Plant Molecular Biology Reporter (2020) 38:189–208
https://doi.org/10.1007/s11105-019-01187-w

ORIGINAL PAPER

# First Expressed TFome of Physic Nut (*Jatropha curcas* L.) After Salt Stimulus

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Published online: 6 January 2020


## Abstract

Physic nut (*Jatropha curcas* L.), a small oleaginous tree spontaneously occurring in arid and semi-arid tropical regions, is a sustainable and renewable energy source for biodiesel. However, the *J. curcas* yield in such areas should consider soil salinity and its consequences. Transcription factor (TF) proteins recognize *cis*-regulatory elements in promoters of genes to be expressed. In the present work, differentially expressed genes (DEGs) encoding putative TFs from physic nut plants responding to NaCl (150 mM), after 3 h of exposition, covered 23 TF families. The expressed profiles of members from AP2/ERF and NAC families basically showed induction after the salt stimulus, while members of bHLH, FHY3-FAR1, and ARF families presented repression. Concerning the induced TF DEGs, the gene ontology (GO) enrichment analysis highlighted terms related to abiotic stress responses, while those terms representing the repressed TF DEGs stood out the basal metabolism. In turn, the TF enrichment analysis predicted those TFs targeting promoters of induced TF DEGs. Some of the enriched TFs may be good candidates as transgenes in transgenic events. Also, RT-qPCR analyses validated the up-regulation of six TF DEGs (*RAV1*, *ERF9*, *ZAT12*, *PTI5*, *MYB340*, and *BZIP4*) of eight candidates selected from the expressed TFome. The generated data could help breeders to better understand the molecular basis of physic nut plants responding to salinity, to select potential candidates for transgenic studies, as well as to develop functional molecular markers to assist selection steps in breeding programs.

**Keywords** *Jatropha curcas* · RNA-Seq · Transcriptome · Abiotic stress · Salinity

**Key Messages**
- First TFome expressed by *J. curcas* roots after 3 h of NaCl exposition (150 mM)
- TFome covering 148 differentially expressed genes (DEGs) of 23 TF families
- TF BPC6 was predicted to regulate more than 40 induced DEGs of *J. curcas* plants responding to the salt stimulus
- Eight TF DEGs evaluated by a second gene expression technique (RT-qPCR analysis)

**Electronic supplementary material** The online version of this article (https://doi.org/10.1007/s11105-019-01187-w) contains supplementary material, which is available to authorized users.

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## Introduction

Physic nut (*Jatropha curcas* L.) is a perennial tropical plant belonging to the Euphorbiaceae family that has proven an alternative source of renewable biofuel producer (Openshaw 2000). *J. curcas* presents some advantages over the so-called oleaginous biodiesel plant producers, including the high (30–50%) oil content in its seeds allied to the relatively easy biofuel conversion (Deore and Johnson 2008); in addition, it does not compete with human food destination. Since it is a spontaneous species occurring in arid and semi-arid tropical regions (Johnson et al. 2011), it is important to address two main issues: soil salinity and plant salt stress. Crop production in arid and semi-arid regions must consider natural saline/sodic soils, high plant evapotranspiration, low rainfall, and unfavorable physical/physicochemical soil properties, which associated with irrigation problems cause soil salinization and consequences to plant growth (Campos et al. 2012). In plants growing in regions with low water availability, the lower osmotic potential at the root zone by the high salt levels in the soil solution is sufficient to reduce water absorption (Dasgan et al. 2002). Additionally, ions acting on protoplasm disturb mineral plant nutrition (Munns 2002), limiting the plant growth (Gurgel et al. 2003).

Plants exposed to environmental stresses change their metabolisms according to the genes properly activated or repressed (Seki et al. 2002). Genes are expressed and transcriptomes are reprogrammed based on the set of transcription factors (TFs) activated through signal transduction in response to a stimulus. The TF proteins recognize the *cis*-regulatory elements (CRE) in promoters of genes to be expressed, which, in turn, regulate the expression (Wang et al. 2009). Therefore, TFs play a key role in biotic and abiotic stress responses and plant development (Riechmann et al. 2000) by spatially and temporally regulating their targets (Zhang et al. 2011; Jin et al. 2014). Thus, characterizing the expressed TFome of *J. curcas* plants after a salt stimulus benefits the understanding on the transcriptional dynamic modulation of genes involved in the salt response, in addition to improving the *J. curcas* salt tolerance.

## Materials and Methods

### Plant Material and the Salinity Assay

We performed two Brazilian *J. curcas* accessions—Jc183 and Jc171 (Lozano-Isla et al. 2018)—through a salt treatment assay using plants growing in a greenhouse (March 2016) at the Federal University of Alagoas (UFAL/CECA, Rio Largo, AL, Brazil; geodesic coordinates 09°28′02″S; 35°49′43″W, altitude 127 m). The regional climate is classified according to Thornthwaite and Mather (1955) as wet, megathermic, and moderately water deficient in the summer (December to March), but with some excess water in the winter (July to September). For the salt assay, we sown homogeneous seeds (size and weight) of both accessions in pots (50 L) filled with 20 kg of washed sand. The seedlings from the first eophiles (5–10 days after germination, DAG) were thinned, leaving only the most vigorous plant per pot. Sampling followed a completely randomized design containing three half-siblings' plants of each accession, two accessions, and two treatments (with and without salt). Cultivation of the plants involved irrigation (4 p.m.) every 3 days with Hoagland nutrient solution (20% w/v) (Epstein 1972). A week before the salt treatment, plants received a 100% Hoagland solution (full strength) on a daily basis. In the salt treatment, the plants (60 DAG) were provided (9 a.m.) with NaCl added to the Hoagland solution (150 mM, final concentration) over a 3-h exposition period. The negative control treatment comprised plants irrigated only with the Hoagland solution. After the NaCl exposure time, we collected the root samples to be immediately frozen in liquid nitrogen ($N_2$) and maintained at − 80 °C until RNA extraction.

### RNA Isolation, RNA-Seq Libraries, and Its Sequencing

We isolated the total RNA from the root samples using the SV Total RNA Isolation System (Promega) and estimated the RNA concentration on NanoDrop spectrophotometer (Thermo Scientific NanoDrop 2000). The RNA quality assessment developed through absorbance ratios (OD 260/280 nm ≥ 1.9 and OD 260/230 nm ≥ 1.9) and 1.5% (w/v) agarose gel electrophoresis. In addition, we verified the integrity of the RNAs using the Agilent Bioanalyzer 2100 system (Santa Clara, CA, USA). Samples showing RNA Integrated Number (RIN) ≥ 9.0 generated the RNA-Seq libraries at the Genomic Center of the "Luiz de Queiroz" College of Agriculture (ESALQ/USP, Piracicaba, SP, Brazil). The 12 libraries (three half-siblings' plants × two accessions × two treatments) were sequenced (2 × 100 bp *paired-end*) using the Illumina HiSeq2500 Platform (Eurofins MGW, Germany).

### Transcriptome Assembly and the Transcript Annotation

We visualized the base sequence quality and content of reads generated from the RNA-Seq *paired-end* libraries on FastQC software (v.0.11.5) pre- and post-adapter filtering and trimming (paired-end) steps using the Trimmomatic tool (v.0.36; Bolger et al. 2014) and default parameters. We discarded low-quality reads containing unknown adapters and nucleotides and used pairs of high-quality reads (*Phred* ≥ 30, all bases) to perform the de novo transcriptome assembly performed on Trinity 2.2.0 software (Grabherr et al. 2011). We estimated the expression levels of assembled transcripts and unigenes on

RSEM software (Li and Dewey 2011) and applied the alignment package Bowtie (v4.4.7; Langmead et al. 2009) to map reads back to unigenes. The normalized FPKM (Fragment Per Kilobase of cDNA Per Million fragments mapped) matrices derived from the RSEM counts and the differential expression analyses performed on the edgeR package (Robinson et al. 2010). In turn, putative transcripts encoding TFs appeared after BLASTx alignments (*e-value* $\leq e^{-10}$) against specific proteins sets downloaded (August 2018) from the following public databases: NCBI (*J. curcas*; https://www.ncbi.nlm.nih.gov/), Phytozome v.12 (*Ricinus communis* and *Manihot esculenta*; https://phytozome.jgi.doe.gov/pz/portal.html), and UniProtKB/SwissProt (http://www.uniprot.org/).

### Identification of the Differential Expressed Genes

Unigenes showing *p value* $\leq 0.0001$, false discovery rate (FDR) $\leq 0.005$, and $Log_2FC \geq 1$ (classified as up-regulated, UR) or $\leq -1$ (down-regulated, DR) were considered differentially expressed genes (DEGs). Fold change (FC) value represented the unigene abundance modulation in the stressed library in relation to the negative control (henceforth, S vs. C, for brevity). Hierarchical clustering analysis performed on Cluster software (v.3.0; https://cluster2.software.informer.com/3.0/) based on the ratio of $Log_2FC$ values of the unigenes, comparing two treatments and generated heatmaps, visualized on JavaTreeview software (v.1.1; http://jtreeview.sourceforge.net).

### The GO and TF Enrichment Analyses

We performed the Gene Ontology analysis using the PlantRegMap tool (http://plantregmap.cbi.pku.edu.cn; Jin et al. 2014) and the GO terms enrichment analysis applying a tool from the same database to identify the over-represented terms (Fisher's exact tests, *p value* $\leq 0.01$), considering the input files individually represented by unigenes encoding TFs, induced or repressed DEGs, or non-DEGs (n.s.). A similar procedure included the TF enrichment analysis from the same database as well. In turn, we generated the Venn diagrams using the online tool Venny (http://bioinfogp.cnb.csic.es/tools/venny/).

### Gene Expression Validation Through RT-qPCR Assay

The gene expression of DEGs encoding TF candidates selected based on the in silico RNA-Seq expression included *RAP2-3* (ethylene-responsive transcription factor RAP2-3), *RAV1* (AP2/ERF and B3 domain-containing transcription factor RAV1), *ERF9* (ethylene-responsive transcription factor 9), *DREB1H* (dehydration-responsive element-binding protein 1H), *ZAT12* (Zinc finger protein ZAT12), *PTI5* (pathogenesis-related genes transcriptional activator PTI5), *MYB340* (Myb-related protein 340), and *BZIP4* (basic leucine zipper 4); Table S1. The analyses of such candidates developed through RT-qPCR assays with the primer pairs designed based on the transcript sequences using the *online* Primer 3 tool (Rozen and Skaletsky 2000) with the following some parameters adjusted: amplicon size (between 70 and 200 bp), melting temperature [50 °C (minimum), 70 °C (optimum), and 80 °C (maximum)], and GC content (45–55%). Primers (Supplementary Table S1) were synthesized by Invitrogen Life Technologies (USA) and previously tested amplifying cDNAs through conventional PCR. Subsequently, we performed RT-qPCR reactions on a real-time thermocycler LineGene 9600 (Bioer®, Hangzhou, China) using SYBR Green detection system. The PCR reaction (10 μL) included 5 μL of SYBR Green SuperMix (Applied Biosystems, Foster City CA, EUA), 1 μL of diluted cDNA (1/10), 0.3 μL of each primer (5 μM), and 3.4 μL $ddH_2O$. The reactions occurred according to the following programming settings: initial denaturation of 95 °C for 2 min, 40 cycles of 95 °C for 15 s, and 60 °C for 60 s. We conducted the RT-qPCR reactions on 96-well plates containing the three half-siblings of each accession, and three technical replicates, negative controls, and two reference genes properly tested for the assays [*β-tubulin* and *actin* (Ma et al. 2015)]. The dissociation curves resulted from heating the amplicons from 65 to 95 °C for 20 min after the RT-qPCR cycles. The LineGene software (v.1.1.10) estimated Cq values and the absolute and relative quantifications, while REST 2009 software (Relative Expression Software Tool v.2.0.13; Pfaffl et al. 2002) assessed the relative expression data through a randomization test including 2000 permutations and the hypothesis of significant differences between the control and treatment groups. For the purpose of data reliability, the procedures followed the MIQE (The Minimum Information for Publication of Quantitative Real-Time PCR Experiments; Bustin et al. 2009).

## Results

### The *J. curcas* De Novo Transcriptome and the DEGs Encoding TFs

The high-throughput sequencing of the 12 *J. curcas* RNA-Seq libraries of roots exposed to NaCl (150 mM, three hours) generated 238,286,823 raw reads. After removing adapters and trimming the low-quality bases, 230,140,599 high-quality *reads* (*Phred* $\geq 30$, all bases; 96.58% of the *reads*) allowed the de novo transcriptome assembly, comprising 145,422 assembled transcripts (101 Mb) or 126,342 unigenes (76 Mb) with a GC% of 41.55. Concerning the transcripts, the $N_{50}$ comprised 1308 bp, while unigenes, 993 bp. Our reports do not address the global transcriptome, but only the transcripts/unigenes encoding potential TFs. Thus, based on

the BLASTx analysis (*e-value* $e^{-10}$) of the assembled transcripts against the annotated proteins from the Euphorbiaceae species (Fig. 1), we identified 1876 transcripts encoding TF candidates. The inclusion of *R. communis* and *M. esculenta* (Phytozome database), both *J. curcas*-related species, provided high sequence similarities (Fig. 1) and higher annotation process efficiency.

The difference (Jc171/4646 and Jc183/57) in the number of DEGs detected per accession [*p value* ≤ 0.0001, FDR ≤ 0.005, $Log_2FC \geq 1$ (UR) or ≤ −1(DR)] in response to the salt stimulus highlights the great effort of Jc171 accession to minimize damages, some only visible in its leaves (Fig. 2).

Based on that, the present investigation of TFs differentially expressed in response to the applied salt was restricted to the Jc171 accession. One hundred forty-eight of the Jc171 DEGs (78 UR and 70 DR; Table S4) potentially encoding TF candidates, encompassing 23 TF families (Fig. 3), comprised the proposed first TFome expressed after the salt stimulus. The following TF families outstanded in isoforms members: AP2/ERF, MYB, bHLH, FHY3/FAR1, WRKY, NAC, ARF, HD-zip, and bZIP (Fig. 3).

Regarding a single TF family, the proportion of induction to the repressed DEGs varied (Fig. 4). The following TF families had more induced DEGs: AP2/ERF (22), MYB (14), NAC (9), and WRKY (7), while the families containing more repressed DEGs were FHY3/FAR1 (15), bHLH (13), ARF (9), and MYB (6) (Fig. 4). Additionally, some TF families presented only UR or DR isoforms members (Fig. 4).

## The GO Enrichment Analysis

The PlantRegMap tool identified 71 of the 78 induced DEGs encoding TF candidates indicating 128 as the enriched GO terms (*p value* ≤ 0.01). For 57 of the 70 repressed TF DEGs (TFs) identified, the enriched GO terms reported 143. The analysis of the 958 non-DEGs encoding potential TFs revealed enriched GO terms of 435. Supplementary Table S2 provides the enriched terms distributed into the three main GO categories [Biological Process (BP), Molecular Function (MF), and Cellular Component (CC)]. Comparing the three sets of enriched terms using a Venn diagram associated with the UR TF DEGs, the following six GO terms stood out: metabolic process (GO:0008152), response to wounding (GO:0009611), death (GO:0016265), cell death (GO:0008219), heterocyclic compound binding (GO:1901363), and organic cyclic compound binding (GO:0097159) (Fig. 5a). The following enriched GO terms (eight) highlight in the DR TF DEGs (Fig. 5a): single-organism cellular process (GO:0044763), vegetative phase change (GO:0010050), cell proliferation (GO:0008283), single-organism process (GO:0044699), negative regulation of growth (GO:0045926), regulation of cell proliferation (GO:0042127), cell fate commitment (GO:0045165), and regulation of circadian rhythm (GO:0042752).

## The TF Enrichment Analysis

By defining the induced TF DEGs as the target genes (72), the TF enrichment analysis predicted 1164 regulations by 245 TFs, but the TFs considered enriched numbered 126. Upon the repressed TF DEGs comprising the target genes (58), the analysis predicted 729 regulations/185 TFs, while the enriched ones numbered 55. When the non-DEGs codifying TFs (n.s.) comprised the target genes (1000), the analysis predicted 11,936 regulations/302 TFs, out of which 123 were enriched TFs. Supplementary Table S3 lists the enriched TFs, their TF families, and number of predicted target genes from the UR, DR, or non-DEGs. A comparison of the three

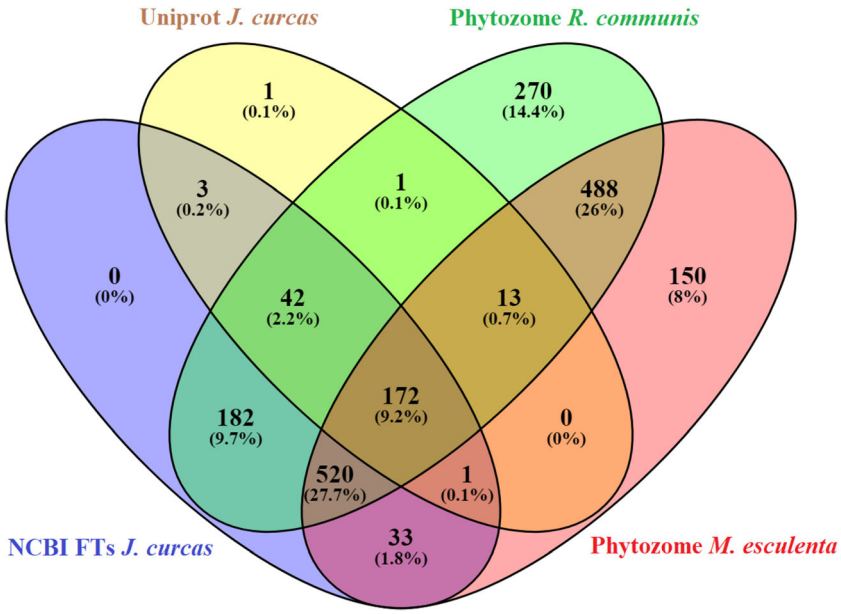


**Fig. 1** Venn diagram showing numbers of *Jatropha curcas* RNA-Seq transcripts (from roots of plants after a 3-h NaCl exposition; 150 mM) encoding transcript factor proteins similar (*e-value* ≤ $e^{-10}$) to those from different public proteins databases (NCBI, https://www.ncbi.nlm.nih.gov/.; Phytozome, https://phytozome.jgi.doe.gov/pz/portal.html; UniProt, https://www.uniprot.org/)

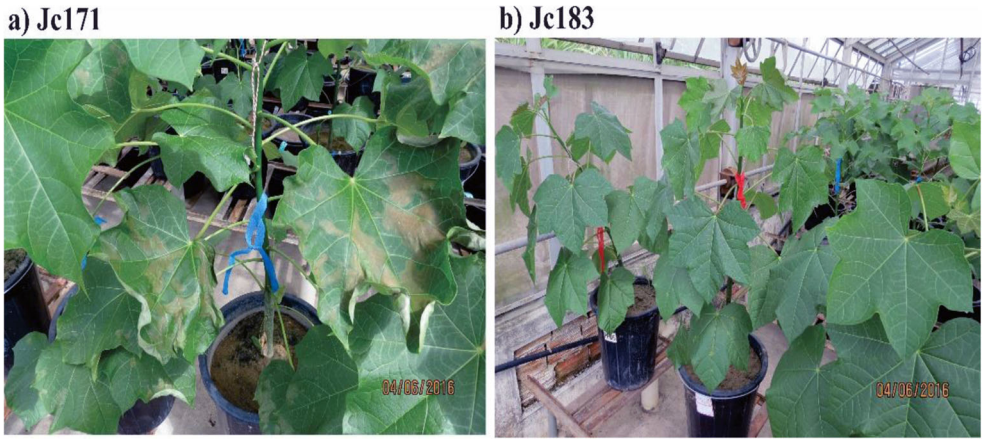


**Fig. 2** Visual damages on leaves of *Jatropha curcas* Jc171 accession, after a 3-h NaCl exposition (150 mM), and not found in the Jc183 accession

sets of enriched TFs in a Venn diagram revealed 39 enriched TFs interacting exclusively with promoters of induced TF DEGs (as their targets), while those interacting only with the repressed TF DEGs numbered 19 TFs, and those associated only with the non-DEGs counted for 34 TFs (Fig. 5b). Enriched TFs from the ERF family (22) comprised most of those predicted interacting exclusively with induced TF DEGs, but ERF family members (28) also stood out in the non-DEGs codifying TFs. In turn, Dof family members (9) interacted mostly with the DR TF DEGs. Figure 6 illustrates the TF families and their enriched TFs predicting targeting promoters of unigenes (UR or DR DEGs, or non-DEGs) codifiers of TF candidates expressed in *J. curcas* roots after the salt stimulus. Additionally, Supplementary Table S3 provides the number of possible target genes.

## Expressed Profiles of the Most Representative TF Families Associated with Salt Response

Figure 7 shows the heatmaps indicating the expressed profiles of the most representative TF family members. In addition, Supplementary Table S4 provides the expression data based on the ratio of $Log_2FC$ values modulated by the Jc171 accession after the salt stimulus in relation to the negative control. The nt sequences are also provided. Almost all AP2/ERF family members were up-regulated after the salt stimulus (Fig. 7a). Similar profile was observed in members of the NAC family (Fig. 7e). Members of MYB (Fig. 7b), WRKY (Fig. 7f), and bZIP (Fig. 7h) family showed more up- than down-regulation. A balance with up- and down-regulation comprised the HD-ZIP

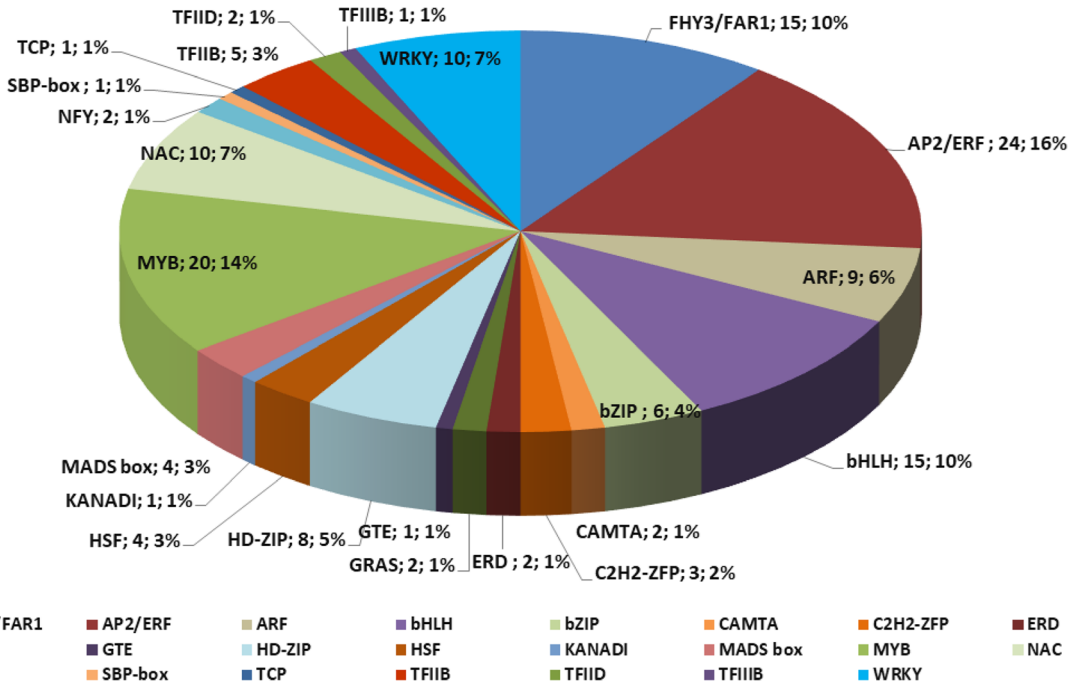


**Fig. 3** Transcription factor (TF) families associated with differentially expressed genes [DEG: $p$ value $\leq 0.0001$, FDR $\leq 0.005$, $Log_2FC \geq 1$ or $\leq -1$] from *Jatropha curcas* Jc171 accession after salt treatment (150 mM NaCl). The TF family name is followed by the total of DEGs and the corresponding percentage

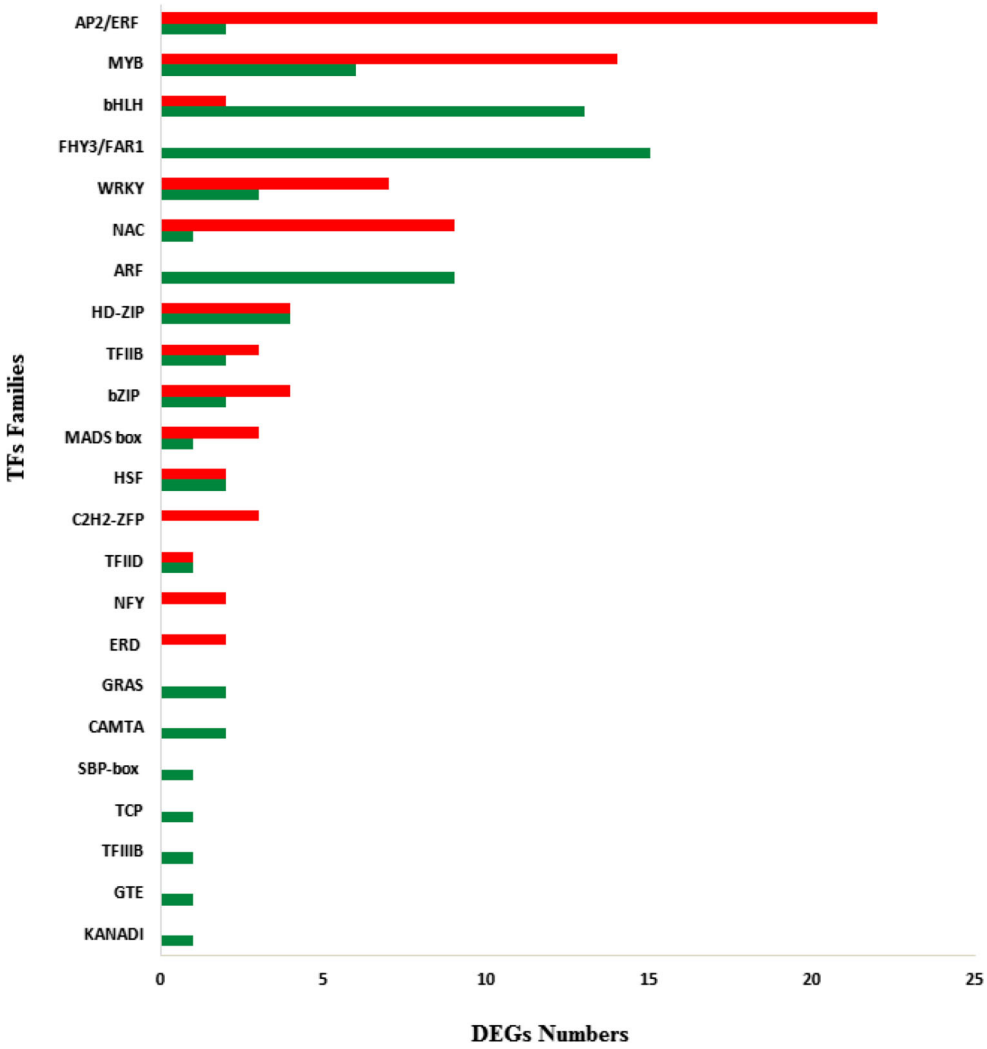


**Fig. 4** Families of transcription factors showing differentially expressed genes [DEG: $p$ value ≤ 0.0001, FDR ≤ 0.005, $Log_2FC \geq 1$ or ≤ − 1] from Jc171 accession after salt treatment (150 mM NaCl): the induced DEGs are represented by red bars and the repressed DEGs by the green bars

family members (Fig. 7i). In turn, almost all members of the bHLH family were down-regulated (Fig. 7c) and the totality of the FHY3-FAR1 (Fig. 7d) and ARF (Fig. 7g) members exhibited down-expression after the salt stimulus.

## Expression Validation of TF DEGs Through RT-qPCR Analysis

We assessed eight DEGs encoding TF candidates through RT-qPCR assays to confirm the in silico expressed profiles. The

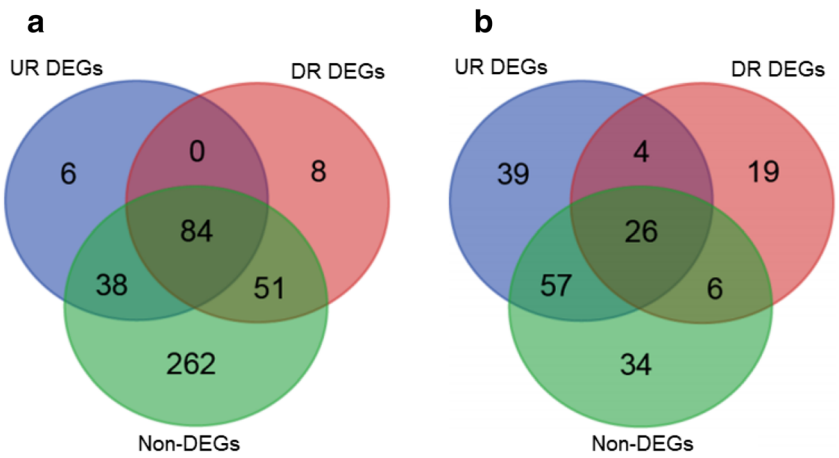


**Fig. 5** Venn diagram comparing the enriched GO terms (**a**) or the enriched TFs (**b**) identified by the respective PlantRegMap tool using individually different input gene list: the UR DEGs, the DR DEGs, or the non-DEGs. DEG. differentially expressed gene (thresholds: $p$ value ≤ 0.0001, FDR ≤ 0.005, $Log_2FC \geq 1$ (UR, up-regulated) or ≤ − 1 (DR, down-regulated))

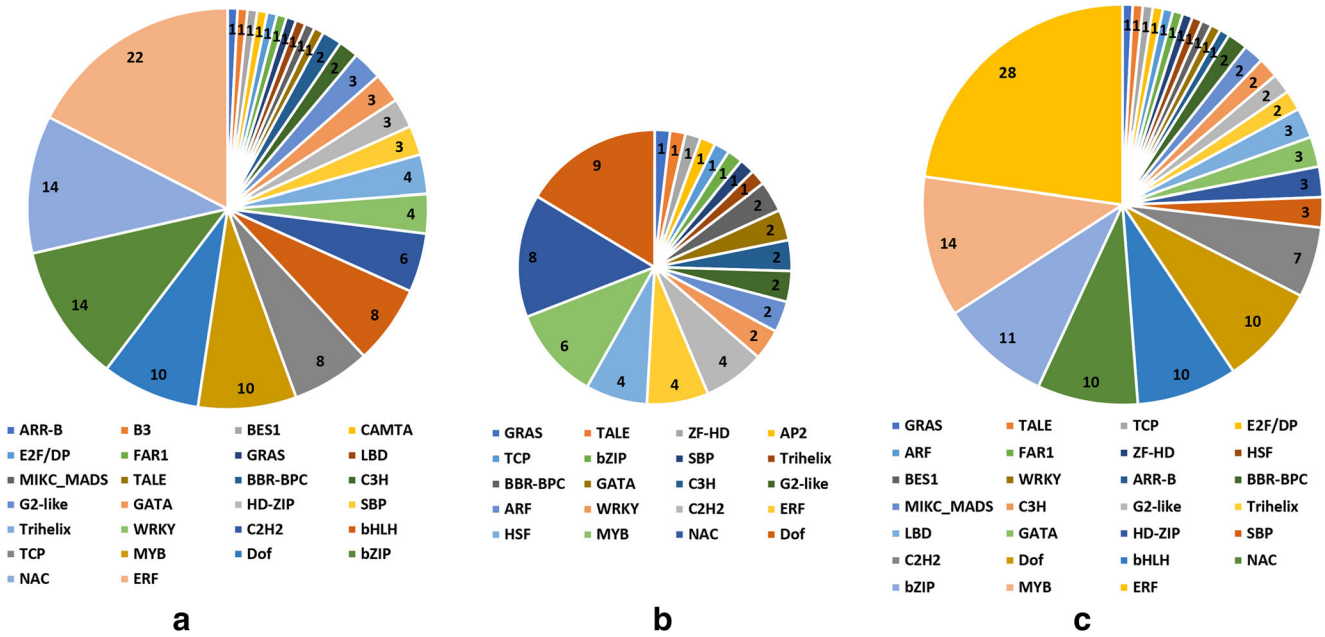


**Fig. 6** Distribution of enriched FT family members predicting targeting promoters of different sets of TF genes: the up-regulated DEGs (**a**), the down-regulated DEGs (**b**), and the non-DEGs (**c**) expressed in roots of *J. curcas* after salt treatment (150 mM NaCl, 3 h). DEGs (threshold: $p$ value $\leq 0.0001$, FDR $\leq 0.005$, $Log_2FC \geq 1$ or $\leq -1$)

selected DEGs (*RAP2-3*, *RAV1*, *ERF9*, *DREB1H*, *ZAT12*, *PTI5*, *MYB340*, and *BZIP4*) and the reference genes (*β-tubulin* and *actin*) presented the expected amplicon, according to the respective dissociation curves (Supplementary Fig. S1). The RT-qPCR parameters [amplification efficiency (*E*), slope (*S*), and correlation coefficient (*R*)] derived from standard curves generated using serial dilution of cDNAs samples and each primer pair presented acceptable values (Table 1), following the recommendation in the MIQE protocol (Bustin et al. 2009). In general, most of the RT-qPCR results (75%) confirmed the in silico gene expression (except for *RAP2-3* and *DREB1H*), suggesting the reliability of the expressed TFome (Fig. 8, and Table 2).

## Discussion

Transcriptomic studies have been performed in plants and some of the identified TFs associated with plant abiotic stress responses, showing interactions with the transcriptional reprogramming activation in living cells (Seki et al. 2002). Since many TFs described in plant abiotic stress responses play a crucial role in stress tolerance processes (Lata and Prasad 2011), the expression modulated by TFs usually results in dramatic metabolic changes (Liu et al. 1998). Here, a de novo RNA-Seq transcriptome analysis uncovered the proposed first TFome differentially expressed in roots of *J. curcas* plants (Brazilian Jc171 accession) early responding a NaCl stimulus (150 mM). Jc171 seeds presented a particular ability in germination, despite the presence of NaCl until that concentration (Lozano-Isla et al. 2018). In the present study, 10 weeks after germination plants of the Brazilian *J. curcas* accessions were exposed to 150 mM NaCl, during 3 h. Since TFs are involved in gene regulation, the work aimed to study the early response of the two previously known cultivars differentially responding to salt stimulus. Thus, the repertory of the identified FT candidates (the TFome) and their respective gene expression modulation by each cultivar could reflect the salt perception and the early salt response. Considering the transcriptomic approaches applied to *J. curcas* plants in response to abiotic stresses, the literature includes low temperatures (Wang et al. 2013; Wang et al. 2014), flooding (Juntawong et al. 2014), drought (Cartagena et al. 2015; Sapeta et al. 2015; Zhang et al. 2015), and salinity (Zhang et al. 2014). Concerning salinity, Zhang et al. (2014) reported transcriptomic data (Illumina 21 bp tags) from roots and leaves of the cultivar GZQX0401 (the GenBank reference genome, GCA_000696525.1, 8 weeks germinating plants), after 100 mM NaCl exposition (2 hs, 2 days, and 7 days). The mentioned authors described more regulated genes in roots, 2 h after the stress, than after 2 days.

Also concerning the present salt assay, it should be mentioned that an automatic weather station monitored the temperature and the relative air humidity inside the greenhouse, and vapor pressure deficit (VPD) values were calculated based on those data. Besides, pyranometers measured the photosynthetically active radiation (PAR). Taking all these into account, in the day of salt application, the values of average daytime air temperature (27.93 °C), vapor pressure deficit (VPD of 0.99 kPa), and integrated global radiation

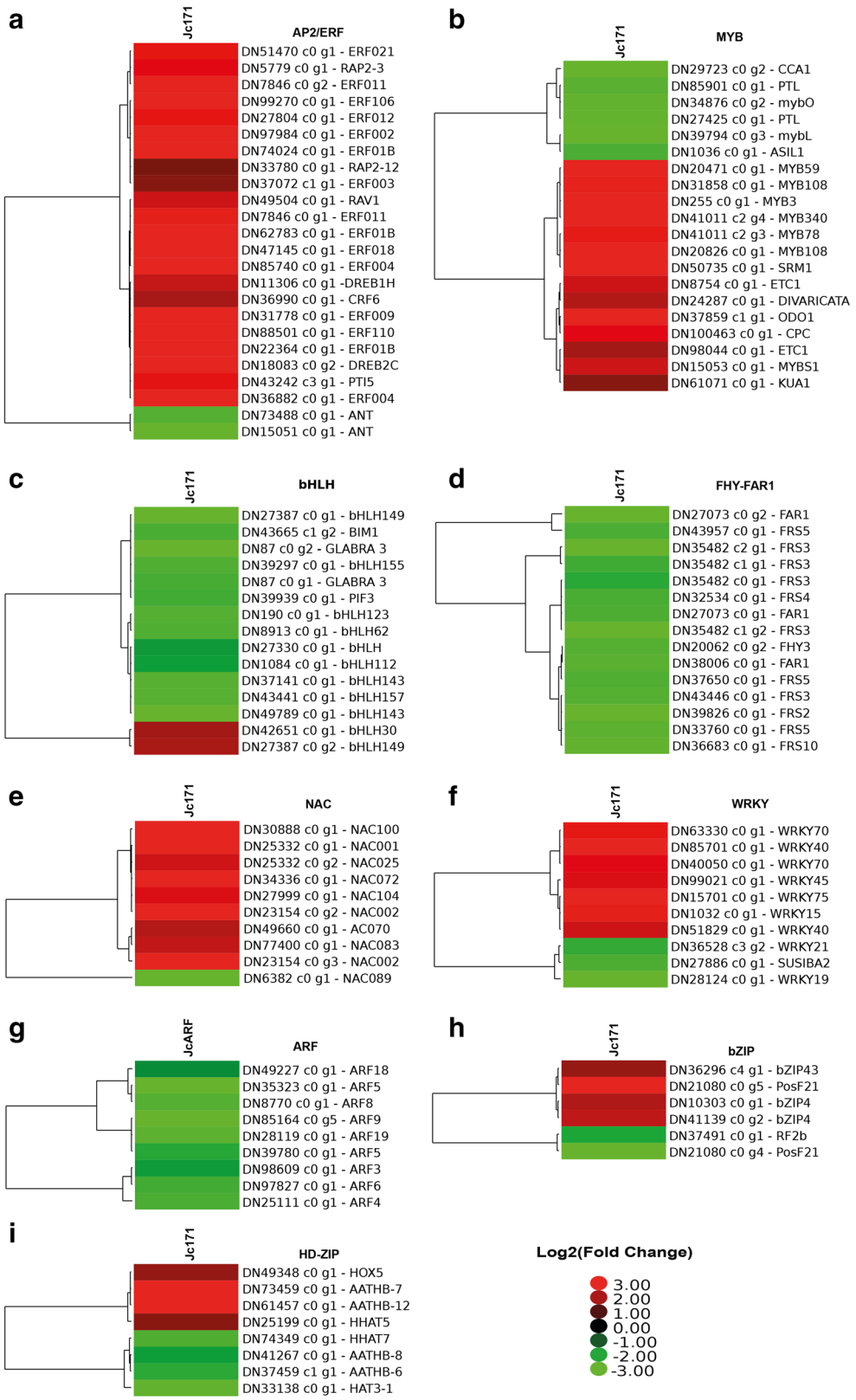


**Fig. 7** Heatmaps based on gene expression modulation of TFs family members identified in *Jatropha curcas* Jc171 roots after a 3-h NaCl exposition (150 mM), in relation to the negative control without salt (ratio of $Log_2FC$ values). The up- and down-regulation of the differentially expressed genes are indicated in red and green, respectively, and the intensity of the colors follows the legend

over 24 h (5.50 $MJ.m^{-2}.day^{-1}$) remained within the range of the days before the salt treatment (M. Pompelli, personal communication, August, 30, 2019), and the analyzed plants were considered in their steady-state condition. In this way, if the transcriptomic analyses showed significant transcriptional modulations after the salt treatment, the changes

**Table 1** RT-qPCR parameters [amplification efficiency (*E*), slope (*S*), correlation coefficient (*R*), and Y intercept] derived from the standard curves using serial dilution of *Jatropha curcas* root cDNAs samples (accessions and treatments) and each primer pair

| Gene (candidate/reference[a]) | *E* (%) | *R* | *S* | Y intercept |
|---|---|---|---|---|
| *RAP2-3* | 91.51 | − 0.994 | − 3.54 | 27.78 |
| *RAV1* | 91.30 | − 0.998 | − 3.55 | 36.14 |
| *ERF9* | 105.45 | − 0.992 | − 3.20 | 34.68 |
| *DREB1H* | 98.69 | − 0.996 | − 3.35 | 33.64 |
| *ZAT12* | 104.71 | − 0.927 | − 3.21 | 33.88 |
| *PTI5* | 104.91 | − 0.915 | − 3.21 | 32.55 |
| *MYB340* | 109.78 | − 0.974 | − 3.11 | 34.12 |
| *BZIP4* | 91.03 | − 0.999 | − 3.56 | 32.59 |
| *β-tubulin*[a] | 96.00 | − 0.986 | − 3.42 | 30.90 |
| *Actin*[a] | 90.15 | − 0.998 | − 3.58 | 26.99 |

[a] Reference gene: *actin* (Tang et al. 2016) and *β-tubulin* (Xu et al. 2016)

could be consequence of the salt stimulus. Phenotypically, after 3 h of the salt exposure (150 mM NaCl), visible symptoms (wilting, dehydration, and necrosis) were observed on leaves of Jc171 (the salt-sensitive accession). Similar visible damages (wilting and leaves dehydration) on *G. hirsutum* leaves of the cotton salt-sensitive Nan Dan Ba Di Da Hua genotype were associated to the saline stress (200 mM NaCl) after 0.5 h of the salt treatment (after 4 h, the wilting was more severe; Peng et al. 2014).

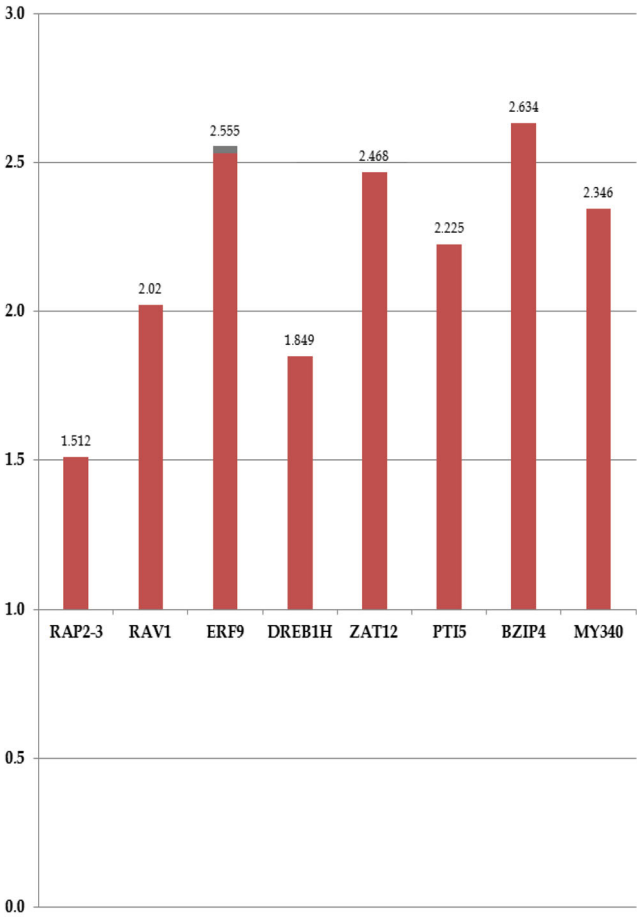


**Fig. 8** RT-qPCR results of eight candidate genes encoding TFs using cDNAs of *Jatropha curcas* root after a 3-h of NaCl exposition (150 mM). Expression data calculated by the REST software (v.2.0.13) (Pfaffl et al. 2002) considering biological (half-siblings' plants) and technical triplicates, and actin and β-tubulin as the reference genes

Considering the generated RNA-Seq transcriptome, the identified TFs candidates differentially expressed after the salt stimulus provided insights on metabolic strategies of plants early responding to salinity. From the annotated assembled transcripts encoding TFs (1876), almost 8% were declared DEGs ($p$ value ≤ 0.0001, FDR ≤ 0.005, $Log_2FC \geq 1$ or $\leq -1$) after the salt treatment. The gene ontology characterization of the two set of TF DEGs, those comprising the up-expressed TFs or the down-expressed TFs, showed distinct enriched GO terms. In addition to the enriched GO terms related to stress responses, as expected, terms related to cell death were also highlighted considering the up-expressed TF DEGs. Programmed cell death (PCD) is a critical process in eukaryotic cells (Lam 2008) mediating adaptive responses of plants to environmental stresses (Shabala 2009). The ionic imbalance induced by salt stress may promote PCD (Katsuhara and Shibasaka 2000; Huh et al. 2002). Plants of the Jc171 accession after 3 h of the salt stimulus presented visible damages on their leaves; some of them are likely to progress to necrosis. Otherwise, the transcription factor MYB108, despite suppressing PCD dissemination in *A. thaliana* injury sites (Mengiste et al. 2003), associated with oxidative stress, salinity, and water deficit responses. In this study, two DEGs MYB108-related showed up-expression after the salt stimulus (DN31858_c0_g1 and DN20826_c0_g1).

In turn, enriched GO terms associated with the down-expressed DEGs highlighted more plant developmental activities, despite regulation of circadian rhythm, which is also involved in adaptive stress responses (Hotta et al. 2007; Legnaioli et al. 2009; Grundy et al. 2015; Seo and Mas 2015). Some of the metabolic and biochemical processes affected by circadian rhythms include cellular $Ca^{2+}$ levels oscillations (Johnson et al. 1995), water uptake by roots (Takase et al. 2011), stomatal opening (McClung 2001), and photosynthesis and respiration (Kreps and Kay 1997). In this study, the MYB-related TF CCA1 (circadian clock associated1) was encoded by the DEG DN29723_c0_g2. CCA1 is a transcriptional activator strictly involved in circadian rhythm regulation binding promoters of at least two genes encoding proteins related to the photosystem II (Lhcb, light-harvesting chlorophyll a/b-protein; Wang and Tobin 1998). Saline stress is known to cause disturbances in photosynthesis since salinity increases soil osmotic potential, reduces water uptake by roots, and leads to a decrease in plant growth (Sudhir and Murthy 2004; Barhoumi et al. 2007) by compromising roots and leaves growth rates (Munns and Tester 2008), finally reducing the photosynthesis (Julkowska and Testerink 2015).

**Table 2** Selected putative transcript factor genes (DEGs) with the respective in silico expressions based on RNA-Seq data and their expression by RT-qPCR analysis with *Jatropha curcas* cDNAs from roots after 3 h of NaCl exposition (150 mM)

| Method | *RAP2-3* | *RAV1* | *ERF9* | *DREB1H* | *ZAT12* | *PTI5* | *BZIP4* | *MY340* |
|---|---|---|---|---|---|---|---|---|
| In silico[a] | 2.665 (UR) | 2.413 (UR) | 3.390 (UR) | 2.294 (UR) | 3.659 (UR) | 2.738 (UR) | 2.072–2.260 (UR) | 4.392 (UR) |
| RT-qPCR[b] | 1.512 (n.s.) | 2.023 (UR) | 2.555 (UR) | 1.849 (n.s.) | 2.468 (UR) | 2.225 (UR) | 2.634 (UR) | 2.346 (UR) |

DEGs (differentially expressed genes: $p\ value \leq 0.0001$, false discovery rate (FDR $\leq 0.005$), and fold change (FC) based on $Log_2$ (FC) $\geq 1$ (up-regulated, UR) or $\leq -1$ (down-regulated, DR))

[a] $Log_2$FC values (FC: ratio of normalized transcript abundance observed in the stressed library in relation to the respective abundance in the control library)

[b] Relative expression by REST software (v.2.0.13) (Pfaffl et al. 2002), UR ($p \leq 0.05$) considering biological (half-siblings' plants) and technical triplicates, and *actin* and *β-tubulin* as the reference genes

Concerning the TFs possible regulating the observed TFome, the enriched TFs showing predicted interactions with the up-expressed TF DEGs were more comprehensive and broadly distributed into TF families than those based on the down-expressed TF DEGs, probably indicating an increased demand for particular TFs regulating the Jc171 salt response. In the analysis, two enriched TFs from the BBR-BPC family [BPC1 (BASIC PENTACYSTEINE1) and BPC6 (BASIC PENTACYSTEINE6)] stood out inducing 29 and 41 UR TF DEGs, respectively, including 25 common DEGs. The TF BPC1 regulates the floral homeotic *STK* gene (seedstick), which controls tissue identity through the regulation of several processes (Kooiker et al. 2005), while TF BPC6 is a transcriptional regulator of *LHP1* (like heterochromatin protein1) gene, which is associated with a polycomb repressive complex (PRC) component involved in plant epigenetic control by histone methylation (Schuettengruber and Cavalli 2013; Hecker et al. 2015). Additionally, enriched TFs members of the Dof family presented meaningful interactions with the UR TF DEGs. The enriched Dof zinc finger proteins DOF3.1 and DOF3.6 probable induced 28 and 33 of the UR TF DEGs targeting common promoters of 22 of those DEGs. The TF DOF3.6 acts in plant growth and development targeting genes induced by salicylic acid, such as *ORG1*, *ORG2*, and *ORG3* (OBP3-responsive genes; Kang et al. 2003). OBP3 is also a Dof TF. Additional enriched TFs from the Dof family were DOF5.6 and DOF3.4, inducing 23 UR TF DEGs (13 shared targets). DOF5.6 acts on the regulation of vascular tissue development (Guo et al. 2009), while DOF3.4 is involved in the cell cycle regulation (Skirycz et al. 2008). Two enriched TFs members of the AP2/ERF family, ERF1B (Ethylene-responsive transcription factor 1B) and ERF5 (Ethylene-responsive transcription factor 5), also stood out, regulating 15 and 16 UR TF DEGs, respectively (sharing 12 targets). The TF ERF1B associated to salinity tolerance in *Avicennia officinalis* (Krishnamurthy et al. 2017), while ERF5 associated with drought and salinity responses in *Solanum lycopersicum* (Pan et al. 2012). Concerning the TF C2H2 family, the enriched TF IIIA probable regulates 23 UR TF DEGs; the over expression of *TFIIIA* gene was previously associated with the salt tolerance in *Medicago truncatula* (De Lorenzo et al. 2007). From the TF WRKY family, interactions of three enriched TFs were predicted for two/three UR DEGs, e.g., the TF WRKY1, already associated with salinity and drought tolerance in *Triticum turgidum* (Mondini et al. 2012), can target promoters of *ERF1B* and *ZAT10* (Zinc finger protein ZAT10) DEGs. All the above-mentioned enriched TFs could be candidates, as transgenes in events of transgeny in breeding programs. Since pyrimidization of transgenes is a valuable strategy, combining desirable characteristics of each transgene, the use of the proposed candidates could also improve the expected response to the salt stimulus.

Although the TF involvement in abiotic stress tolerance has been established (Reyes et al. 2004; Yanhui et al. 2006; Du et al. 2009; Yang et al. 2011; Cabello et al. 2012; Xie et al. 2012; Zhu et al. 2014; Zhang et al. 2014b), and TFs families reported to orchestrate stress responses in plants, such as MYB, AP2/ERF, bZIP, MYC, NAC, HD-zip, and WRKY (Singh et al. 2002; Shameer et al. 2009), a comprehensive TFome covering TFs differentially expressed in *J. curcas* roots after salt stimulus has not been presented. Concerning the almost 70 TF families identified in plants (Pérez-Rodríguez et al. 2010; Hong 2016), based on the DNA-binding domains (Riechmann et al. 2000), the presented TFome covered 23 TF families and encompassed 148 members differentially expressed after the salt stimulus. Until now, TF families presenting a *J. curcas* genome-wide analysis include WRKY (Xiong et al. 2013), NAC (Wu et al. 2015), MYB (Zhou et al. 2015), and AP2/ERF (Tang et al. 2016). Basically, in the mentioned reports, the authors explored Digital Gene Expression (DGE) analysis identifying TFs from the families in tissues (root, stem, leaf, or seed) of plants under stress (drought, phosphate or nitrogen starvation, and salinity). In the case of salinity, the salt stress involved plants/seedlings under 100 mM NaCl for 2 h, in addition to 2 or 7 days. In this study, plants presented similar development were submitted to 150 mM NaCl for a 3-h exposition. Additionally, gene expression including validation developed through semi-quantitative RT-PCR (Xiong et al. 2013; Zhou et al. 2015; Tang et al. 2016) or RT-

qPCR analysis (Wu et al. 2015; Tang et al. 2016). In our case, selected RNA-Seq assembled transcripts were validated only through RT-qPCR analysis using at least two reference genes. However, despite the wide distribution covering 23 TF families, some described plant from TF families did not present declared DEGs responding to the salt stimulus. Such TF families included ABI3VP1, LFY, SBP, Alfin-like, CCAAT, LIM, Sigma70-like, CPP, LOB, SRS, CSD, TAZ, ARR-B, DBP, mTERF, TCP, BBR/BPC, E2F-DP, Tify, BES1, EIL, TIG, BSD, FHA, NOZZLE, TUB, G2-like, OFP, ULT, GeBP, SAP, VARL, Dof, PBF-2-like, VOZ, GRF, PLATZ, YABBY, RWP-RK, HRT, S1Fa-like, Zn-clus, and C3H. Among these families, TFs members of Dof (Li et al. 2016; Wen et al. 2016; Ma et al. 2015), TCP (Zhou et al. 2013; Yin et al. 2018), and CCAAT families (Nelson et al. 2007; Kuromori et al. 2014) had been associated with abiotic stress tolerance, including salinity in specific cases. Furthermore, regarding those families, a broad RNA-Seq analysis on *Hippophae rhamnoides* plants under drought stress presented induced TFs members from the families mTERF, PLATZ, TUB, and LIM, while repressed TF members appeared in the families ABI3VP1, Dof, YABBY, CCAAT, FHA, G2-like, and C3H (Ye et al. 2018). In our RNA-Seq analysis, the main results covering the proposed TFome included the following:

**AP2/ERF Family** Members have fundamental roles in plant development and biotic or abiotic stress responses (Tang et al. 2017). Some potential members encoded by DEGs include the following:

- ERF3 (Ethylene-responsive transcription factor 3; DN37072_c1_g1): Gene over-expression confirmed in plants under cold and drought stresses (Cao et al. 2006; Trujillo et al. 2008); TF probably promoting positive regulation of the physiological adaptive response to drought/salinity tolerance by increasing proline content, chlorophyll accumulation, and cell redox homeostasis regulation, as determined in wheat (*Triticum aestivum*) transgenic plants (Rong et al. 2014).
- ERF1 (Ethylene-responsive transcription factor1; DN7846_c0_g1): Gene expression modulated by jasmonic (JA; Dombrecht et al. 2007), gibberellic acid (GA; Liu and Hou 2018), and some abiotic stress (Vergnolle et al. 2005); TF contains a repressor domain that interacts with dehydration-responsive element (DRE) in the *ACS2/5* (1-Aminocyclopropane-1-carboxylic acid synthase) gene promoter, affecting the ETH biosynthesis under higher ABA levels (Li et al. 2011).
- ERF21 (Ethylene-responsive transcription factor 21; DN51470_c0_g1): TF binding to the promoter of *RD29A* gene (Mitsuda et al. 2010), known to regulate mechanisms of perception and fast induction in water deficit situations (Yamaguchi-Shinozaki and Shinozaki 1993).
- ERF12 (Ethylene-responsive transcription factor ERF12, also known as DREB26; DN27804_c0_g1): TF highly responsive to salt (200 mM NaCl), heat, and drought (Krishnaswamy et al. 2011); as a DREB subfamily member (Guo et al. 2005) has an amphiphilic repression motive (Zhao et al. 2014), characteristic to repressor proteins that inhibit the expression of stress-related genes (Kazan 2006).
- DREB1H (Dehydration-responsive element-binding protein 1H; DN11306_c0_g1): TF playing a crucial role in plant development and gene expression mediated by abiotic stresses (Zhao et al. 2014); however, the RT-qPCR analysis did not confirm the DEG up-regulation.
- DREB2C (Dehydration-responsive element-binding protein 2C; DN18083_c0_g2): Transcriptional activator of genes, such as *COR15A* (cold-regulated 15a; salinity tolerance; Song et al. 2014), *HsfA3* (heat shock factor a3; heat stress response; Chen et al. 2010), *NCED9* (9-cis-epoxycarotenoid dioxygenase 9; ABA biosynthesis; Je et al. 2014a), *CYS4* (phytocystatin 4; thermotolerance; Je et al. 2014b).
- ERF1B (Ethylene-responsive transcription factor 1B; DN74024_c0_g1): TF related to the ETH signaling (Corbacho et al. 2013); the transcript up-regulation has been reported in plant responding to drought in soybean (Ferreira Neto et al. 2013) and tomato (Egea et al. 2018).
- RAV1 (AP2/ERF and B3 domain-containing transcription factor RAV1; DN49504_c0_g1): Acts in ABA signaling during seed germination and early seedling development (Feng et al. 2014); the RT-qPCR analysis validated the DEG up-regulation.
- ERF9 (Ethylene-responsive transcription factor 9; DN31778_c0_g1): The respective gene is induced in leaves and roots at different development stages under saline stress in tomato (Gharsallah et al. 2016); the RT-qPCR analysis confirmed the DEG up-regulation.
- RAP2-3 (Ethylene-responsive transcription factor RAP2-3; DN5779_c0_g1): TF modulating osmotic tolerance inducing genes like *PDC1* (pyruvate decarboxylase1), *SUS1*, and *SUS4* (sucrose synthases) when associated with ABA signaling (Gibbs et al. 2015; Papdi et al. 2015); unfortunately, the RT-qPCR analysis did not confirm the DEG up-regulation.
- PTI5 (Pathogenesis-related genes transcriptional activator PTI5; DN43242_c3_g1): TF activating genes regulated by salicylic acid (SA), such as *PR1* and *PR2* (pathogenesis-related genes) (Gu et al. 2002), involved in the systemic acquired resistance (SAR) process during phytopathogen infection (Ryals et al. 1996; Feys and Parker 2000); the RT-qPCR analysis confirmed the DEG up-regulation.

**WRKY Family** Members of this family are involved in the control of biotic and abiotic stress responses (Ulker and Somssich 2004; Rushton et al. 2010). Some potential members encoded by DEGs include the following:

- WRKY40 (WRKY transcription factor 40; DN51829_c0_g1, and DN85701_c0_g1): TF negatively modulating the expression of JA repressors signaling pathway (JAZ7, JAZ8, and JAZ10) and participating in the defense systems (Glazebrook 2005). It acts primarily on plant defense susceptibility, but is influenced by previous stresses (stressors may have an antagonistic, synergistic, or additive effect on plant; Anderson et al. 2004; Asselbergh et al. 2008).
- WRKY70 (DN63330_c0_g1): This TF is a saline stress-response regulator interacting with another TF (Cys2/His2 zinc finger Zat7); both TFs were involved in higher salt tolerance (Ciftci-Yilmaz et al. 2007).
- WRKY45 (DN99021_c0_g1): The respective gene is induced in ABA hormone-related response and stress responses, including NaCl, dehydration, cold, heat, and pathogens infections (Yu and Qiu 2009).
- WRKY57 (DN40050_c0_g1): TF interacting with promoters of genes, such as *RD29A* (Yamaguchi-Shinozaki and Shinozaki 1993) and *NCED3* (Chernys and Zeevaart 2000), assisting the plant adaptation regarding water stress tolerance by increasing ABA levels (Finkelstein et al. 2002); the phytohormone ABA regulates essential processes in plants (germination, seed dormancy, and stomatal behavior; Liotenberg et al. 1999); under ABA influence and abiotic stress (osmotic, salinity, and drought; Jiang et al. 2012), which TF affects *A. thaliana* germination.

**MYB Family** Members of this family have been investigated regarding their biotic and abiotic stress responses (Denekamp and Smeekens 2003; Seo et al. 2009). Some potential TF encoded by DEGs include the following:

- MYB108 (DN20826_c0_g1): TF regulating abiotic stresses responses (e.g., salinity, drought, and cold) through the JA pathway and the ROS-mediated cellular signaling (Mengiste et al. 2003; Schmid et al. 2005).
- KUA1 (DN61071_c0_g1): Transcriptional repressor of genes encoding peroxidases (PRXs; Lu et al. 2014); PRXs also promote ROS generation, such as $H_2O_2$, which can cleave the polymers of the cell wall, restricting plant growth (Passardi et al. 2004).
- MYB340 (DN41011_c2_g4): This TF activates the *PAL* gene (phenylalanine ammonia-lyase) transcription binding to its promoter (Moyano et al. 1996); the PAL enzyme is involved in the phenylpropanoid metabolism, and stresses (e.g., drought, and salinity) stimulating such metabolism (Cabane et al. 2012) generate precursors for lignin biosynthesis (Davin and Lewis 1992), which also associates with stress tolerance (Liu et al. 2018); the RT-qPCR analysis confirmed the DEG up-regulation.
- MYBS1 (DN15053_c0_g1): TF recognizes the TATCCA motif in promoters of genes (e.g., α-amylase gene), inducing its expression (Lu et al. 2002); however, during salt stress, the α-amylase activity degrading starch and releasing soluble sugar molecules is reduced (Lin and Kao 1995; Siddiqui and Khan 2011), affecting processes such as germination and plant growth (Mei and Song 2008).
- SRM1 (Salt-Related MYB1; DN50735_c0_g1): This TF regulates the synthesis and signaling of ABA during germination and seed development in salinity conditions activating the expression of the *NCED3/STO1* gene, a mediator of the ABA biosynthesis (Iuchi et al. 2001; Barrero et al. 2006).
- ETC1 (enhancer of try and cpc 1; DN98044_c0_g1): MYB-like transcription factor ETC1 acts as a negative regulator of trichome development, but also promotes an increased root hair development (Kirik et al. 2004).
- MYB59 (DN20471_c0_g1): TF involved in cell cycle regulation and root growth (Mu et al. 2009); TF also responding to ETH and JA (Razzaque et al. 2017).

**HD-ZIP Family** Members of this family play a significant role in plant growth and development responding to several phytohormone stimuli and stresses (Ge et al. 2015; Mao et al. 2016); in wheat (*Triticum aestivum*) plants, the salt-sensitive CS genotype presented 21 induced HD-Zip genes, while the salt-tolerant DK presented 18 (Yue et al. 2018). Potential members encoded by DEGs include the following:

- HAT5 (DEG DN25199_c0_g1): This TF (homeobox-leucine zipper protein) associated with salt stress tolerance in *Thellungiella halophila* (halophytic plant; Wang et al. 2004).
- ATHB-12 (DN61457_c0_g1): In transgenic plants under drought conditions, ATHB-12 and ATHB-7 act as negative plant development regulators in response to the ABA levels (Olsson et al. 2004); plants in salinity conditions induce ABA biosynthesis (Mahajan and Tuteja 2005) responding to the osmotic and water deficit stresses (Popova et al. 1995; He and Cramer 1996).
- ATHB-7 (DN73459_c0_g1): The respective gene was strongly induced by drought and ABA (Söderman et al. 1996); in addition, the ectopic expression of *ATHB7* gene in tomato provided drought tolerance (Mishra et al. 2012).

**NAC Family** Members of the NAC (**N**AM, **A**TAF, and **C**UC) family present crucial roles in plant development (Kunieda

et al. 2008; Ohtani et al. 2011) and stress responses (Takasaki et al. 2015). Potential NAC members encoded by DEGs include the following:

- NAC72 (NAC domain-containing protein 72; DN34336_c0_g): The respective gene was induced by ABA (100 μM ABA), salinity (250 mM NaCl), and drought (Tran et al. 2004), which was associated with stress level (Wu et al. 2016); the TF NAC72 (*Poncirus trifoliata*) is the transcriptional repressor of *ADC* (arginine decarboxylase) gene (Wu et al. 2016), whose enzyme is critical to putrescine (Put) biosynthesis (Put is an osmoprotectant compound reducing oxidative damages in roots; Zhang et al. 2014a); the TF NAC72 binds to the CATGTG motif in promoters of genes, such as *ERD1* (early responsive to dehydration stress 1) gene whose protein (ClpA, ATP-dependent CLP protease ATP-binding subunit clpA; Tran et al. 2004) is essential for the maintenance of the chloroplast enzymatic apparatus (Sjögren and Clarke 2011).
- NAC100 (DN30888_c0_g1): TF binding promoters of cell expansion-related genes, such as *CESA2* (cellulose synthase2), and *PIP* (Plasma Membrane Intrinsic Protein) aquaporins (Pei et al. 2013), gateways for cell membrane water exchange (Yaneff et al. 2015).
- NAC2 (DN23154_c0_g2, and DN23154_c0_g3): Induction of *NAC2* gene in roots of *A. thaliana* plants responding to saline stress (200 mM NaCl) has been reported previously (He et al. 2005).

**bZIP Family** Members of this family mediate several biological processes, including energetic metabolism (Baena-González et al. 2007), cell expansion (Fukazawa et al. 2000), tissue and organ differentiation (Silveira et al. 2007), seed maturation, and embryogenesis (Lara et al. 2003); bZIP members also participate in biotic (Thurow et al. 2005) and abiotic stress responses (Ji et al. 2018), including drought and salinity (Ying et al. 2012; Liu et al. 2014). Potential bZIP members encoded by induced DEGs comprised the following:

- bZIP43 (Basic leucine zipper 43; DN36296_c4_g1): A positive regulator of *bHLH109* gene (Nowak and Gaj 2016), associated with increasing LEA (late embryogenesis abundant) protein and enhancing plant stress tolerance (Nowak and Gaj 2016).
- bZIP4 (DN10303_c0_g1, and DN41139_c0_g2): In addition, a positive regulator of the *bHLH109* gene (Nowak and Gaj 2016), the up-regulation of the DEG (DN41139_c0_g2) corroborated with the RT-qPCR results.

**$C_2H_2$-ZFP ($C_2H_2$ Type Zinc Finger Protein) Family** Members of this family are involved in several biological processes (Gourcilleau et al. 2011), including growth mediation, plant development, and abiotic stress responses (Ding et al. 2016). The following potential member was encoded by DEG:

- ZAT12 (Zinc finger protein 12; DN26908_c0_g1): TF regulating the expression of several oxidative-stress-response genes, including *APX* (Ascorbate Peroxidase), *CAT* (Catalase), *GR* (Glutathione Reductase), *POD* (Guaiacol Peroxidase), and *SOD* (Superoxide Dismutase) (Rizhsky et al. 2004; Davletova et al. 2005; Rai et al. 2012); the RT-qPCR analysis confirmed the DEG up-regulation.

## Conclusions

This study represents the first TFome differentially expressed in roots of *J. curcas* plants after salt stimulus (3 h of NaCl exposition, 150 mM), based on RNA-Seq de novo assembly strategy followed by gene expression validation in RT-qPCR assays. The proposed TFome comprised 148 DEGs (78 UR and 70 DR) codifying TFs encompassing 23 TF families. The gene ontology enrichment analysis identifying over-represented terms exclusively associated with the UR DEGs indicated GO terms related to stress responses, while those representing the DR DEGs were more related to the basal metabolism. In addition to pointing the cognate TFs regulating the DEGs bound to their promoters, the TF enrichment analysis emphasizing the most representative TFs regulating the expression of TF DEGs also highlighted enriched TFs showing predicted interactions with over 40 UR DEGs. The enriched TFs, some sharing over 20 targets (UR DEGs), are promising candidates, such as the transgenes in transgenic events simulating the strategy of transgenes pyrimidization. In turn, the RT-qPCR analysis confirmed the in silico gene expression of 75% of eight selected DEGs (from different TF families) revealing that some could be functional molecular markers for marker-assisted selection on plant breeding programs benefiting the development of *J. curcas* salt-tolerant accessions. The results also improve the understanding on the molecular mechanisms involved in *J. curcas* plants responding to salt exposure.

**Acknowledgments** The authors would like to thank the *Empresa Brasileira de Pesquisa Agropecuária* (EMBRAPA SOJA, Londrina, PR, Brazil) and Universidade Federal de Alagoas (UFAL) for offering us with the infrastructure facilities.

**Authors' Contributions** LE, MFP, EB, and EAK conceived and designed the experiments; GALC, MCPS, MDS, and JRCFN carried out the experiments; GALC, MCPS, MDS, and JRCFN analyzed the data; GALC and EAK wrote and revised the paper. All authors read and approved the final manuscript.

**Funding Information** This work was supported (grants and fellowships) by the following Brazilian agencies: *Conselho Nacional de Desenvolvimento Científico e Tecnológico* (CNPq 404357/2013-0, and 311894/2017-8), *Fundação de Amparo à Ciência e Tecnologia do Estado de Pernambuco* (FACEPE; IBPG-0271-5.01/14), *Coordenação de Aperfeiçoamento de Pessoal de Nível Superior* (CAPES), and *Universidade Federal de Pernambuco* (UFPE).

## Compliance with Ethical Standards

**Competing Interests** The authors declare that they have no competing interests.

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