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Gene expression analysis reveals function of *TERF1* in plastid-nucleus retrograde signaling under drought stress conditions

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Abstract

Ethylene response factor (ERF) is a key transcription factor of plant ethylene signaling pathway, which plays an important role in plant response to abiotic and biotic stresses by regulating the expression of downstream genes. However, little is known about the mechanisms of the regulation of gene expression by ERF proteins. Chloroplast is an essential organelle that is important for photosynthesis and biosynthesis of many essential metabolites. There exists an interaction between chloroplasts and the nucleus. Chloroplasts can send multiple kinds of signals to regulate the nuclear gene expression known as retrograde signaling. In our study, we have analyzed the expression of the components related to plastid retrograde signaling pathway to elucidate the mechanism of tomato ethylene responsive factor 1 (*TERF1*) in response to drought stress. Our results showed that *TERF1* can regulate different biogenic and operational retrograde signals to regulate nuclear genes expression, which can improve plant tolerance to drought stress. We also propose a new potential of *TERF1* in regulating nuclear gene expression, including regulation of different phytohormone signaling pathways and gene posttranscriptional modification triggered by different retrograde signals. Our results have enriched our knowledge about the function of ERF proteins and ethylene signaling pathway.

Additional key words: chloroplast-nucleus interactions, ethylene response factor, *Solanum lycopersicum*, tomato.

Introduction

Drought is one of the most important abiotic stresses that severely affects plant growth, development, and final yield. Ethylene, an important phytohormone, regulates plant response to abiotic and biotic stresses. Ethylene response factors (ERFs), unique to plant, are key components of ethylene signaling pathway, which belong to the apetala2/ethylene response factor (*AP2/ERF*) gene family (Liao *et al*. 2016). ERF proteins bind the GCC-box (AGCCGCC) to regulate the downstream target genes expression, which can increase or decrease plant stress tolerance (Maruyama *et al*. 2013, Wan *et al*. 2014).

The mature chloroplast is responsible for photosynthesis and biosynthesis of many essential compounds, such as amino acids, fatty acids, vitamins, and tetrapyrroles (Neuhaus and Emes 2000). Function of the chloroplast is regulated by internal and external factors. The chloroplast acts in plant response to abiotic stresses and stresess can trigger different signals from the chloroplast to regulate the nuclear genes expression (Glasser *et al*. 2014, Kmiecik *et al*. 2016, Sun and Guo 2016).

Owing to its endosymbiotic origin, the chloroplast encodes fewer than 100 open reading frames, and chloroplast proteins are mostly translated in the cytoplasm and imported into the chloroplast, referring as anterograde control (Abdallah *et al*. 2000, Woodson and Chory 2008). Additionally, the chloroplast is also the hub

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Abbreviations: 12-OPDA - 12-oxophyto-dienoic acid; ABA - abscisic acid; ABI4 - ABA insensitive 4; AOS - allene oxide synthase; CSK - chloroplast sensor kinase; ERF - ethylene response factor; GLK - golden 2-like; GUN - genomes uncoupled; HPL - hydroxyperoxide lyase; JA - jasmonic acid; MBS - methylene blue sensitivity; PAP - 3'-phosphoadenosine 5'-phosphate; PEP - plastid-encoded plastid RNA polymerase; PhANGs - photosynthesis-associated nuclear genes; PRANGs - plastid redox-associated nuclear genes; PRIN2 - plastid redox insensitive 2; PS - photosystem; ROS - reactive oxygen species; RpoTp - RNA polymerase of the phage T3/T7 type in plastid; RpoTmp - RNA polymerase of the phage T3/T7 type in plastid and mitochondria; SA - salicylic acid; SIG - sigma factors;TERF1 - tomato ethylene responsive factor 1; WT - wild-type; XRN - 5'-3' exoribonuclease.

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for regulating nuclear genes expression, referring as retrograde signaling (Barajas-Lopez *et al*. 2013). Chan *et al.* (2016) proposed a broader definition of retrograde signaling as a process in which a stimulus perturbs plastid homeostasis and gives rise to one or more retrograde signals that alter nuclear genes expression from transcriptional to posttranslational level and ultimately feeds back to regulate plastid function. Now different retrograde signaling pathways have been confirmed. They are generally divided into biogenic and operational signaling. The biogenic signaling mainly derives from tetrapyrroles and plastid genes expression (Chan *et al*. 2016). The operational signaling mainly derives from oxidative stress, plastid redox state changes, and plastid metabolites (Chan *et al*. 2016). Retrograde signaling regulates the expression of photosynthesis-associated nuclear genes (*PhANGs*), singlet oxygen-responsive genes (*SORGs*), as well as plastid redox-associated nuclear genes (*PRANGs*) (Chan *et al*. 2016). *PhANGs*, especially the genes encoding the Rubisco small subunit (*RBS*) and the light harvesting chlorophyll *a/b* binding proteins (*CAB*), which are related to light capture and photosynthesis and directly regulates leaf growth and development, are significantly regulated by plastid retrograde signals (Ankele *et al*. 2007).

Plant hormonal signaling networks are regulated by different chloroplast retrograde signals. Auxin signaling is related with chloroplast homeostasis and communication (Tognetti *et al*. 2012, Xiao *et al*. 2012). Jasmonate production and programmed cell death are regulated by $^1O_2$ production (Goltsev *et al*. 1987, Van Wijk *et al*. 1993, Ramel *et al*. 2013). β-cyclocitral correlates with salicylic acid (SA) through enhanced disease susceptibility 1 (*EDS1*), which induces the expressions of reactive oxygen species (ROS) detoxification genes (Lv *et al*. 2015). Additionally, sensing and communication of plastid redox state and 3'-phosphoadenosine 5'-phosphate (PAP) accumulation is related with abscisic acid (ABA) signaling (Xiong *et al*. 2001, Galvez-Valdivieso *et al*. 2009, Chen *et al*. 2011). ERF proteins are found to be regulated by the retrograde signal derived from sugars in plastids (Vogel *et al*. 2014). On the contrary, the regulation of retrograde signaling pathway by plant hormonal signaling networks is rarely reported.

Tomato ethylene responsive factor 1 (TERF1) is an ERF protein isolated from tomato and its overexpression in tobacco shows constitutive triple response of ethylene (Huang *et al*. 2004). *TERF1* can be induced by ethylene or NaCl and improves plant tolerance to abiotic stresses (Huang *et al*. 2004). It is still not clear how *TERF1* works in response to abiotic stresses. In this study, we analyzed plastid retrograde signaling using the transgenic tobacco overexpressing *TERF1* under drought stress in order to elucidate the interaction between ethylene and plastid retrograde signaling.

Materials and methods

Plants and *Agrobacterium*-mediated transformation: *Nicotiana tabacum* L. cv. NC89 was used for plant transformation. A construct PROKII, containing the ORF of *TERF1*, was introduced into *Agrobacterium tumefaciens* by the freeze and thaw method (Hofgen and Willmitzer 1988). Tobacco (5-week-old) transformation mediated by *Agrobacterium tumefaciens* was carried out by the leaf disk transformation method of Maiti *et al.* (1993). Tobacco was regenerated on Murashige and Skoog (MS) medium containing 300 mg dm^{-3} kanamycin for screening the transgenic ones. Kanamycin-resistant tobacco was grown in a greenhouse and seeds (T_1) were collected from the primary transformants. The T_1 progeny selected by 300 mg dm^{-3} kanamycin was used for PCR analysis. Genomic DNA was isolated from leaves of 6-week-old plants using *DNAiso* (*Takara*, Tokyo, Japan).

Drought stress treatment: Transgenic (T_2) and wild-type (WT) tobacco plants were grown from seeds in a growth chamber at day/night temperatures of 22/20 ± 2 °C, a relative humidity of 50 %, a 16-h photoperiod, and an irradiance of 300 μmol m^{-2} s^{-1}. Transgenic and WT plants were fully irrigated. When the third new leaf expanded, the irrigation was stopped and after 22 d the WT tobacco showed more severe wilting in comparison with the transgenic ones. Leaves were collected with 3 replicates for transgenic and WT plants during day time for further analyses.

RNA isolation and real-time quantitative (q)PCR): About 100 mg of leaves were utilized to extract total RNA using *MiniBEST* plant RNA extraction kit (*Takara,* Tokyo, Japan). The RNA quantity was determined by *ND-1000* spectrophotometer (*NanoDrop Technologies*, Wilmington, DE, USA), and RNA integrity was confirmed by electrophoresis. The RNA from WT and transgenic tobacco was used for reverse transcription (RT) using *PrimeScript*™ RT reagent kit with genomic DNA eraser (*Takara*). All RT-qPCR reactions were performed in three biological replicates with *CFX96* real-time PCR detection system (*Bio-Rad*, Hercules, USA) and *SYBR® Premix Ex Taq™ II* (*Tli RNaseH Plus*) (*Takara*). Tobacco *β-tubulin* (GenBank accession number AJ421411) was used as an internal control to normalize the expression of other genes. Gene specific primers were designed by *Beacon designer 8.0* (Table 1 Suppl.). The reactions were carried out at 95 °C for 5 min, followed by 40 cycles (95 °C for 30 s, 60 °C for 30 s, and 72 °C for 30 s), followed by melting curve analysis: at 50 °C for 30 s and then at 65 - 95 °C (0.5 °C increments, 5 s for each). We retrieved

the gene sequences of tobacco from the database of *Sol Genomics Network* according to the latest tobacco genome annotation (Fernandez-Pozo *et al*. 2015).

Data analyses and statistics: Mean Ct value was calculated from the triplicates of each sample and the PCR specificity was determined by the melt curve analysis. Relative expression of each gene was calculated as $2^{-\Delta\Delta Ct}$ (Dussault and Pouliot 2006). The differentially expressed genes in WT and transgenic plants were identified by two criteria: fold change ≥ 1.5 and $P \leq 0.05$. The *SAS* software was used for statistical analysis.

Results and discussion

The *TERF1* induces genomes uncoupled 1 (*GUN1*) by more than 2-folds under drought stress conditions (Fig. 1). The *gun1* mutant can induce the *PhANGs* expression in the nucleus independently of chloroplast development (Mochizuki *et al*. 2001). As described in Fig. 1 Suppl. GUN1 acts as a hub for relaying the plastid retrograde signals to nucleus. GUN1 can relay different chloroplast signals to nucleus, including tetrapyrroles, plastid genes transcription (Kindgren *et al*. 2012, Tameshige *et al*. 2013), and nuclear-encoded proteins import into chloroplast (Kakizaki *et al*. 2009, Waters *et al*. 2009). Furthermore, *GUN1* also regulates the accumulation of plastid ribosomal protein S1 and plastid protein homeostasis (Tadini *et al*. 2012).

The ABA insensitive 4 (*ABI4*), significantly induced by *TERF1* (Fig. 1), acts downstream of *GUN1* because promoters of nuclear genes in response to *GUN1* are enriched with ABA response elements and over-expression of *ABI4* can rescue the *gun1* phenotype (Koussevitzky *et al*. 2007) The ABI4 directly regulates the expression of *PhANGs*, such as light-harvesting chlorophyll *a*/*b* binding protein 1.2 (*LHCb1.2*) gene (Fernandez-Pozo *et al*. 2015). Roles of a full plant homeodomain (PHD) type transcription factor with transmembrane domain (PTM) in GUN1-mediated signaling is controversial (Sun *et al*. 2011, Page *et al*. 2017). Our result showed that GUN1-mediated signaling did not correlate with significant induction of *PTM* (Fig. 1), which is in line with the results of Page *et al*. (2017). The above results have shown that TERF1 significantly activated the GUN1-mediated signaling pathway under drought stress conditions.

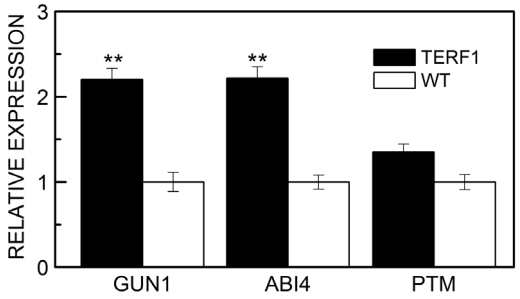

Fig. 1. Real-time quantitative PCR analysis of *GUN1*, *ABI4*, and *PTM* expressions in WT and TERF1 tobacco under drought stress. Means ± SDs, $n = 3$; * and ** - significantly different at 5 and 1 % level of probability, respectively.

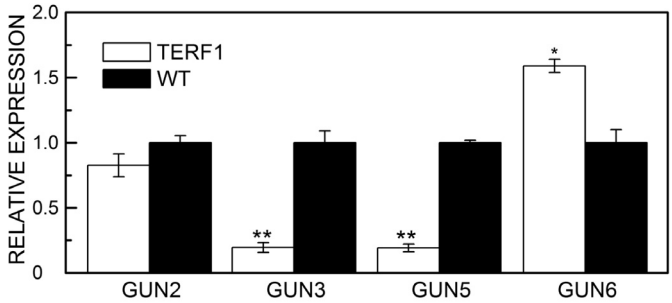

Fig. 2. Relative expression of genes involved in the metabolism of tetrapyrroles (GUN2 - GUN6) in WT and TERF1 tobacco under drought stress. Means ± SDs, $n = 3$; * and ** - significantly different at 5 and 1 % level of probability, respectively.

Another five *GUN* genes (*GUN2* - *GUN6*) were involved in the retrograde signaling. *GUN6* and *GUN3* were significantly induced and repressed by *TERF1*, respectively (Fig. 2), which can promote the heme accumulation. Heme is proposed to be the major tetrapyrrole signal that positively regulates the expression of *PhANGs* under stress conditions (Woodson *et al*. 2011). *GUN5* worked in the chlorophyll biosynthesis pathway and it was significantly repressed by *TERF1* (Fig. 2), which might divert the intermediates for chlorophyll synthesis into heme pathway. The *gun5* mutant could promote the accumulation of heme under stress conditions and so it prevents the accumulation of Mg-protoporphyrin IX (Mg-ProtoIX), leading to the derepression of *PhANGs* in the nucleus (Woodson *et al*. 2011, Schlicke *et al*. 2014). Induction of *GUN6* along

with repression of *GUN5* and *GUN3* leads to positive regulation of the *PhANGs* expression.

The *GUN1* can relay the plastid transcription signals to regulate nuclear gene expression (Kindgren *et al*. 2012). RNA polymerase of the phage T3/T7 type in plastids (RpoTp) and RNA polymerase of the phage T3/T7 type in plastids and mitochondria (RpoTmp) are encoded by the nucleus (NEPs). They were significantly repressed by *TERF1* (Fig. 3*A*). RpoTp and RpoTmp regulate chloroplast biogenesis and leaf morphogenesis, the concurrent repression of RpoTp and RpoTmp may cause severe growth retardation (Hricova *et al*. 2006). Plastid redox insensitive 2 (*PRIN2*) was significantly activated by *TERF1* (Fig. 3*A*). The *PRIN2* positively regulates plastid-encoded RNA polymerase (*PEP*) function and *PhANGs* expression (Kindgren *et al*. 2012). Moreover, the function of *PRIN2* is partially dependent on *GUN1* (Kindgren *et al*. 2012), so the concurrent induction of *PRIN2* and *GUN1* acts as a positive signal for *PhANGs* expression.

The nuclear-encoded sigma factors (SIGs) also account for plastid gene transcriptions, which confer *PEP* ability to recognize the specific promoter and initiate transcription (Schweer *et al*. 2010). Six sigma factors (*SIG1* - *SIG6*) have been identified in plants. Apart from *SIG4*, *SIG1*, *2*, *3*, *5*, *6* were all significantly repressed (Fig. 3*A*). The *SIG1* correlates with the balanced expression of components of photosystem (PS) I and II (Shimizu *et al*. 2010). Transcription of $tRNA^{Glu}$, starting precursor for tetrapyrrole biosynthesis, is dependent on *SIG2* and *SIG6* (Woodson *et al*. 2013). *GUN1* is involved in the signaling pathway partially through regulating the tetrapyrrole synthesis (Woodson *et al*. 2013). The *SIG5* is related to plant responses to abiotic stresses, changes of irradiance, and circadian rhythms (Belbin *et al*. 2017, Zhao *et al*. 2017).

Chloroplast sensor kinase (CSK) and chloroplast casein kinase 2 (cpCK2) are two kinases involved in plastid gene transcriptions, which regulate the activity of SIGs and PEP at posttranslational level (Steiner *et al*. 2011). The *CSK* was significantly induced by *TERF1* and no significant difference was observed for *cpCK2* (Fig. 3*A*). The CSK is a modified two-component sensor kinase for plastoquinone (PQ) redox state and SIG1 is its functional partner, which work together to regulate photosystem stoichiometry adjustments (Puthiyaveetil *et al*. 2012).

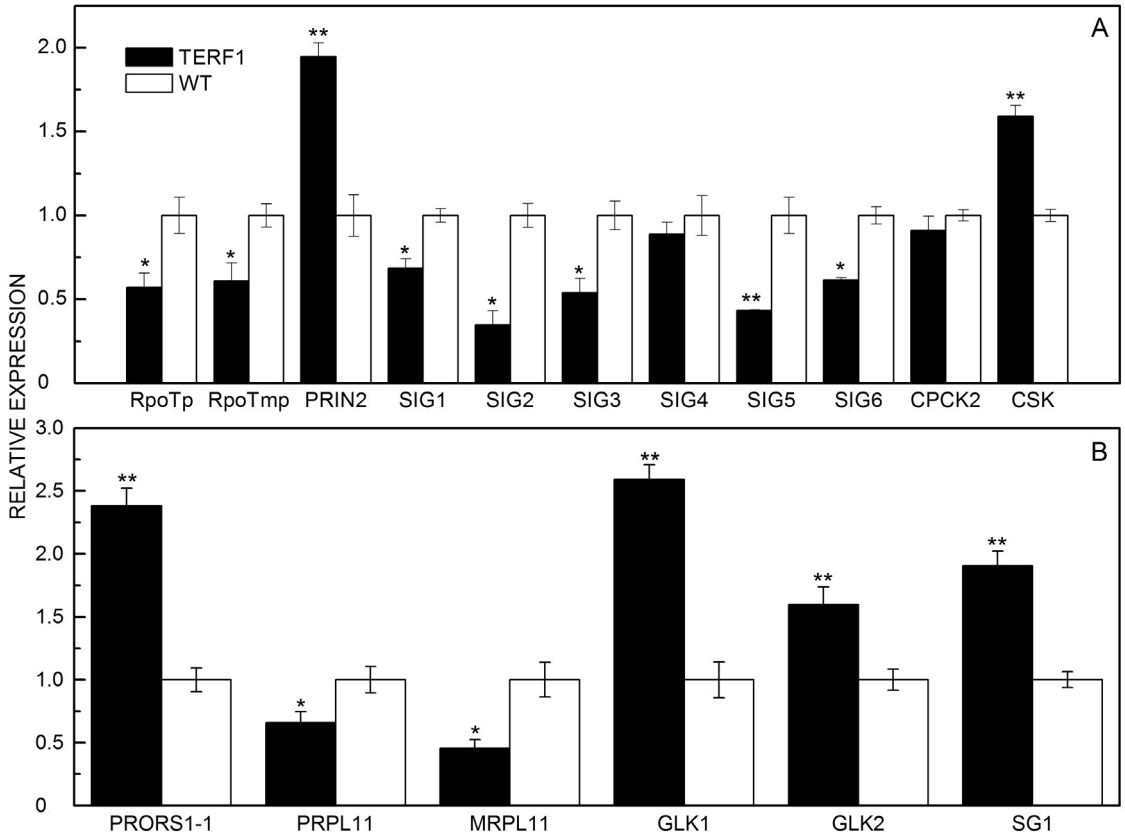

Fig. 3. Relative expression of genes involved in plastid gene transcription (*A*) and translation (*B*), protein import, and homeostasis in WT and *TERF1* tobacco under drought stress. Means ± SDs, $n = 3$; * and ** - significantly different at 5 and 1 % level of probability, respectively.

Plastid genes translation can also act as retrograde signals. Prolyl-tRNA synthetase 1-1 (PRORS1-1) positively regulates protein translation in chloroplasts and mitochondria (Pesaresi *et al*. 2006). The induction of *PRORS1-1* can significantly induce the expression of nuclear-encoded genes related with light reactions of photosynthesis (Pesaresi *et al*. 2006). The genes encoding plastid ribosomal protein L11 (*PRPL11*) and mitochondrial ribosomal protein L11 (*MRPL11*) were both significantly repressed by TERF1 (Fig. 3*B*). The *PRPL11* and *MRPL11* work together to regulate *PhANGs* expression (Pesaresi *et al*. 2006). The slow green 1 (*SG1*) is involved in plastid protein biosynthesis and/or degradation (Hu *et al*. 2014); it is also significantly induced by *TERF1* (Fig. 3*B*). The SG1 is also regulated by *GUN1* and regulates *PhANGs* expression and chloroplast development (Hu *et al*. 2014).

Golden 2-like (*GLK*) transcription factors, regulating the protein import from cytoplasm to chloroplast, are activated by plastid perturbations and regulate *PhANGs* expression dependent on *GUN1* (Kakizaki and Matsumura *et al*. 2009, Leister and Kleine 2016). The *GLK1* and *GLK2* are functionally redundant and they were both significantly induced by *TERF1* (Fig. 3*B*). The *GLK1* can induce the expression of glutamyl-trna reductase (*GLUTR*), the rate-limiting step for chlorophyll biosynthesis (Maekawa *et al*. 2015). The GLKs are also closely related with leaf growth and development, accumulation of GLK proteins is related with light harvesting and electron transport in PS II (Waters *et al*. 2008, Maekawa *et al*. 2015). Except for *CSK* and *SIG4*, all the nuclear-encoded genes for plastid transcription were repressed, but for the genes related with protein translation only *PRPLL11* was found to be repressed by TERF1. So we propose that *TERF1* exerted more negative effect on plastid genes transcription than their translation.

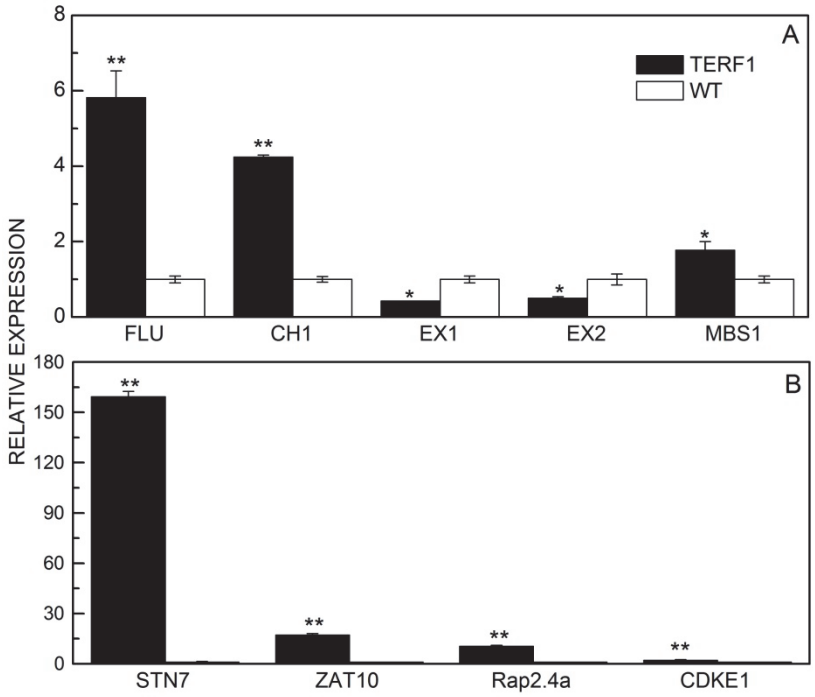

Fig. 4. Relative expression of genes involved in singlet oxygen (*A*) and plastid redox (*B*) signaling in WT and TERF1 tobacco under drought stress. Means ± SDs, $n = 3$; * and ** - significantly different at 5 and 1 % level of probability, respectively.

Singlet oxygen ($^1O_2$) and carotenoid oxidation products (β-cyclocitral and dihydroactinidiolide) regulate the expression of *PhANGs* and *SORGs* in plastids. Fluorescent (*FLU*) and Chlorina 1 (*CH1*) were significantly induced by *TERF1* (Fig. 4*A*). They regulate $^1O_2$ production and prevent β-cyclocitral and dihydroactinidiolide accumulation in plastids (Op den Camp *et al*. 2003, Ramel *et al*. 2013). Executer proteins (EX1 and EX2), responsible for the perception and transduction of the $^1O_2$ signals and for programmed cell death resulting from $^1O_2$ production (Lee *et al*. 2007), were significantly repressed by TERF1 (Fig. 4*A*). So, TERF1 not only inhibited the $^1O_2$ production but also blocked the $^1O_2$ signaling transduction under drought stress, which prevented the cell damage caused by $^1O_2$.

Methylene blue sensitivity (MBS) proteins (MBS1 and MBS2) and small zinc-finger proteins accumulate in distinct granules in the cytosol under stress conditions and positively regulate plant response to photooxidative stress, and their overexpression in plants improves stress tolerance (Shao *et al*. 2013). Only MBS1 was significantly induced by TERF1 (Fig. 4*A*). The MBS1 is supposed to act downstream of β-cyclocitral and to regulate plant growth and development (Shumbe *et al*.

2017). The MBS proteins acts in the cytoplasm and regulate untranslated mRNA (Shao *et al*. 2013), indicating that $^1O_2$ may also participate in the posttranscriptional regulation.

The environmental fluctuations change the redox state of photosynthetic electron transport chain through conversions between plastoquinol (PQH_2) and PQ as well as the oxidation or reduction of thioredoxin. These redox state changes regulate the expression of *PhANGs* and *PRANGs* (Fey *et al*. 2005, Brautigam *et al*. 2009). The state transition 7 (*STN7*) mediates state transition through phosphorylating LHC II and regulates the expression of *PRANGs* (Bellafiore *et al*. 2005), which was induced by more than 160-folds in *TERF1* plants (Fig. 4*B*). Phosphorylation of LHC II by *STN7* can maintain the thylakoid redox state and ROS in balanced conditions (Tikkanen *et al*. 2012). The induction of *PRIN2* (Fig. 3*A*) and *PRORS1* (Fig. 3*B*) in *TERF1* tobacco were also involved in the expression of *PhANGs* (Pesaresi *et al*. 2006, Kindgren *et al*. 2012). Nuclear response to redox changes involved transcription factors [salt tolerance zinc finger (*ZAT10*), related to *AP2.4* (*Rap2.4a*); Hiltscher *et al*. 2014, Rossel *et al*. 2007] and cyclin dependent kinase E1 (*CDKE1*) (Blanco *et al*. 2014), which were all significantly induced by *TERF1* (Fig. 4*B*).

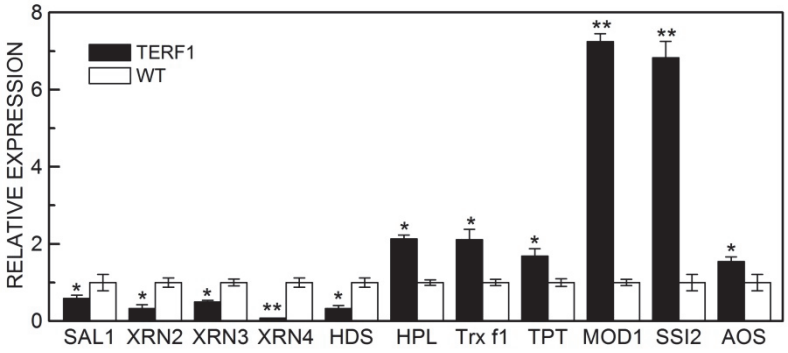

Fig. 5. Relative expression of genes involved in plastid metabolism in WT and TERF1 tobacco under drought stress. Means ± SDs, $n = 3$; * and ** - significantly different at 5 and 1 % level of probability, respectively.

The *PAP* can act as a retrograde signal and regulate nuclear gene expression. Repression of 3'(2'),5'-bisphosphate nucleotidase (*SAL1*) by *TERF1* (Fig. 5) could promote the accumulation of PAP and the inhibition of 5'-3' exoribonucleases (XRNs; Fig. 5) through prevention of the conversion of PAP into adenosine monophosphate (AMP; Estavillo *et al*. 2011). Repression of *XRN2, 3, 4* by *TERF1* (Fig. 5) could activate the expression of *PRANGs* and other stress-responsive genes (Estavillo *et al*. 2011), leading to decreased ROS accumulation and membrane damage, accumulation of osmoprotectants, and oxidative stress tolerance (Rossel *et al*. 2006, Wilson *et al*. 2009). The XRN2 and XRN3, located in the nucleus, are also found to act on uncapped RNAs, including precursor mRNA transcripts (Merret *et al*. 2013), demonstrating the potential of TERF1 in post-transcriptional regulation of gene expression, including gene silencing and mRNA turnover.

Methylerythritol cyclodiphosphate (MEcPP) can induce accumulation of the chloroplast-targeted hydroxyperoxide lyase (HPL) protein and SA under stress conditions (Xiao *et al*. 2012). The 1-hydroxy-2-methyl-2-(E)-butenyl-4-diphosphate synthase (HDS) can convert MEcPP into hydroxymethylbutenyl diphosphate (HMBPP) in the methylerythritol phosphate (MEP) pathway, which was significantly repressed by *TERF1* (Fig. 5). In plants, MEcPP is also proposed to be related with chromatin remodeling (Grieshaber *et al*. 2004), indicating another layers of gene expression regulation by *TERF1*. Additionally, MEcPP also participates in the induction of unfolded protein response (UPR) in endoplasmic reticulum (ER) by inducing one signaling branch of inositol-requiring enzyme 1 (IRE1), which functions in maintaining cellular protein homeostasis (Iwata and Koizumi 2012, Howell 2013).

Sugars in plastids act as signals regulating nuclear genes expression by sensing the sugars amount in cytosol, chloroplasts and nucleus (Hausler *et al*. 2014). The intermediates of the Calvin-Benson cycle and starch synthesis are the sources of retrograde signals. A plant thioredoxin protein Trx f1 was significantly induced in *TERF1* plants (Fig. 5). The Trx f1 regulates starch synthesis and Calvin-Benson cycle, and *Trx f1* mutant shows the inhibition of photosynthetic electron transport and disruption of the signals of starch synthesis and the Calvin-Benson cycle to the nucleus (Thormahlen *et al*. 2015, Geigenberger *et al*. 2017). Triose phosphate translocator (TPT) transported dihydroxyacetone phosphate (DHAP) from chloroplasts to cytosol and was significantly induced in *TERF1* plants (Fig. 5). The DHAP export from chloroplasts can cause the phosphorylation and activation of mitogen-activated protein kinase 6 (MPK6) as well as the *ERF-TF* genes (Vogel *et al*. 2014).

Fatty acids represent the last kind of retrograde

signals in chloroplasts. *MOD1* encoding enoyl-acyl carrier protein reductase, was significantly induced in TERF1 plants (Fig. 5). The induction of MOD1 can inhibit programmed cell death and development defects partially through modulating the ROS in mitochondria (Mou *et al*. 2000, Wu *et al*. 2015).

More than 6-folds induction of suppressor of salicylic acid insensitivity 2 (*SSI2*) in *TERF1* plants (Fig. 5) could induce the oleic acid accumulation and the expression of *R* gene (Kachroo *et al*. 2007). Oleic acid also correlates with NO synthesis as well as signaling mediated by NO (Mandal *et al*. 2012). Additionally the interaction between oleic acid and NO can lead to the accumulation of modified fatty acids, resulting in the improvement of plant stress tolerance (Mata-Perez *et al*. 2016).

Jasmonates and C6 aldehydes, the oxidative products of linoleic acid and linolenic acid in plants, are synthesized by the allene oxide synthase (AOS) and in HPL pathway, respectively (Chehab *et al*. 2008). The induction of HPL by *TERF1* (Fig. 5) could trigger the biotic stress signal (Frost *et al*. 2008). *AOS* expression was also significantly induced by *TERF1* (Fig. 5), resulting in the accumulation of 12-oxophyto-dienoic acid (12-OPDA) and the biosynthetic precursor for jasmonic acid (JA) and methyl jasmonate (Schaller and Stintzi 2009). So *TERF1* can induce the accumulation of jasmonates and aldehydes, simultaneously. The 12-OPDA itself also acts as retrograde signal independent of jasmonates, leading to the stomatal closure related to ABA signaling pathway in response to drought (Park *et al*. 2013, Savchenko *et al*. 2014).

The *TERF1* is a transcription factor belonging to ERF family that regulates multiple plastid retrograde signals under drought stress conditions, demonstrating the interaction between ethylene and plastid retrograde signaling pathway under drought stress conditions (Fig. 1 Suppl.). *TERF1* may initiate other plant hormone signaling through retrograde signals in plastids under drought stress. It may activate ABA signaling through 12-OPDA accumulation (Park *et al*. 2013, Savchenko *et al*. 2014) and *ABI4* activation, an important transcription factor in ABA signaling pathway (Shu *et al*. 2013). *ABI4* also participates in the biosynthesis of gibberellins (Shu *et al*. 2013), in the enhancement and in the inhibition of SA and JA signaling pathways, respectively (Foyer *et al*. 2012).

The fatty acid retrograde signaling in *TERF1* plants can activate the JA and NO-mediated signaling by inducing *AOS* and *SSI2*, respectively. *TERF1* may also negatively regulate auxin biosynthesis, transport, and, homeostasis through repressing *SAL1*, which leads to the positive regulation of ABA signaling and inhibition of JA biosynthesis (Robles *et al*. 2010, Rodriguez *et al*. 2010, Chen *et al*. 2011, Zhang *et al*. 2011). *TERF1* also positively regulates the sugar signaling mediated by *Trx f1* and *TPT*.

TERF1 regulates plant growth and development through retrograde signals. The upregulation of *GUN1* in *TERF1* plants can promote hypocotyl elongation and cotyledon expansion (Ruckle and Larkin 2009). *GUN1* also promotes the establishment of photoautotrophic growth, influences the cell differentiation at shoot apex and regulates plant circadian clock (Mochizuki *et al*. 2001, Hassidim *et al*. 2007, Wilson *et al*. 2016). Signals of plastid gene expression regulate leaf growth and development through *GUN1*, including regulating adaxial-abaxial specification in leaf primordium (Tameshige *et al*. 2013). The *SIG6*, *GLKs*, and *SG1* also regulate chloroplast development, leaf growth, plant development, and senescence through *GUN1* (Pesaresi *et al*. 2001, Rauf *et al*. 2013, Hu *et al*. 2014, Garapati *et al*. 2015).

MEcPP accumulation in *TERF1* plants positively correlates with early flowering and dwarfed phenotype through downregulation of B-boxdomain protein 19 (*BBX19*) (Xiao *et al*. 2012, Wang *et al*. 2014, 2015, Wang and Dehesh 2015). The upregulation of *MBS1* by *TERF1* also has positive effects on plant growth and development (Shumbe *et al*. 2017). However, downregulation of *NEP*, *PRPL1*, and *MRPL11* by *TERF1* negatively affect plants growth and development (Hricova *et al*. 2006, Pesaresi *et al*. 2006).

The *TERF1* regulates nuclear gene expression by GCC box and dehydration responsive element (Huang *et al*. 2004). We found that *TERF1* might regulate gene expression in many diversified ways. Firstly, *TERF1* could regulate the plastid genes transcription and translation (Fig. 2). Secondly, *TERF1* could also alter the organization of the chromatin structure through regulating the MEcPP content (Xiao *et al*. 2012). Thirdly, *TERF1* might regulate nuclear genes expression through regulation of plant hormone signaling pathway as described above. Fourthly, *TERF1* might also regulate gene expression at posttranscriptional level by regulating *XRNs*.

TERF1 plays diversified roles in plant response to drought stress through regulating different chloroplast retrograde signals. The retrograde signals from chloroplasts mediated by *TERF1* may regulate nuclear genes expression through multiple ways, including different plant hormone signaling pathways and gene expression at different levels. Elucidating the detailed mechanism of the above process may improve our knowledge of ERF proteins and ethylene signaling pathways.

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