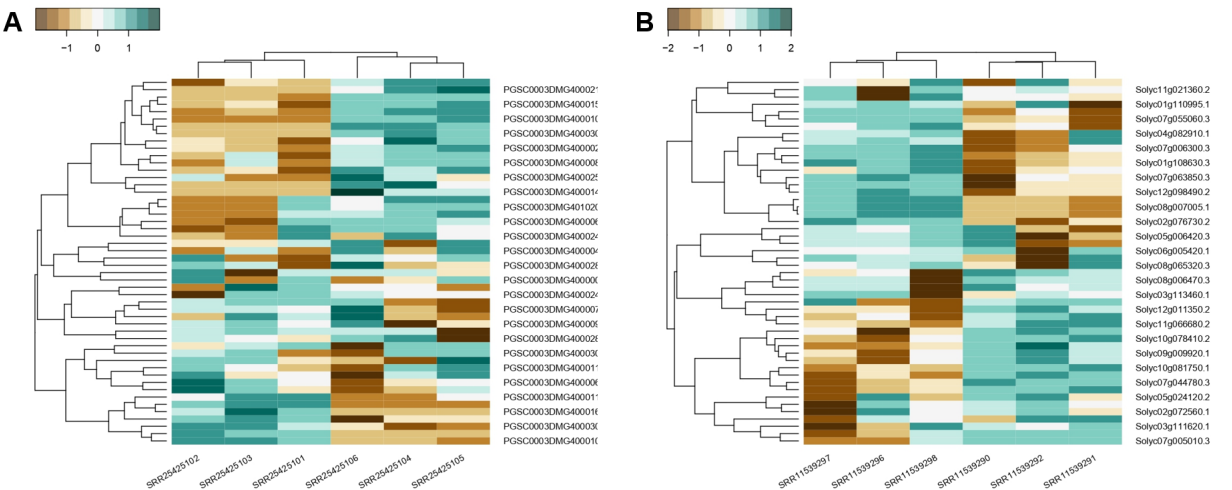


Figure 8. Heatmap visualization of the top 50 differentially expressed genes in *Solanum tuberosum* under drought stress: (A) potato, (B) tomato.

4. Discussion

Drought stress is a major environmental constraint that significantly reduces crop productivity and poses a serious threat to global food security, particularly under moderate drought conditions where plant growth rates are substantially diminished (Vadez et al., 2024). The genus *Solanum* includes several globally important vegetable crops, notably tomato (*Solanum lycopersicum*) and potato (*Solanum tuberosum*), which collectively contribute substantially to food production and nutritional security. Nevertheless, the increasing frequency and severity of climate change-associated phenomena, particularly elevated temperatures and declining precipitation levels, have intensified drought occurrences in many agricultural regions. Consequently, water-deficit stress has emerged as a major constraint affecting the growth and productivity of *Solanum* species, leading to significant yield losses and posing challenges to sustainable crop production (Flores-Saavedra et al., 2023). In the present study, comparative transcriptomic analysis demonstrated that drought treatment induced substantial transcriptional alterations in both tomato and potato. The observed transcriptomic changes support the initial working hypothesis that drought stress triggers differential regulation of stress-responsive genes in Solanaceae crops, although the magnitude and organization of the responses vary between species.

Principal component analysis (PCA) revealed clear clustering separation between drought-treated and control samples in both species, indicating that drought stress strongly influenced global transcriptomic profiles. In tomato, PC1 accounted for 71% of the total variance, whereas potato exhibited 61% variance along PC1. The relatively distinct clustering patterns observed in both datasets suggest that drought treatment generated reproducible transcriptional responses across biological replicates. Similar transcriptomic separations under drought conditions have been reported in previous RNA-seq studies involving tomato and potato, indicating that water-deficit stress consistently induces extensive reprogramming of gene expression associated with stress adaptation pathways (Aliche et al., 2021; Nicolas et al., 2022).

Interestingly, the transcriptomic response observed in potato appeared broader and more pronounced than that observed in tomato. Volcano plot and MA plot analyses demonstrated wider fold-change distributions and more extensive differential expression patterns in potato compared to tomato. This finding may reflect species-specific differences in drought sensitivity and stress adaptation mechanisms. Potato is generally considered more susceptible to drought stress due to its shallow root system, high transpiration rate, and elevated water demand during growth and tuber formation (Nasir & Toth, 2022; Salehi-Soghadi et al., 2023; Yang et al., 2024). Consequently, exposure to drought conditions may trigger more extensive transcriptional reprogramming in potato tissues as part of an intensified stress response (Aliche et al., 2021). Compared with tomato, potato exhibited a more extensive transcriptomic response to drought stress, suggesting greater transcriptional reprogramming under water-deficit conditions. However, whether this response reflects enhanced stress adaptation or increased drought sensitivity requires further physiological and functional validation.

The heatmap analysis of the top differentially expressed genes further supported the existence of coordinated transcriptional regulation during drought stress. In both species, drought-treated samples clustered separately from control samples and displayed distinct expression profiles involving simultaneous upregulation and downregulation of multiple genes. Such coordinated expression patterns are commonly associated with activation of complex stress-responsive pathways involving ABA signaling, osmotic adjustment, ROS detoxification, and transcriptional regulation. Previous studies have demonstrated that drought stress frequently induces genes associated with DREB, NAC, WRKY, and MYB transcription factor families, in addition to genes involved in antioxidant defense systems and osmoprotectant biosynthesis (Shinozaki & Yamaguchi-Shinozaki, 2007). These findings suggest that the clustering patterns observed in this study reflect the activation of integrated molecular defense mechanisms in response to water-deficit conditions.

The statistical quality assessment further indicated that the RNA-seq datasets and downstream analyses were reliable. Sample-to-sample distance heatmaps demonstrated strong consistency among biological replicates, while dispersion estimate plots showed appropriate variance fitting during DESeq2 normalization and modeling. Additionally, enrichment of low p-values in the p-value histograms supported the presence of biologically meaningful differential expression signals rather than random statistical noise. The consistency observed across multiple quality assessment metrics suggests that the analytical workflow involving FastQC, Trim Galore, HISAT2, featureCounts, and DESeq2 successfully generated robust transcriptomic datasets suitable for comparative drought-response analysis.

Importantly, the stronger transcriptional response observed in potato should not be interpreted as direct evidence of superior drought tolerance. A common misconception in transcriptomic studies is the assumption that broader gene expression changes necessarily indicate enhanced stress resistance. Extensive transcriptomic alterations may also reflect increased physiological stress sensitivity and greater disruption of cellular homeostasis (Marais et al., 2012). The broader differential expression patterns detected in potato may represent activation of adaptive defense mechanisms, a heightened physiological response to stress, or a combination of both processes (Aliche et al., 2021). Determining the biological significance of these responses requires additional physiological, biochemical, and functional validation. This distinction is particularly important when interpreting transcriptomic datasets for crop improvement and stress adaptation research.

The findings of this study contribute to the broader understanding of drought-responsive transcriptional regulation in Solanaceae crops. Comparative transcriptomic approaches provide valuable opportunities to identify conserved and species-specific stress-response pathways that may serve as targets for future crop improvement strategies. Genes consistently associated with drought-responsive pathways could potentially be utilized in molecular breeding programs, marker-assisted selection, or genetic engineering approaches aimed at improving drought resilience in economically important crops.

Despite the meaningful insights generated in this study, several limitations should be acknowledged. First, the analysis relied on publicly available RNA-seq datasets with relatively limited biological replicates, which may influence statistical power and DEG detection sensitivity. Second, the study focused primarily on transcriptomic alterations without incorporating physiological or metabolomic validation. Third, *Solanum melongena* (eggplant) could not be included in downstream comparative analyses due to limitations in genome annotation compatibility and insufficient feature annotation required for accurate read quantification. These limitations highlight the importance of high-quality genome annotation resources for comparative transcriptomic studies.

Future studies should integrate transcriptomic analysis with physiological measurements, metabolomics, proteomics, and functional validation experiments to provide a more comprehensive understanding of drought adaptation mechanisms in Solanaceae species. In particular, characterization of key drought-responsive genes identified through RNA-seq analysis may help clarify their specific biological functions and regulatory roles during stress adaptation. Furthermore, comparative studies involving additional Solanaceae species and diverse environmental stress conditions may contribute to a broader understanding of conserved stress-response networks in economically important crop plants.

5. Conclusions

This comparative transcriptomic analysis demonstrated that drought stress substantially altered gene expression patterns in both tomato and potato. PCA, sample clustering, differential expression, and heatmap analyses consistently distinguished drought-treated samples from controls, confirming a strong transcriptional response to water-deficit conditions. Potato exhibited broader differential expression patterns and larger fold-change distributions than tomato, indicating more extensive transcriptomic reprogram-

ming under drought stress. These findings highlight species-specific differences in drought-responsive molecular regulation within the Solanaceae family. The generated transcriptomic datasets provide a valuable resource for identifying candidate genes associated with drought response and may support future studies aimed at improving drought resilience through molecular breeding and functional genomics approaches.

Supplementary Materials: No supplementary materials are available for this study.

Acknowledgments: This study was conducted as part of the Omics Technology course project under the academic supervision of Dr. Rizky Dwi Satrio, S.Si., M.Si. The author acknowledges the National Center for Biotechnology Information (NCBI) for providing publicly accessible RNA-seq datasets through the Sequence Read Archive (SRA), which served as the primary data source for this study. During the preparation of this manuscript, the author used ChatGPT (OpenAI) for language refinement, scientific writing assistance, and manuscript editing. All generated content was critically reviewed, revised, and verified by the author, who assumes full responsibility for the accuracy and integrity of the final manuscript.

Conflicts of Interest: The author declare no conflicts of interest.

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