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Comparative transcriptomic profiling of field-grown cassava genotypes across season transitions

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Cassava (*Manihot esculenta*, Crantz) is a perennial crop cultivated in tropical and subtropical areas. In its cultivation cycle, it encounters environmental stresses related to changes in temperature and water fluctuations during seasonal transitions. We profiled the transcriptomes of four field-grown genotypes to investigate the molecular basis of adaptation to season transitions. 3'mRNA-seq libraries were prepared from samples collected from storage roots to capture gene expression changes associated with shifts from rainy to dry and dry to rainy seasons. Reproducibility and variability within the dataset were evaluated using correlation analysis and principal component analysis, providing confidence in data quality and consistency across samples. The usability of these data was proved by differential expression analysis during the rainy-to-dry and dry-to-rainy transitions, and by functional enrichment analysis. The detailed information of the experimental environmental conditions and of the workflow from planting to final DEGs analysis provided, make this dataset a useful resource for future research on plant responses to environmental fluctuations and to identify candidate genes for crop improvement strategies for climate-resilient varieties.

Background & Summary

Cassava (*Manihot esculenta*, Crantz), a crucial crop in tropical and subtropical regions, is the third most important source of calories in the tropics, providing a reliable carbohydrate source for hundreds of millions of people worldwide¹. Its global production exceeds 300 million metric tons annually, with the majority cultivated in Africa, Asia, and Latin America^{2,3}.

Cassava's global significance stems from its remarkable adaptability to diverse environmental conditions. This resilient crop thrives in diverse climate conditions, from humid tropics to arid and semi-arid regions. Its resilience to challenging growing conditions, including poor soils, pests, and diseases, supports its role as a dependable crop for smallholder farmers in areas with limited access to modern agricultural inputs⁴. These capabilities become increasingly crucial as agriculture confronts escalating challenges due to climate change, where rising temperatures and more frequent extreme weather events threaten crop productivity worldwide⁵.

As a tropical root crop cultivated in an annual cycle, cassava experiences distinct seasonal transitions, from rainy to dry periods and back to rainy conditions, each imposing unique biotic and abiotic stresses that impact its growth, physiology, and overall resilience⁶. During rainy seasons, cassava benefits from ample moisture, promoting nutrient uptake and growth⁷. However, the dry season brings reduced soil moisture, increased temperatures, and solar radiation, inducing drought-like conditions that challenge cassava's physiological and cellular mechanisms⁸. To withstand these seasonal shifts, cassava activates a variety of adaptive responses, including

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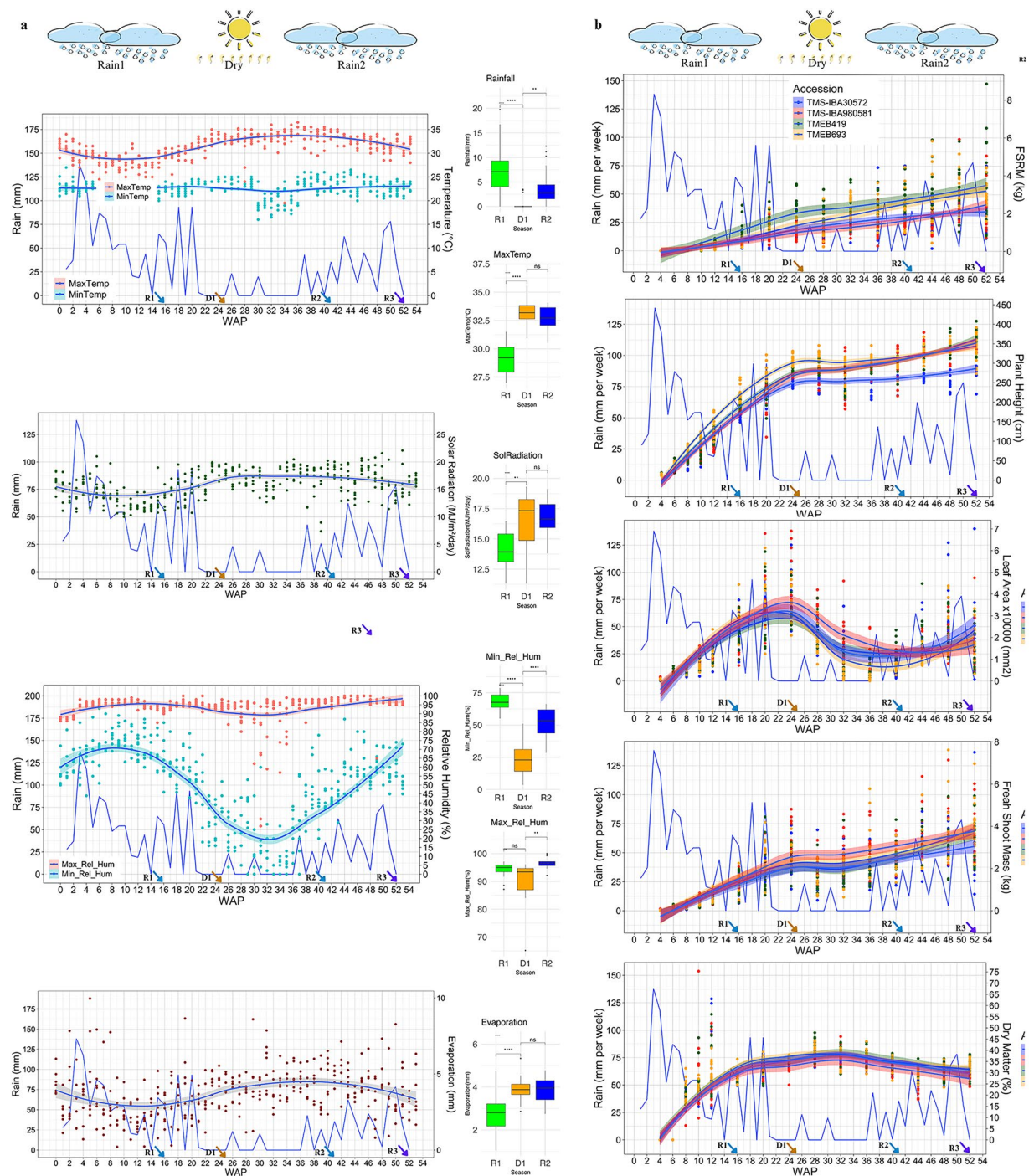


Fig. 1 Weather parameters and cassava agronomical trait trends across seasonal transitions. **(a)** Weekly average of daily measurements of weather parameter: temperature ($^{\circ}\text{C}$), relative humidity (%), solar radiation (MJ/m^2), and evaporation (mm). Alongside box plots summarizing these averages. The rainfall graph (mm) indicates the cumulative rain per week. **(b)** Trends of agronomical traits, including fresh storage root mass (FSRM, kg), plant height (PH, cm), leaf area (LA, mm^2), shoot mass (kg), and dry matter content (DM, %) across the seasonal transitions. Data represent the average of 12 replicate for each time point and each of the four genotypes (TMEB419, TMEB693, TMS30572, TMS980581). WAP, week after planting. Arrows indicate key sampling points at 16 WAP (R1, Rain1), 25 WAP (D1, Dry), 41 WAP (R2, Rain2), and 52 WAP (R3, Rain3).

reducing leaf area, changing stomatal conductance to conserve water, modifying root architecture to enhance water uptake, and altering gene expression to regulate stress-responsive proteins^{9–11}.

Investigating the transcriptomic changes associated with these seasonal patterns is critical for understanding the mechanisms underlying cassava's resilience, with general implications for crop improvement under fluctuating climate conditions. While previous studies have considered cassava's drought responses under controlled

conditions, understanding its adaptation to natural seasonal transitions remains limited. Controlled environments often fail to capture the complexity of field environments, where multiple stressors interact dynamically.

Based on this foundation, this study adopts a broader approach by profiling transcriptomes of field-grown cassava across natural seasonal transitions within a single growing season. We applied 3'mRNA Illumina sequencing, reducing sequencing depth and costs and allowing accurate quantification of gene expression. The depth and quality of obtained data confirms and encourages the use of such technology for comparative transcriptome analysis.

The discovery of shared gene expression patterns across four cassava genotypes, with diverse growth habits, disease resistance, and yield performance (Table S1), indicates common adaptive strategies to seasonal environmental changes, providing broadly applicable insights into its molecular responses useful for breeders and biotechnologists. Linking transcription factors to their target genes further validates the dataset. Unlike controlled studies, this field-based approach moves beyond controlled stress conditions, offering a dynamic perspective on cassava's natural adaptation to environmental changes.

Methods

Plant materials and experimental conditions. For this study, four cassava genotypes, TMEB419, TMEB693, TMS-IBA30572, and TMS-IBA980581 (Table S1), were cultivated in the field, in a randomized complete block design, at IITA Forest Reserve, Westbank (7.490708° N, 3.883849° E). Their growth parameters: plant height (PH), leaf area (LA), fresh shoot mass (FSM), fresh storage root mass (FSRM), and dry matter (DM), were monitored bi-weekly for the first 3 months (until bulking of storage roots) and then monthly during seasonal transitions (Growth parameters). Daily weather monitored at the IITA weather station throughout the growing season characterized the environmental conditions experienced by the crop and defined the seasonal transitions (Weather data). These sub-tropical seasonal transitions, from the first rainy season to the following dry season and to the second rainy season, coincide with pronounced variations in environmental conditions, including temperature, rainfall, solar radiation, evaporation, and relative humidity that can shape transcriptional reprogramming can shape transcriptional reprogramming, and were, therefore, monitored throughout the field experiment (Fig. 1a).

To expand the possibility to use these transcriptomic data in future analysis, we also measured agronomical traits indicative of cassava's physiological and developmental responses to seasonal transitions. (Fig. 1b).

RNA extraction and sequencing. For transcriptomic analysis, storage root of the four field-grown genotypes were sampled in triplicate at four time points: R1, 16 WAP during Rain1; D1, 25 WAP during Dry, R2, 41 WAP at start of the Rain2, and R3, at 52 WAP during the second rains (Fig. 1).

Destructive samples comprised a mixture of three different roots for each plant replicate. Total RNA was extracted from storage root tissue of the four above-mentioned genotypes (3 independent biological replicates per genotype) by combining cetyltrimethylammonium bromide (CTAB)-extraction method and spin-column based purification¹². The purified RNA was resuspended in RNase-free water, and RNA quality was preliminarily assessed using a NANODROP 8000 spectrophotometer (Thermo Scientific, Waltham, MA USA). RNA samples with OD260/280 and OD260/230 values ranging between 1.9 and 2.2 were selected for further analysis. The RNA integrity was then assessed by gel electrophoresis using 1.2% agarose gel with 1 × Tris/Borate/EDTA buffer (Sigma-Aldrich, St. Louis, MO, USA), at 80 V for 40 minutes. Based on this analysis, samples were selected for 3'mRNA-Seq library preparation according to the manufacturer's protocol (Quant Seq, Lexogene, Vienna, Austria). Sequencing was performed on an Illumina NextSeq 500 platform, generating 75-bp single-end reads.

RNAseq processing, quality control, and mapping. Raw reads were mapped against the reference genome of *Manihot esculenta* v8.0 in Phytozome¹³ using the splicing site-sensitive mapping tool STAR v2.4.1c and STAR index, including the corresponding GFF annotation file. STAR parameters were set to eliminate low-quality mappings and include: i) only reads aligning with matching read fragments longer than 50% of the full read length, ii) only matching read fragments with less than 4 mismatches (6% of the total read length and iii) only alignments with a score higher than 66% of the full length.

Pre-processing and quantification of transcripts. An in-house-developed Perl script (<https://github.com/gisels4/3primeTag/>) was used to parse the STAR mapping file and create clusters of overlapping read hits. The number of reads in each cluster was counted, reflecting the expression level for each gene (cluster). Within each cluster, the script searched for reads with a polyA tail that had been soft clipped by the STAR aligner. The poly A tail is an indication that the cluster indeed represents the end of a transcript. However, we expect that some clusters, although representing a transcript, is missing reads with a poly A tail. Therefore, the script compares the biological replicates and selects only clusters with at least two poly A tails containing reads and at least one cluster within the three biological replicates should contain these two reads with a poly A tail. The output of this script was a count matrix for each annotated gene across all samples and replicates.

Normalization of gene expression data. Gene-level read counts were analyzed using R v4.4.1 and the DESeq 2 package v1.44.0¹⁴. Raw count matrices were first filtered to exclude low-expression genes (defined as having <5 counts in fewer than 3 samples) to reduce noise and improve statistical power. Filtered counts were then normalized using DESeq 2's median-of-ratios method, which corrects for sequencing depth and compositional differences across libraries by estimating size factors per sample¹⁵. To stabilize variance across a wide range of mean expression values, we applied DESeq 2's variance-stabilizing transformation (VST). The VST approach mitigates the heteroscedasticity inherent in count data, producing a log2-like transformed matrix appropriate for unsupervised analyses¹⁴. This transformed matrix was used for all downstream clustering, dimensionality reduction, and correlation analyses.

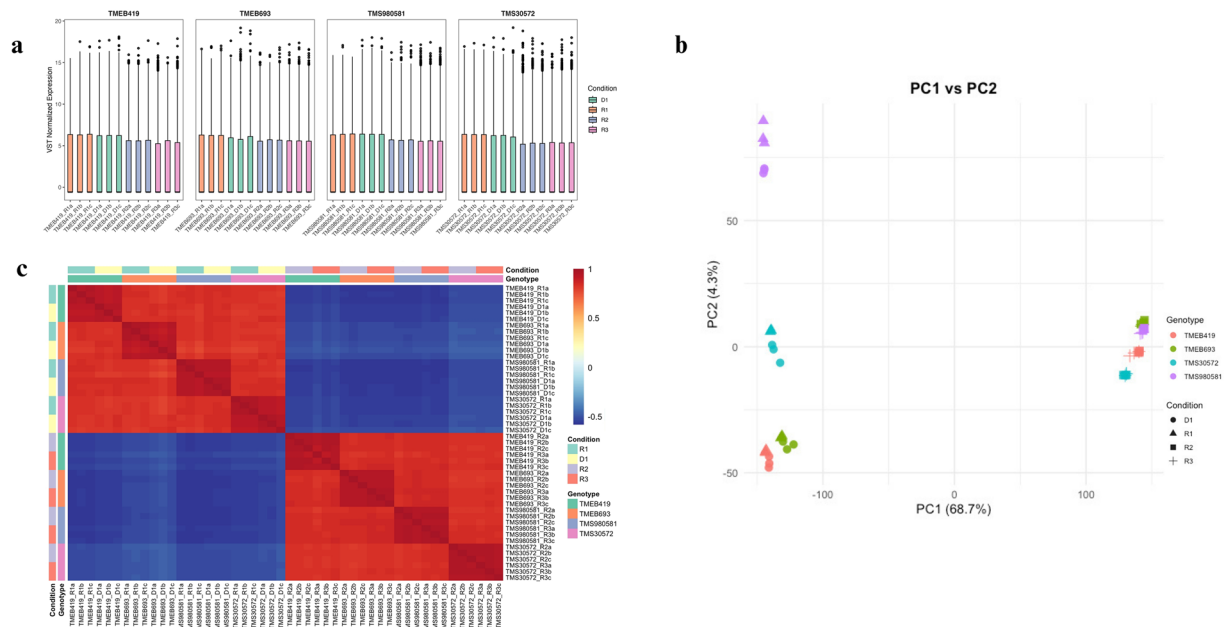


Fig. 2 Quality assessment and exploratory analysis of RNA-seq data. **(a)** Box plots of variance-stabilized transformed (VST) expression values across all expressed genes for each RNA-seq sample. Boxes represent the interquartile range (IQR), with the central line indicating the median. Samples are grouped by genotype and condition, demonstrating consistent normalization, minimal technical variability, and absence of extreme outliers, supporting data quality and comparability for downstream analyses. **(b)** Principal component analysis (PCA) plots based on VST-normalized counts. Left panel: PC1 (68.7% variance) versus PC2 (4.3%), capturing major variance and separating samples by genotype and condition and demonstrating the low variability between biological replicates. **(c)** Heatmap of pairwise Pearson correlations between samples, computed from VST-normalized gene expression. Color scale ranges from low (blue) to high (red) correlation. High intra-group correlations and distinct inter-group patterns confirm replicate consistency and transcriptional divergence driven by genotype and condition.

Principle component analysis. Unsupervised principal component analysis (PCA) was performed using base R on the VST-transformed expression matrix, with centering and scaling enabled. The first two principal components (PC1 and PC2) captured 68.7% and 4.3% of the total variance, respectively. These components effectively separated samples according to genotype and physiological condition, reflecting dominant biological signals. To interrogate treatment-specific transcriptional shifts, separate PCA analyses were conducted on sample subsets (e.g., rain-to-dry and dry-to-rain comparisons), highlighting condition-dependent expression patterns.

Sample correlation and clustering. Sample-level consistency was assessed through Pearson correlation analysis of all pairwise sample comparisons using the VST data. Correlation matrices were visualized using the pheatmap package v1.0.12¹⁶, with hierarchical clustering applied to both rows and columns. Sample annotations by genotype and treatment were overlaid to validate grouping structure. The observed clustering confirmed strong within-group correlations and reproducibility of biological replicates. No technical outliers were detected.

Differential expression analysis. Gene expression data from three biological replicates per genotype at each time point (R1, D1, R2) were analyzed using DESeq2¹⁴. Comparisons were made across seasonal transitions (R1 vs D1 and D1 vs R2) and among genotypes. Genes with a log₂ fold change (LFC) greater than 0.5 or less than -0.5 and a false discovery rate (FDR) < 5% were designated as significantly differentially expressed genes (DEG).

Functional annotation of genes. Gene sets of shared DEG were annotated using the Database for Annotation Visualization and Integrated Discovery (DAVID)^{17,18} with Ensembl gene IDs as input (Gene annotation). Genes labeled as “unknown” were mapped by extracting unspliced transcript sequences from the *Manihot esculenta* version 8.0 genome using the BioMart (Phytozome). The sequences were queried using the PlantRegMap ID mapping tool^{19,20}, leveraging reciprocal best hits (RBHs) to link query sequences with annotated IDs. For uncharacterized genes, transcription factor (TF) prediction, TF target identification, and cis-regulatory element analysis were performed to explore potential functional roles.

Gene ontology and pathway enrichment analysis. Gene ontology (GO) enrichment analysis was conducted using the PlantRegMap GO enrichment tool, incorporating annotations from TAIR 10, UniProt-GOA, InterProScan, and RBHs with *Manihot esculenta* genes as background set. Significant GO terms were identified using Fisher’s exact test in TopGO (p-value ≤ 0.05; GO terms). Pathway enrichment analysis of shared DEGs (intersecting all genotypes per transition) was performed using ShinyGO V0.77²¹. Genes were queried

Genotype	Time point	Samples (n)	Input reads (million)	Uniquely mapped (%)	Multi-mapped (%)	Avg. mapped length (nt)	Mismatch rate (%)
TMEB419	R1	3	9.5–14.9 (mean 11.7)	81.9–92.6 (mean 87.9)	5.8–9.1 (mean 7.6)	69.2–71.7	1.14–1.26
	D1	3	13.1–22.5 (mean 18.0)	81.8–87.5 (mean 83.8)	7.9–9.5 (mean 8.8)	68.5–69.8	1.26–1.32
	R2	3	10.4–12.8 (mean 11.9)	79.9–86.9 (mean 84.1)	9.4–15.7 (mean 12.3)	66.5–69.5	1.07–1.15
	R3	3	7.8–12.7 (mean 9.8)	77.3–88.9 (mean 81.9)	9.1–15.6 (mean 13.4)	65.5–69.8	1.04–1.21
TMEB693	R1	3	11.3–24.8 (mean 16.6)	85.7–87.3 (mean 86.7)	8.3–8.6 (mean 8.4)	70.0–70.6	1.16–1.18
	D1	3	8.4–14.2 (mean 11.7)	66.5–91.1 (mean 80.1)	6.1–9.2 (mean 7.8)	67.0–69.6	1.18–1.32
	R2	3	10.3–15.2 (mean 13.1)	75.1–94.4 (mean 85.3)	5.1–16.8 (mean 10.7)	66.1–71.6	0.92–1.18
	R3	3	9.1–10.0 (mean 9.6)	80.5–89.1 (mean 85.7)	8.9–15.3 (mean 11.4)	66.7–69.6	1.03–1.12
TMS980581	R1	3	11.4–19.6 (mean 15.0)	84.1–91.8 (mean 87.7)	6.4–8.9 (mean 7.9)	69.4–71.4	1.11–1.23
	D1	3	13.3–17.6 (mean 16.1)	85.9–89.5 (mean 88.0)	7.0–8.2 (mean 7.6)	69.9–70.9	1.14–1.21
	R2	3	10.0–15.7 (mean 12.9)	85.7–94.4 (mean 89.7)	4.8–10.4 (mean 7.7)	69.1–72.3	0.98–1.02
	R3	3	10.9–11.7 (mean 11.2)	89.8–91.1 (mean 90.5)	7.2–8.2 (mean 7.6)	69.8–71.0	1.02–1.03
TMS30572	R1	3	18.9–22.2 (mean 20.3)	87.6–89.9 (mean 88.9)	7.3–7.9 (mean 7.6)	70.7–70.9	1.23–1.28
	D1	3	11.0–23.9 (mean 17.6)	81.4–90.0 (mean 86.8)	6.9–7.7 (mean 7.4)	69.9–70.5	1.25–1.27
	R2	3	9.4–12.1 (mean 10.8)	89.1–92.8 (mean 90.9)	5.4–7.6 (mean 6.7)	69.9–72.0	1.07–1.20
	R3	3	10.0–15.2 (mean 12.4)	88.8–90.4 (mean 89.8)	8.0 (consistent)	70.1–70.2	1.09–1.12

Table 1. Summary of sequencing and mapping statistics. RNA-seq libraries (n = 48) from four cassava genotypes (TMEB419, TMEB693, TMS980581, and TMS30572) sampled during four seasonal time points (R1, D1, R2, and R3). Values represent the range and mean across three biological replicates per genotype × time point. Shown are input reads (in millions), uniquely mapped reads (%), multi-mapped reads (%), average mapped read length (nt), and per-base mismatch rate (%).

against the PlantGSAD database²² which integrates KEGG pathways including cellular and viral pathways^{23,24} (KEGG pathways).

Genes re-regulation analysis. DEG that were common across all genotypes (shared DEG) in both transitions were analyzed for re-regulation. A gene was considered re-regulated if it met one of the following criteria: (i) it was a sigDEG in one transition (log2 fold change ≥ 0.5, FDR < 5%) but not in the other, or (ii) its expression pattern was reversed between transitions (i.e., shifting from upregulation to downregulation or vice versa).

Transcription factors identification and enrichment. TFs were predicted from input nucleic acid sequences of shared gene sets using PlantTFDB v5.0, following established family assignment rules^{19,25}. Briefly, input sequences were first processed with EST Scan 3.0 to identify coding regions (CDS) and they were then translated into proteins sequences. TF families were assigned based on the best hit in *Arabidopsis thaliana*. Enrichment analysis was performed using PlantRegMap²⁰, which integrates data from literature, ChIP-seq experiments, and motifs-binding analyses. Fisher’s exact test was used to assess significant enrichment of TF families among target genes at p-value ≤ 0.05.

Technical Validation

Quality control. We sequenced, on average, 13.6 million 3’ mRNA-Seq reads per sample, generated a total of 49.86 Gb across 48 libraries from four cassava genotypes (TMEB419, TMEB693, TMS30572, TMS980581) sampled at four seasonal transition time points (R1, D1, R2, R3), sequencing yielded between ~7.7 and 24.8 million reads per library. Read quality exceeded a score per position of 28 for nearly all libraries (except one sample), with average scores between 28–35.

Mapping quality. 66.5–94.4% (average 86.6%) mapped uniquely to the *Manihot esculenta* version 8.0 reference genome, with a mean mapped read length of ~70 nt (from 76 bp raw reads), a per base mismatch rate of 0.9–1.3%, and 4.8–16.8% mapping to multiple loci. These values indicate good mapping quality and dataset reliability. Consistent expression distribution among replicates further supported data quality (Fig. 2a). Summary statistics by genotype and time point are shown in Table 1, with full replicate level details in Supplementary Fig S2. PCA of full variance-stabilized expression matrix showed a clear structure, with PC1 and PC2 explaining 68.7% and 4.3% of the total variance, respectively (Fig. 2b). A complementary heatmap supports the PCA results, demonstrating reproducible biological signal across replicates and grouping patterns consistent with experimental design (Fig. 2c).

Stress-responsive gene dataset. To confirm the relevance and usability of our dataset, differential expression analysis across seasonal transitions identified extensive transcriptional reprogramming across all genotypes during seasonal transitions as visualised in the heatmaps, the percent proportion of the up- and down-regulated genes, and the UpSet plot matrices of unique and shared genes between genotypes (Fig. 3). During R1-D1, 1,837 DEG were identified, of which 52–60% were downregulated (Table 2). In D1-R2, 830 DEG were found, with 45–51% upregulated. These DEG included well-characterized stress-responsive genes, such as aquaporin PIP2-1 (reduced water loss), osmotic-like proteins (osmotic balance), chaperone protein dnaJ, (protein stabilization), and galacturonosyltransferase 8 (GAUT8), essential for cell wall remodeling. We further identified 26 re-regulated

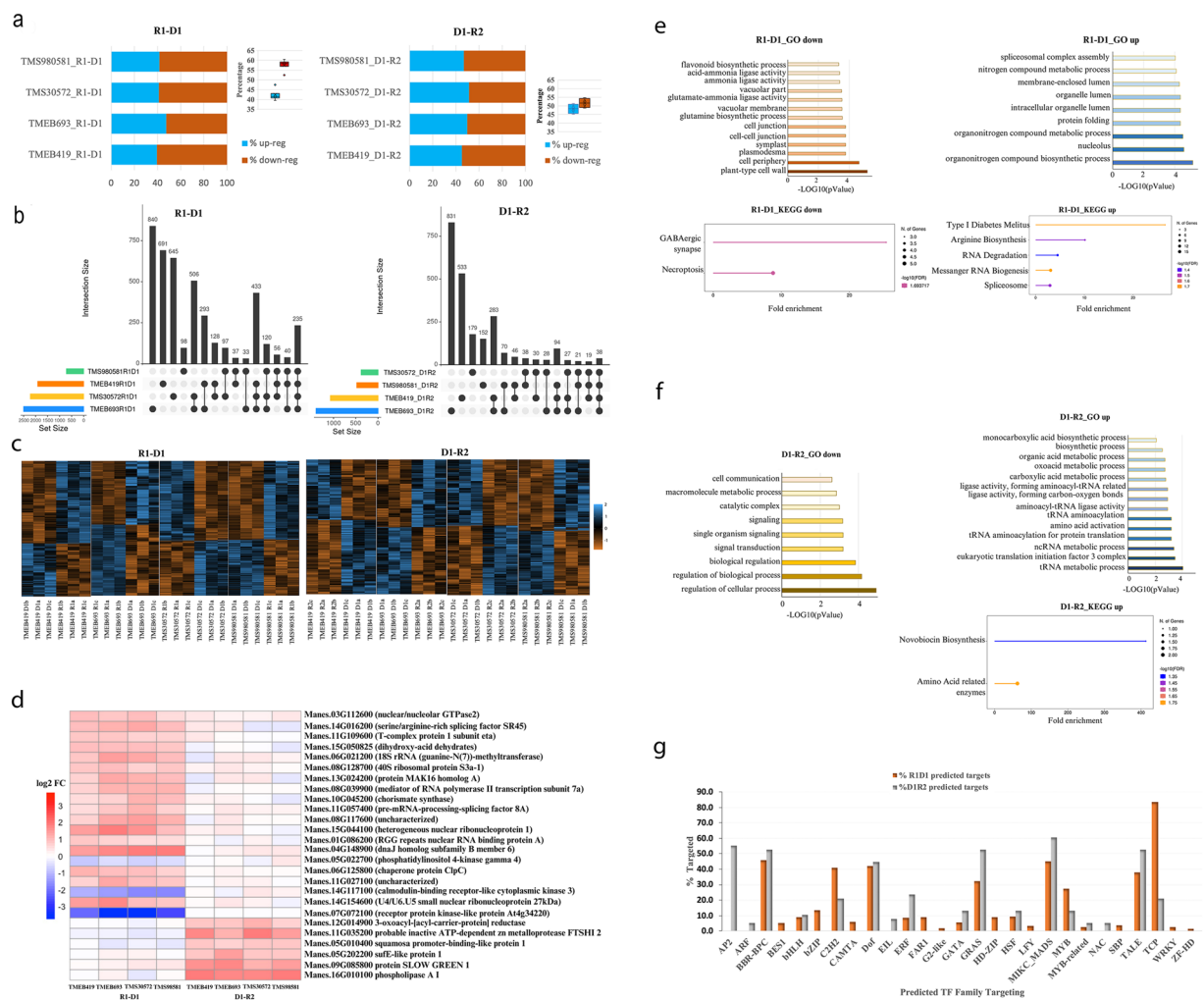


Fig. 3 Gene dataset functional validation **(a)** Percentage proportions of the up- (blue) and down- (brown) regulated genes, and in-set the proportion range among genotypes. **(b)** UpSet plot matrices showing unique genes (single dot) and shared genes (linked dots) within genotypes. Color bars on a scale next to plots indicate gene set size. **(c)** Hierarchically clustered heatmaps per genotype for all sigDEGs revealing up- (blue) and down- (brown) regulated gene expression differences in R1 vs D1, and D1 vs R2 comparisons. **(d)** Shared genes that were differentially expressed in genotypes below or above the threshold ($\log_2 FC$ 0.44, FDR = 5%) and changed to above or below the threshold in the subsequent transition comparison were considered relatively re-regulated (heatmap scale = \log_2 Fold Change). **(e)** Enriched GO terms and KEGG pathways in shared genes R1-D1 downregulated (left) and R1-D1 upregulated (right). **(f)** Enriched GO terms and KEGG pathways in shared genes D1-R2 downregulated (left) and D1-R2 upregulated (right). **(g)** Target TF families and percentage (%) proportion of predicted targets in shared SigDEGs of R1-D1 (Orange) and D1-R2 (Grey) transitions.

genes that returned to baseline expression with the return of the rain season (D1-R2) after stress removal consistent with transcriptional resetting during rehydration (Fig. 3d). Their dynamic expression aligns with known stress-recovery mechanisms, confirming the dataset's utility for studying transcriptional resetting. Enrichment analysis confirmed the involvement of GO and the KEGG pathways associated with abiotic stress and recovery during seasonal transitions (Fig. 3e, f). TF family enrichment revealed both shared (HSF, TCP, bZIP, MYB, Dof) as well as transition specific regulators such as bZIP, BES1, and HD-ZIP in R1D1, and AP2, ARF, and NAC in D1-R2, suggesting seasonal-specific regulatory roles (Fig. 3g).

Our dataset analysis reveals a dynamic blueprint of cassava molecular resilience and can be useful for the study of stress response to climate changes. This stress response comprises a cascade of fundamental elements, including the perception of stress, signal transduction, activation of stress responses or gene regulation/alteration, and subsequent adaptation/acclimation that we have summarized in Supplementary Fig. S1 to facilitate further use of the dataset. Finally, we provide a table of genes and pathways to be considered as potential actionable targets for drought mitigation and recovery strategies (Actionable targets). Experimental validation of these key genes and pathways, combined with field-based studies, will be crucial for translating these into strategies for breeding climate-resilient cassava varieties.

Season transition	Genotype	DEG		
		Up regulated	Downregulated	Total
R1-D1	TMEB419	756	1157	1913
	TMEB693	1188	1312	2500
	TMS30572	915	1305	2220
	TMS980581	298	418	716
	mean	789	1048	1837
D1-R2	TMEB419	484	586	1070
	TMEB693	694	698	1392
	TMS30572	195	185	380
	TMS980581	224	254	478
	mean	399	431	830

Table 2. Number of significantly Differentially Expressed Genes (DEG) identified at a >0.5 logfold change (LFC) threshold and <5% false discovery rate in each genotype and season comparison.

Data Records

High-throughput sequencing data supporting this study’s findings have been deposited at ENA European Nucleotide Archive²⁶.

In addition, plant growth parameters, weather data, gene annotations, GO terms, KEGG pathways, transcription factors (TF) targets, and actionable target genes are uploaded to Zenodo²⁷ (<https://doi.org/10.5281/zenodo.15545011>).

Data availability

High-throughput sequencing data supporting this study’s is accessible without restriction in the ENA European Nucleotide Archive under the following link: <https://identifiers.org/ena.embl:PRJEB79515> (2024). All metadata datasheets: plant growth parameters, weather data, gene annotations, GO terms, KEGG pathways, transcription factors (TF) targets, and actionable target genes are accessible in the Zenodo repository under the following link: (<https://doi.org/10.5281/zenodo.15545011>).

Code availability

Software and their versions used for RNA-seq analysis were described in Methods. Custom codes are available at <https://github.com/gisels4/3primeTag>.

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Author contributions

M.W.-B., L.S., A.G., E.A.: designed the research. M.W.-B., J.E.I., A.G.: performed experiments and data analysis. M.W.-B., L.S., A.G.: wrote the manuscript. M.W.-B., L.S., A.G., E.A.: reviewed and edited the manuscript. All authors read and approved the final manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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