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Research Article

Identification of Genes Related to Cellular Respiration in *Musa acuminata* as Response to Water Stress

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Abstract

Background and Objective: The growth and productivity of banana plants can be disrupted due to water stress. The response of banana plants could be different at the molecular level based on the severity of water stress. This study aimed to profile gene expression in the glycolysis pathway affected by different water stress levels in banana plantlets. **Materials and Methods:** A transcriptome dataset from four cDNA libraries was used to profile the expression of genes related to cellular respiration. The cDNA libraries were generated from *Musa acuminata* (genome AAA, cv. Barangan Merah) plantlets treated at different levels of water stress, i.e., low (2.5% PEG), moderate (7.5% PEG) and high (10% PEG). The transcriptome data were analyzed using DAVID, KEGG and DeSeq2 software. **Results:** Based on DAVID there were 13 genes in glycolysis affected by water stress which were grouped in 6 family proteins. Predominantly, all genes identified in the glycolysis pathway were upregulated in high-stress levels. The 4 family proteins contribute to pyruvate metabolism, while 2 family proteins contribute to fermentative metabolism. It could be indicated that water stress led to hypoxia, so the energy must be produced using anaerobic metabolism. The *MaFBA6*, *MaFBA8* and *MaPDCB* genes were selected and used to validate mRNA-seq and transcriptome analysis. **Conclusion:** Banana plantlets respond to water stress by increasing the expression of glycolysis-related genes. With transcriptomic analysis, respiration-related genes can be identified to add to regarding banana plants' response to water stress.

Key words: Cellular respiration, glycolysis, hypoxia, *Musa acuminate*, transcriptome, water stress

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Competing Interest: The authors have declared that no competing interest exists.

Data Availability: All relevant data are within the paper and its supporting information files.

INTRODUCTION

Water stress is one of the major abiotic factors limiting banana production. On the other hand, the increase in world population causes climate change which adversely affects plant productivity, so the agricultural sector is facing a new challenge to produce plants that are more tolerant of environmental stresses[1]. *Musa acuminata* cv. Barangan Merah, a staple food in Southeast Asia, is grown in tropical areas affected by climate change. Climate change causes erratic rainfall, so banana plant productivity often declines due to the unavailability of water[2]. Banana plants as commercial crops in Indonesia can be affected by water stress, which often is associated with enhanced oxidative damage[3]. To survive, plants respond and adapt to water stress through morphological, physiological, biochemical and molecular changes.

At the morphological levels, changes occur in the number of leaves, roots and plant height. Also, changes in the color of the leaves to yellowish, lead to browning and wilting[4]. At the physiological and biochemical levels, drought-induced stomatal closure, a decrease of chlorophyll content, osmolyte accumulation and reactive oxygen species (ROS) scavenging mechanism[5]. In addition, some protective proteins, such as dehydrins, heat shock proteins and late embryogenesis abundant proteins, are synthesized. This response is a strategy for plants to cope with water stress. At the molecular level, water stress induces signal transduction, drought-responsive transcription factor, protein kinase and secondary metabolite biosynthesis[6]. The molecular response of banana plants to water stress may vary depending on severity, so better knowledge is still needed to reveal the tolerance mechanism in the banana plant.

Knowledge of molecular responses can be studied with a transcriptomic approach. With the development of high-throughput DNA sequencing technology, Next-Generation Sequencing (NGS) can be used to understand transcriptome profiles and their quantity. The NGS technology has been widely studied to obtain transcriptome datasets from banana plants such as *M. acuminata*, *M. balbisiana* and *M. paradisiaca*[6,7].

In other studies, NGS technology was applied to generate a transcriptome dataset of *in vitro* banana plantlet *M. acuminata* cv. Barangan Merah. The 4 cDNA libraries from the water stress treatment induced by polyethylene glycol 6000 (PEG): Control (without PEG), low-stress level (2.5% PEG), moderate stress level (7.5% PEG) and high-stress level (10% PEG) were then sequenced using Illumina MiSeq™2000 and generated transcriptome data which was used as a reference in this study. This study's transcriptome dataset was registered and uploaded to the NCBI BioProject database (BioProject ID PRJNA970186). The statistics of transcriptome analysis showed that 104,118, 407 nucleotide bases had been identified and successfully assembled into 147, 811 contigs. In addition, gene ontology enrichment analysis showed that five major biological processes are affected by water stress, i.e., photosynthesis, response to stress, cellular respiration, morphogenesis, organ development and secondary metabolite biosynthesis.

Cellular respiration is a catabolism process of organic compounds into inorganic that occurs both aerobically and anaerobically. Cellular respiration is a mechanism in energy conversion to produce ATP used for many processes in growth and development. Research on bananas exposed to mild osmotic stress shows an increase in energy demand, which enhances aerobic respiration and leads to hypoxia[2]. Based on the transcriptome analysis results, cellular respiration is one of the biological processes affected by water stress in banana plants. In water-stressed conditions, plants can't absorb water from the medium and tend to close their stomata to avoid water loss. Hence, plants can't get oxygen, so anaerobic processes tend to produce energy. This process may lead to an increase in the process of glycolysis and fermentation to have energy. Increased respiration can also lead to a decrease in oxygen content, resulting in anoxia in plants[8]. Therefore, transcriptome profiling in this process must be analyzed and validated to ensure that the analyzed transcriptome data can reveal the mechanism of banana plant response to water stress at different stress levels.

In the present study, transcriptome data from banana plantlets exposed to different stress levels were analyzed to get information about the response mechanism of bananas against water stress. The reference transcriptome data were obtained from previous research and are currently being deposited in the NCBI database. The current study aimed to profile gene expression in the glycolysis pathway affected by water stress in banana plantlets. Therefore, transcriptome analysis was performed to identify genes related to glycolysis. Selecting some of the genes in glycolysis and validating them by Quantitative Real-time Polymerase Chain Reaction (qRT-PCR) in an independent experiment and confirming the success of RNA-seq for transcriptome profiling of banana plantlets exposed to water stress.

MATERIALS AND METHODS

Study area: The research was conducted in the Transformation and Micropropagation Laboratory, Plant

Science and Biotechnology, Institut Teknologi Bandung, Indonesia. This research was carried out from September, 2022 to February, 2023 consisting of transcriptomic analysis and analysis of gene expression by qRT-PCR.

Plant material, growth conditions and water stress treatment: *In vitro*, banana plantlets (*Musa acuminata* cv. Barangan Merah) were supplied by the Southeast Asian Regional Centre for Tropical Biology SEAMEO BIOTROP (Bogor, Indonesia). Plantlets were maintained in Murashige and Skoog medium[9] containing 2.5, 7.5 and 10% (w/v) PEG 6000. Plantlets grown on a medium without PEG were used as a control. Banana plantlets were grown for 30 days with a 16/8 hrs light/dark period and the temperature was kept constant at 25°C. These samples were used for RNA sequencing to produce four cDNA libraries. The transcriptome data set was used in this research study to analyze glycolysis-related genes. An independent experiment was set up for qRT-PCR validation, including three different PEG concentrations and control treatments.

Gene ontology enrichment and pathway analysis: The 4 cDNA libraries were used as references for transcriptomic analysis. Gene ontology (GO) terms were assigned using DAVID v6.7 (Database for Annotation, Visualization and Integrated Discovery) that links into KEGG (Kyoto Encyclopedia of Genes and Genomes) to perform pathway prediction. Transcriptome data for DAVID were analyzed and identified as *Arabidopsis thaliana* orthologous gene. The GO terms related to glycolysis were selected and analyzed using KEGG to determine specific gene products.

Differential gene expression analyses and selection of candidate genes: The DEG analysis was performed on transcriptome data using DESeq2 software. Transcripts per Million reads (TPM) was used as the DEG evaluation parameter and the genes were grouped based on the ratio of TPM to control. Different gene expressions were analyzed with a cutoff ratio of $\log_{10}>1$ to obtain a list of genes that were affected more than 10 times compared to the control[8]. A total of 3 candidate genes involved in high-stress levels were selected for subsequent analyses. Analysis was performed to validate the mRNA-seq and differential gene expression analysis.

Design and optimization of RT-qPCR primers: Each candidate gene and housekeeping gene were designed using Primer3Plus (Table 1). Chosen parameters were product size range 100-250 bp, primer size 20-22 bp, primer Tm 57-60°C (with maximum Tm difference = 2°C) and GC content 45-60%. Primers were synthesized by the supplier (Macrogen, Singapore) and the primers were optimized and tested at 10 nM concentration for electrophoresis and qRT-PCR. The PCR products were run in a 2% agarose gel for electrophoresis and stained using EtBr. The melting curves in qRT-PCR were checked to confirm a single product in PCR.

qRT-PCR analysis and determination of gene expression levels: For qRT-PCR validation of gene expression levels, total RNA was isolated from the independent experiment. The RNA was extracted from four samples with different water stress treatments using CTAB methods described by Diningrat *et al.*[10]. RNA quality and quantity were measured using Nanodrop™ Lite Spectrophotometer (Thermo Scientific, USA) and confirmed by gel electrophoresis in 1.5% agarose. The cDNA was reverse transcribed of total RNA using the GoScript™ Reverse Transcription kit (Promega, USA). The cDNA synthesis reaction was done by incubating for 5 min at 25°C, followed by incubation for 1 hr at 42°C and deactivating reverse transcriptase for 15 min at 70°C. Validation of gene expression was performed by reverse transcriptase qRT-PCR using QuantStudio 1 (Thermo Scientific, USA). The qRT-PCR was performed using GoTaq® qPCR Master Mix according to the manufacturer manual (Promega, USA). The PCR reaction was done following the procedure from Diningrat *et al.*[10], with some optimization. The reaction program started with pre-denaturation at 95°C for 15 min, followed by 40 cycles of polymerization (15 sec at 95°C, 30 sec at 58°C and 30 sec at 72°C). The 3 technical replicates were performed in the qRT-PCR assay.

Table 1: Primer pairs for the selected genes and housekeeping genes

Gene	Functional annotation	Account number	Forward	Reverse	Product size (bp)
MaACT	Actin	Ma10_p01140.1	CTGACTGGCAGCAGGACATA	CCAAATCGTGCCTTTGAACT	162
MaBT	Beta tubulin	Ma01_p13380.1	AGTCCGGAGCTTCAACCTTT	ACGCTGACGATGGAGAAGAC	221
MaFBA6	Aldolase (FBA6)	Ma05_p27790.1	CTCAGGAGGGCAGAGTGAAG	CTCGCCTTCTCGACATTCTC	162
MaFBA8	Aldolase (FBA8)	Ma05_p27790.1	GAGGCACATCTCCCTCTGAT	TCAGAGAGCCTCCATGTCAA	245
MaPDCB	Thiamine pyrophosphate-dependent pyruvate decarboxylase	Ma05_p30490.1	TGTGCTTCATCGAGGTCATC	AGTCTCGGACGCAAGAACAT	215

Statistical analysis: The DESeq2 in R software version 1.2.5001 was used to perform statistical analysis for DEG by comparing gene expression between control and experimental groups. The SPSS software version 23.0 was used to analyze all gene expression data, with One-way Analysis of Variance (ANOVA). Differences in mean values were considered statistically significant at p<0.05.

RESULTS

Gene ontology and differentially expressed genes (DEGs): This enrichment analysis points towards an essential function in cellular respiration. Analysis of DAVID and KEGG revealed that the glycolysis/gluconeogenesis pathway was induced in all stress levels. In general, 13 genes identified in the glycolysis pathway can be classified into 6 family proteins, i.e., aldolase, alcohol dehydrogenase, phosphoglycerate mutase, pyruvate kinase, pyruvate decarboxylase and glyceraldehyde-3-phosphate dehydrogenase. Genes identified as aldolase family proteins were *MaFBA6*, *MaFBA8* and *MaPDE345*. Genes identified as alcohol dehydrogenase were *MaHOT5* and *MaADH1*. Genes identified as phosphoglycerate mutase were *MaiPGAM1*. Genes identified as pyruvate kinase were *MaPKA* and *MaPKB*. Genes identified as pyruvate decarboxylase were *MaPDC2*, *MaPDCA* and *MaPDCB*. Finally, genes identified as glyceraldehyde-3-phosphate dehydrogenase were *MaGAPC2* and *MaGAPCP-1*.

All genes were analyzed using DESeq2 to gain information on differential gene expression to gain a broader overview of the changes in the glycolytic pathway. In total, 13 genes were identified in the glycolysis pathway, listed in Table S1. Most genes were identified in high-stress levels, while four different genes were identified in low and moderate stress levels. For example, gene *Ma05_p27790.1* (aldolase, *MaFBA6*) was downregulated at low and upregulated at moderate and high-stress levels. Meanwhile, other genes were upregulated in all stress levels (Fig. 1). Pathway visualization using KEGG showed that the affected genes were focused on acetaldehyde production (Fig. 2, Table 2).

Validation of genes by quantitative real-time PCR (qRT-PCR): A subset of three genes affected by water stress in banana plantlets was selected for validation to confirm the statistical analysis's accuracy and robustness. Therefore, an independent experiment was set up with three different PEG concentrations and control treatments. Three genes (*MaFBA6*, *MaFBA8* and *MaPDCB*) were validated using qRT-PCR with 2 house keeping genes (*MaACT* and *MaBT*). Agarose gel electrophoresis of the PCR products showed that each gene had a single band and suit into their PCR product size (Fig. 3). In general, relative gene expression values were similar to mRNA-seq. For example, gene *MaFBA6* was downregulated in low and upregulated in high-stress levels. Similarly, *MaFBA8* and *MaPDCB* genes were upregulated in all stress levels (Fig. 4).

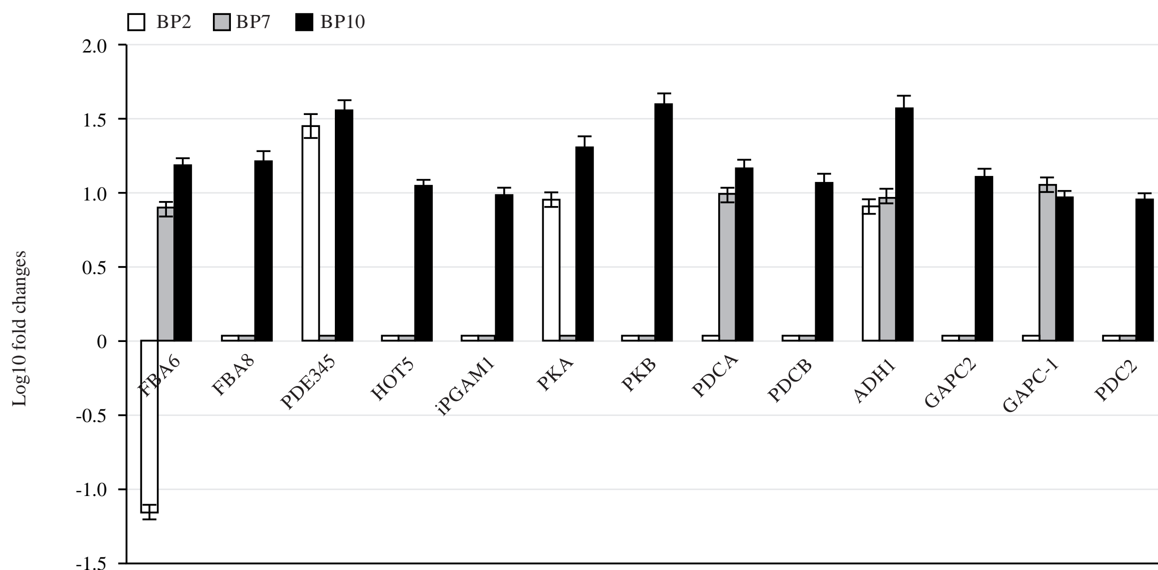

Fig. 1: Relative expression of the genes affected by water stress in banana plantlets under PEG treatments at 2.5% (BP2), 7.5% (BP7) and 10% (BP10) based on mRNA-seq, DEGs were normalized to the control (BK)

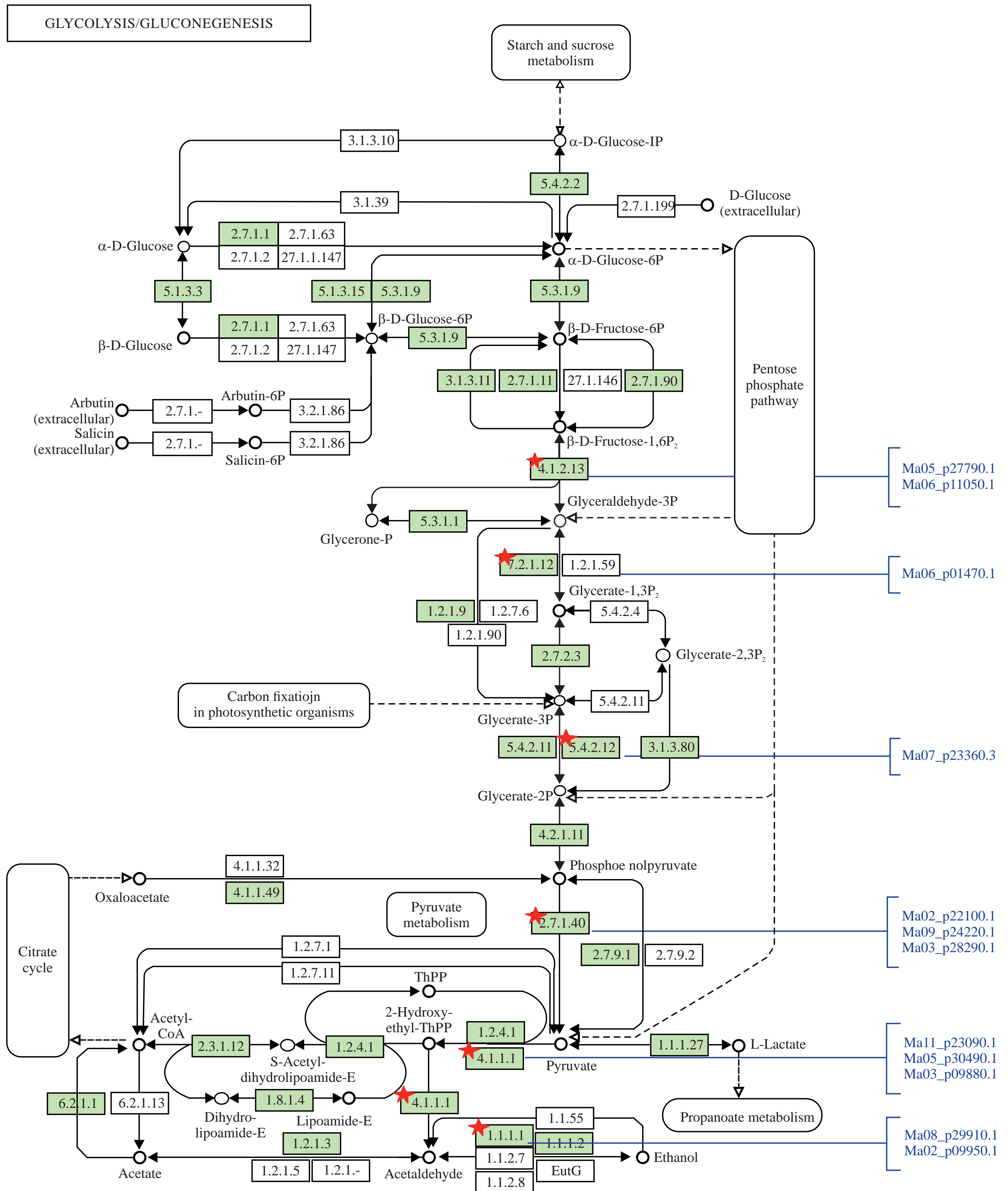

Fig. 2: Water stress affects glycolysis/gluconeogenesis of banana plantlets based on the KEGG pathway illustration

Red stars indicated genes altered by drought stress in the BP10 sample

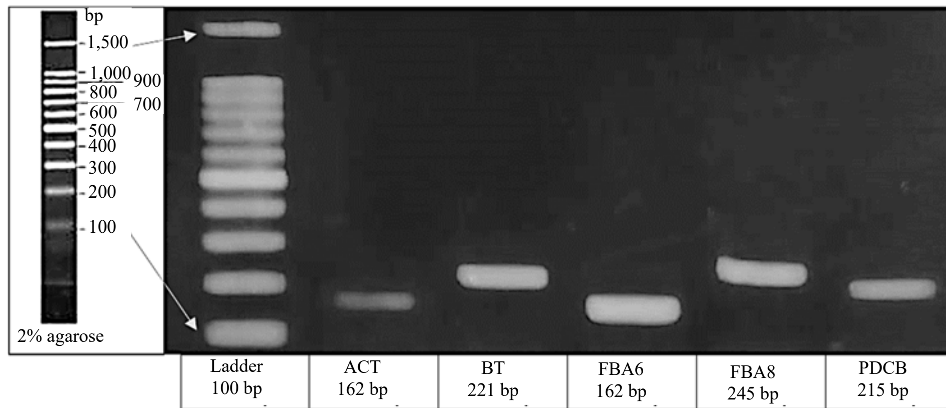

Fig. 3: Agarose gel electrophoresis of the PCR products for genes affected by water stress in banana plantlets, 100 bp ladder was used to compare the PCR band with the amplicon size

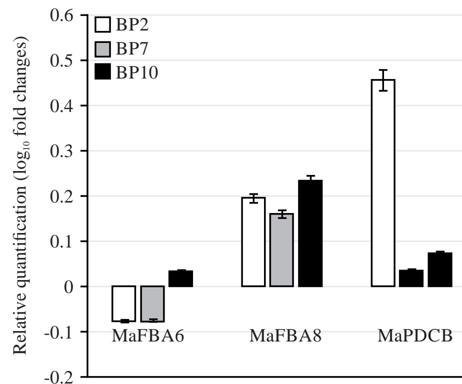

Fig. 4: Relative gene expression value of *Ma05_p27790.1* (aldolase, *MaFBA6* and *MaFBA8*), *Ma05_p30490.1* (Thiamine pyrophosphate dependent pyruvate decarboxylase family protein B, *MaPDCB*) genes in BP2, BP7 and BP10 sample based on qRT-PCR

Table S1: Expression profile of 13 glycolysis/gluconeogenesis-related genes based on mRNA-seq

TAIR_ID	Musa ID	Abbreviation	Gene name	Relative expression values (log10 fold changes) at different water stress levels		
				BP2	BP7	BP10
AT2G36460	Ma05_p27790.1	MaFBA6	Aldolase superfamily protein	-1.1528	0.9046	1.1862
AT3G52930	Ma05_p27790.1	MaFBA8	Aldolase superfamily protein	0	0	1.2263
AT2G01140	Ma06_p11050.1	MaPDE345	Aldolase superfamily protein	1.4602	0	1.5560
AT5G43940	Ma08_p29910.1	MaHOT5	GroES-like zinc-binding dehydrogenase family protein	0	0	1.0448
AT1G09780	Ma07_p23360.3	MaiPGAM1	Phosphoglycerate mutase, 2,3-bisphosphoglycerate-independent	0	0	0.9885
AT2G36580	Ma02_p22100.1	MaPKA	Pyruvate kinase family protein A	0.9612	0	1.3203
AT5G08570	Ma09_p24220.1	MaPKB	Pyruvate kinase family protein B	0	0	1.6033
AT4G33070	Ma11_p23090.1	MaPDCA	Thiamine pyrophosphate dependent pyruvate decarboxylase family protein A	0	0.9942	1.1722
AT5G01320	Ma05_p30490.1	MaPDCB	Thiamine pyrophosphate dependent pyruvate decarboxylase family protein B	0	0	1.0795
AT1G77120	Ma08_p29910.1	MaADH1	Alcohol dehydrogenase 1	0.9206	0.9849	1.5818
AT1G13440	Ma06_p01470.1	MaGAPC2	Glyceraldehyde-3-phosphate dehydrogenase C2	0	0	1.1121
AT1G79530	Ma06_p01470.1	MaGAPCP-1	Glyceraldehyde-3-phosphate dehydrogenase of plastid 1	0	1.0630	0.9685
AT5G54960	Ma05_p30490.1	MaPDC2	Pyruvate decarboxylase 2	0	0	0.9583

Table 2: List of genes affected by water stress in glycolysis/gluconeogenesis metabolism

Enzyme code	Musa ID	Abbreviation	Gene name
4.1.2.13	*Ma05_p27790.1*	*MaFBA6*	Aldolase superfamily protein
4.1.2.13	*Ma05_p27790.1*	*MaFBA8*	Aldolase superfamily protein
4.1.2.13	*Ma06_p11050.1*	*MaPDE345*	Aldolase superfamily protein
1.1.1.1	*Ma08_p29910.1*	*MaHOT5*	GroES-like zinc-binding dehydrogenase family protein
5.4.2.12	*Ma07_p23360.3*	*MaiPGAM1*	Phosphoglycerate mutase, 2,3-bisphosphoglycerate-independent
2.7.1.40	*Ma02_p22100.1*	*MaPKA*	Pyruvate kinase family protein A
2.7.1.40	*Ma09_p24220.1*	*MaPKB*	Pyruvate kinase family protein B
4.1.1.1	*Ma11_p23090.1*	*MaPDCA*	Thiamine pyrophosphate dependent pyruvate decarboxylase family protein A
4.1.1.1	*Ma05_p30490.1*	*MaPDCB*	Thiamine pyrophosphate dependent pyruvate decarboxylase family protein B
1.1.1.1	*Ma08_p29910.1*	*MaADH1*	Alcohol dehydrogenase 1
1.2.1.12	*Ma06_p01470.1*	*MaGAPC2*	Glyceraldehyde-3-phosphate dehydrogenase C2
1.2.1.12	*Ma06_p01470.1*	*MaGAPCP-1*	Glyceraldehyde-3-phosphate dehydrogenase of plastid 1
4.1.1.1	*Ma05_p30490.1*	*MaPDC2*	Pyruvate decarboxylase 2

DISCUSSION

Fructose 1,6-bisphosphate aldolase (FBA) is a key enzyme in plants involved in glycolysis and gluconeogenesis in the cytoplasm. These genes can catalyze the reversible condensation of D-glyceraldehyde 3-phosphate and dihydroxyacetone phosphate to form fructose 1,6-bisphosphate[11]. The FBA is also found in the Calvin cycle to catalyze the condensation of fructose-1,6-bisphosphate and the condensation of sedoheptulose-1,7-bisphosphate. FBA family was classified into 2 subfamilies in *Arabidopsis thaliana*, including 3 members (FBA1-3) occurring at the plastid and five (FBA4-8) localized in the cytoplasm[12]. In this study, *MaFBA6* and *MaFBA8* were affected by water stress in all stress levels. Interestingly, *MaFBA6* was downregulated in low and upregulated in high-stress levels. This pattern was also validated with qRT-PCR analysis. The *MaPDE345* gene (also called FBA3) has upregulated low and high-stress levels based on transcriptome analysis. Increased FBA gene expression was also reported in *Sesuvium portulacastrum* as a response to drought tolerance[13].

Glyceraldehyde-3-Phosphate Dehydrogenase (GAPDH) is an enzyme that converts glyceraldehyde 3-phosphate to glycerate-1, 3-bisphosphate. This reaction produced NADH and it catalyzed by GAPDH into NADPH in the cytoplasm[14]. The NADPH was synthesized through the pyruvate-oxaloacetate-malate cycle (POM cycle) for electron donor. In this study, 2 genes (*MaGAPC2* and *MaGAPCP-1*) were affected by water stress. The MaGAPC was specifically expressed in the cytosol, while *MaGAPCP-1* was expressed in the plastid. In glycolysis, these genes are essential to break down glucose for energy. Research conducted in *Arabidopsis thaliana* showed that GAPC2 was expressed higher simultaneously with sucrose concentration[15]. The upregulation of *MaGAPC2* and *MaGAPCP-1* indicates that sucrose was consumed higher to meet energy needs for survival capability.

The 2,3-bisphosphoglycerate-independent phosphoglycerate mutase (iPGAM) is a key enzymatic activity in glycolysis and catalysis of the reversible interconversion of 3-phosphoglycerate to 2-phosphoglycerate. In this study, *MaiPGAM1* was highly expressed in high-stress levels of water stress. Furthermore, research in *Arabidopsis thaliana* showed that iPGAM has a critical role in stomatal movement, vegetative growth and pollen production[16].

Pyruvate kinase catalyzes glycolysis's last step, essential for generating Adenosine Triphosphate (ATP). Pyruvate kinase can catalyze the phosphate group transfer from phosphoenolpyruvate (PEP) to adenosine diphosphate (ADP), yielding one molecule of pyruvate and one molecule of ATP. In this study, *MaPKA* and *MaPKB* were upregulated in banana plantlets exposed to water stress. Pyruvate kinase that is highly expressed indicates higher energy production in response to water stress conditions. In sugarcane, drought stress can induce pyruvate kinase gene expression[17]. Pyruvate kinase regulation in glycolysis is crucial under stress situations. Soluble sugars play an important role in plant metabolism as sources of carbon and energy in cells, therefore plants under stress have to constantly adjust the supply and usage of carbon.

Alcohol dehydrogenase (ADH) and pyruvate decarboxylase (PDC) are keys to establishing the fermentative metabolism in plants during oxygen shortages. In this study, the ADH family protein (*MaADH1* and *MaHOT5*) and PDC family protein (*MaPDCA* and *MaPDCB*) were significantly upregulated based on transcriptome data. These family proteins play a role in fermentation due to hypoxia. Hypoxia occurs in drought stress by stomatal closure instead

of maintaining water in plants. Higher expression of ADH and PDC genes indicates that banana plantlets produce energy from fermentation in response to water stress. Research conducted in *Arabidopsis thaliana* showed that ADH1, PDC1 and PDC2 genes were expressed higher in aerobic conditions[18].

Identification of the genes in the banana plantlets experiencing water stress shows a list of genes that play a role in maintaining homeostasis of energy. Overall, the genes in the glycolytic pathway show increased expression at high-stress levels. In this study, the identification of genes was only based on transcriptomic analysis and validation of gene expression by qRT-PCR. The phenotypic analysis is needed as a comparison to explain how changes in gene expression in the glycolysis pathway can affect plant phenotypic conditions when stressed by water stress. However, the results of this research can be utilized as a reference to offer insight into the molecular response of banana plants to water stress.

CONCLUSION

Transcriptome profiling in bananas indicated changes in cellular respiration after applying low, moderate and high water stress. Based on transcriptome analyses, it can be concluded that banana plantlets respond to water stress by producing energy from glycolysis and fermentative metabolism. The mRNA-seq was also validated using qRT-PCR so that transcriptome analyses could be confirmed. This work contributes to a better understanding of the molecular mechanisms and provides a workflow to study responses to water stress.

SIGNIFICANCE STATEMENT

Several genes related to cellular respiration are already detected in *Musa* spp. and play a role in plant response to water stress. *Musa acuminata* plantlets were cultured *in vitro* with water stress induction using PEG6000 in different stress levels. Transcriptome datasets were used to get information about the gene profile related to cellular respiration. The glycolysis/gluconeogenesis pathway was affected by water stress in all stress levels. A total of 13 genes were identified in the glycolysis/gluconeogenesis pathway that can be classified into 6 family proteins. Current results contribute to a better understanding of the molecular mechanisms and provide a workflow to study responses to water stress.

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