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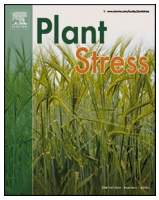

Peroxisome-dependent transcription factors respond to biotic and abiotic stresses in Arabidopsis and tomato

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ABSTRACT

Plants adapt to environmental challenges through complex mechanisms. They rapidly activate metabolic pathways in response to stress, relying on signaling molecules such as reactive oxygen species (ROS) for cell-to-cell communication. Peroxisomes, key subcellular organelles that regulate ROS metabolism and signaling, house a wide enzymatic antioxidant system including catalases (CAT) and the ascorbate-glutathione cycle enzymes. This study identifies a set of catalase-dependent transcription factors (TFs) transcriptionally regulated during abiotic and biotic stress responses in Arabidopsis. Additionally, it examines whether their regulation is conserved in an important crop like tomato, aiming to deepen our understanding on the functions of peroxisomes in plant stress responses. The orthologues of these Arabidopsis TFs in tomato were all regulated under stress, responding to different adverse conditions, including salt and heat stress, and pathogen and/or herbivore attack, supporting their conserved functionality in stress responses. The results pinpoint these selected TFs, regulated in response to multiple stresses in Arabidopsis and tomato, as targets for biotechnological applications to enhance crop resilience to cope with climate change challenges.

1. Introduction

Plants, growing in ever-changing environments, have to cope with very diverse stressors. They have to fine-tune the more appropriate response to cope with them, and for that, they have developed complex regulation networks shaping mechanisms for stress sensing and protection (Suzuki *et al.*, 2015; Kollist *et al.*, 2019). Recent research has shown that plants can react to some of these stresses within seconds, activating different responses at the molecular and metabolic levels. Cell-to-cell communication and long-distance signaling are essential for plants to coordinate their responses to harsh environmental conditions (Miller *et al.*, 2009; Kollist *et al.*, 2019). Some signals involved in plant response to stress include molecules such as calcium and reactive oxygen species (ROS), as well as hydraulic and electrical waves (Fichman and Mittler, 2020). In fact, plants have evolved to use low concentrations of ROS as signals under specific physiological and stress conditions (Xie *et al.*, 2019). Different genetic and pharmacological approaches have shown that diverse ROS types can influence nuclear gene expression in response to environmental stimuli. In particular, due to its stability compared with other ROS, hydrogen peroxide (H_2O_2), plays a crucial role in plant signal transduction (Nazir *et al.*, 2020). However, a precise balance between ROS production and scavenging is essential to control their dual role as both cytotoxic agents and signaling molecules (Romero-Puertas and Sandalio, 2016). One mechanism to protect cellular components from the harmful effects of ROS is organelle compartmentalization, which also increases the efficiency of cellular processes (Kao *et al.*, 2018). Peroxisomes, which are single membrane-enclosed organelles, housing different phytohormone biosynthesis pathways and producing signaling molecules such as ROS and reactive nitrogen species (RNS) through different metabolic pathways, are now recognized as critical decision-making hubs in the cell (Sandalio *et al.*, 2023). The complete antioxidant system of peroxisomes allows them to regulate ROS and RNS levels, and as a consequence, their signaling function during stress responses (Sandalio and Romero-Puertas, 2015; Giulietti *et al.*, 2024).

One of the antioxidant enzymes considered to be primarily localized

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in peroxisomes is catalase (CAT), which converts H_2O_2 into water and oxygen (Mhamdi *et al.*, 2012). So far, three catalase genes have been identified in Angiosperm species, being *CAT2* the crucial isoform for preventing redox imbalances under ambient air conditions (Queval *et al.*, 2007). Arabidopsis CAT mutants, mainly *cat2*, have been extensively analysed to underscore the potential role of this enzyme and in particular, of peroxisomal H_2O_2 in plant physiology (Mhamdi *et al.*, 2010a; Foyer and Noctor, 2020). Therefore, a decrease in CAT and as a consequence, an increase in peroxisomal H_2O_2 has been shown to have an impact on plant responses to pathogens (Chaouch *et al.*, 2010), inducing defence mechanisms associated with hormone signaling, mainly related to jasmonic acid (JA), salicylic acid (SA) and auxins (Chaouch *et al.*, 2012; Gao *et al.*, 2014; Yuan *et al.*, 2017). Hundreds of genes related to metabolic redox signaling are also altered in *cat2* mutants (Vanderauwera *et al.*, 2005; Queval *et al.*, 2012; Phua *et al.*, 2021; Sandalio *et al.*, 2021). These results suggest that ROS produced in peroxisomes can activate hypothetical retrograde signaling, to regulate defence systems (Sewelam *et al.*, 2014; Su *et al.*, 2019; Terrón-Camero *et al.*, 2022) although the precise mechanisms are yet to be uncovered. Retrograde signaling from organelles adjusts nuclear gene expression according to their developmental and physiological states. While this process is more studied in mitochondria and chloroplast during stress responses, it is hardly known in peroxisomes (Phua *et al.*, 2021). Currently, retrograde signaling has expanded to include metabolites, cytosolic signaling cascades, and transcription factors (TFs) involved in operational control (Klein and Leister, 2016). TFs play a crucial role in regulating cellular functions, as they coordinate transcriptional regulation of responses to stress. Their primary roles involve locating specific DNA sequences for binding and recruiting other proteins to these sites (Strader *et al.*, 2022). During signal transduction, they function as molecular switches by directly regulating the expression of selected genes. Remarkably, several transcription factors were quickly regulated in *cat2* mutants exposed to high light, confirming that they are dependent on peroxisomal H_2O_2 (Mhamdi *et al.*, 2010b). Only a few of these TFs are now well-established as regulators of abiotic stress responses (Mhamdi *et al.*, 2010b; Davletova *et al.*, 2005b; Ogawa *et al.*, 2007).

A previous report identified a list of genes hypothetically regulated by peroxisomal H_2O_2 in Arabidopsis, the so-called peroxisomal transcriptional footprint (PTF; Terrón-Camero et al., 2022). In this study, we look for transcription factor activity within the PTFs and identify key transcription factors that are essentially dependent on peroxisomal H_2O_2. We analysed their transcriptional regulation in Arabidopsis in response to abiotic and biotic stress, and confirmed that they are regulated by different stressors. We then aimed to explore if these findings in the model plant allows the identification of key transcription factors on other plant species of agronomic importance. Accordingly, we looked for the tomato orthologues of these Arabidopsis TFs, and analysed if their regulation in plant response to stress could be conserved between species. Our analysis revealed a conserved regulation pattern and suggest that the selected TFs are likely ROS regulated hubs in the transcriptional networks regulating plant responses to diverse stresses. The results would help us to unravel peroxisomes' function, and the mechanisms mediating their function in plant response to stress. The results aim to contribute to identify targets for biotechnological applications to improve crop resilience.

2. Material and methods

2.1. Plant material and growth conditions

For Arabidopsis bioassays, *Arabidopsis thaliana* wild type and *cat2–2* seeds (Col-0 as background; Queval et al., 2007) were used. After surface sterilization and stratification for 24–48 h, seeds were grown for 2 weeks on MS medium (Murashige and Skoog, 1962) at 22/20 °C day/night, 60 % humidity, 16/8 h light/dark photoperiod and 100 μE irradiation for control conditions. For salinity treatment, plants were acclimated for 24 hours in liquid MS and then transferred to liquid MS with or without (control conditions) 100 mM NaCl. Seedlings were then harvested at 1, 3, and 24 hours post-treatment. For heat stress conditions, the temperature was raised to 33 °C for 1, 3, and 24 hours prior to harvesting. A minimum number of 3 seedlings per replicate for Arabidopsis genotype, treatment and time point were harvested. The experiments were independently repeated twice and representative data from one of them is shown.

For tomato bioassays, *Solanum lycopersicum* cv Moneymaker and cv Castelmart were used. Seeds were surface sterilized and placed in humid sterile vermiculite for germination. Before the true leaves appeared, the seedlings were transferred to 300 mL pots containing 1:1 sand:vermiculite substrate and were grown in a greenhouse at 24/20 °C (day/night), 60 % humidity and 16/8 hours of light/dark period. Twice a week, plants were added with 0.5x Long Ashton nutrient solution (Hewitt, 1953). For abiotic stress experiments, four-week-old plants were challenged with 100 mM NaCl or 35 °C heat stress for 1, 3, and 24 hours. Just before treatments, pots were watered to field capacity. For chemical elicitation with the damage-associated signals oligogalacturonides, eight-week-old *Solanum lycopersicum* cv Castelmart tomato plants were treated with aqueous oligogalacturonides solution (50 μg/mL in MilliQ water) in shoots. Oligogalacturonides, with a degree of polymerization between 10 and 15, were obtained from a PGA solution (2 % w/v; Alfa Aesar) incubated with endo-polygalacturonase II (0.1 RGU/ml), purified from *Aspergillus niger* Pectinase (Sigma) as previously described by Gamir and collaborators (2021). Finally, for addressing responses to biotic stress, we analysed plant responses to the necrotrophic fungal pathogen *Botrytis cinerea* or to infestation by chewing herbivores. For *B. cinerea* bioassay, *the fungus* was cultivated in potato dextrose agar plates and incubated at 20 °C for three weeks. Then, the spores were collected from plates in 0.5x potato dextrose broth as previously described (Sanmartín *et al.*, 2020). Pathogen inoculation was performed on four-week-old *Solanum lycopersicum* cv Moneymaker plants by spraying either with a conidia suspension (1×10^6 spores/ml) of *Botrytis cinerea* or a mock solution as a control, and leaves were harvested 24 h post infection (Dejana et al., 2022). For the herbivore bioassays *Solanum lycopersicum* cv Moneymaker plants were challenged by applying 2 larvae of the L2 stage from either *Spodoptera exigua* or *Manduca sexta* as previously described (Lidoy *et al.*, 2024). A minimum number of 3 biological replicates for tomato plants were harvested for each treatment and time point.

2.2. RNA isolation and expression quantification

Total RNA was isolated using TRIzol reagent (Invitrogen), and DNase was used according to the manufacturer's protocol (Ambion DNA-free). 1 μg RNA was reverse transcribed with 5x PrimeScript RT Master Mix (Takara) as described elsewhere (Rodríguez-Serrano et al., 2016). Quantitative real-time PCR was performed on a QuantStudio3 thermocycler (Applied Biosystems) using TB Green Premix ExTaq (Takara). The samples were initially denatured by heating at 95 °C for 3 min followed by 35-cycle amplification and a quantification program (95 °C for 30 s, 50–60 °C for 30 s, and 72 °C for 45 s). Amplification efficiency was calculated using the formula $E = [10\ (1/a) - 1] \times 100$, where "a" is the slope of the standard curve. The relative expression of each gene was normalized to that of *TUB4* (tubulin) for *Arabidopsis thaliana* and *EF* (elongation factor) for *Solanum lycopersicum*, and the results were analysed using the method described by Pfaffl (2001). The primers used in this genetic expression assay are described in Supplementary Table S1.

2.3. In silico analyses

We used the genes so-called peroxisomal transcriptional footprints (PTFs) provided by Terrón-Camero *et al.* (2022) to obtain the transcription factors described in the present manuscript. This group was filtered by GOs (Gene Ontology terms) associated with transcription

regulation categories such as GO:0006,355, GO:0003,700 and GO:0044, 212. Then, the TFs that were in common with the differentially expressed genes (DEGs) obtained in the Arabidopsis triple knock-out catalase mutant were selected (Su *et al.*, 2018) by using Venny 2.1.0 (Oliveros, 2007–2015). For Classification of the Arabidopsis TFs into different GOs categories, an analysis using the Classification Super Viewer tool (https://bar.utoronto.ca/ntools/cgi-bin/ntools_classification_superviewer.cgi), StringDB (https://string-db.org/) and GeneMania (Warde-Farley *et al.*, 2010) using the background for *A. thaliana* and running on default parameters was carried out. To search for all the described Arabidopsis orthologues in *Solanum lycopersicum*, ePLANT, ENSEMBLplants and PANTHER databases (Fucile *et al.*, 2011; Thomas *et al.*, 2022; Yates *et al.*, 2022) were used.

2.4. Analysis of transcriptome databases

Heatmaps of expression profiles were generated using the GEO DATASETs web interface with the default parameters and other public repositories depending on the author's supplementary material provider. The transcriptome datasets analysed on *Arabidopsis thaliana* are 3 groups of cytosolic, mitochondrial and chloroplastic ROS sources studies summarized in Supplementary Fig. S2 (1a to 3b) and 42 more studies that are reflected in Fig. 3 encompassed in wounding, herbivory, necrotrophic, damage and microbe-associated molecular pattern and hormone treatment conditions (4 to 45). Their respective GSE code is included in the references enlisted in the Supplementary Table S2. Genes were considered as differentially expressed regarding the authors' criteria.

2.5. Statistics

To test the effect of the different abiotic and biotic stresses on the gene expression of the selected TFs, pairwise comparisons between stress treatments and their corresponding controls were performed with a two-tailed Student's *t*-test using Excel software. When data did not follow a normal distribution, Wilcoxon signed-rank non-parametric test was followed. Values marked with "+" in relative expression data, represent a tendency but with a p-value ≤ 0.1 while values marked by an asterisk represent significantly different comparisons with control conditions (p-value ≤ 0.05). A number sign (#) is added when significant differences due to the genotype are found (p-value ≤ 0.05). Error bars shown in the figures represent standard error (SEM). To create the figure plots R software was used, including ggplot2 (Wickham, 2016), plotly (Sievert, 2020) and heatmaply (Galili *et al.*, 2017) packages.

3. Results and discussion

3.1. Peroxisomal-dependent transcription factors in Arabidopsis

A key feature of peroxisome function in plant development and plant response to stress is supposed to be the regulation of gene expression networks (Rosenwasser *et al.*, 2013; Sewelam et al., 2014). However, the molecular mechanisms underlying the organization of these gene networks need to be established. Previously, we identified several peroxisomal-dependent genes (Peroxisomal Transcriptional Footprint, PTF) in Arabidopsis following the interrogation of data sets from transcript profiling in mutants with altered peroxisomal H_2O_2 metabolism (Terrón-Camero *et al.*, 2022). Transcription factors (TF) directly regulate their target genes by binding to short cis-regulatory DNA sequences. Aiming to identify PTF genes that could regulate peroxisomal-dependent gene networks, we look for transcription factor activity within the PTF set. A total of 22 peroxisomal-related TFs were extracted from the PTF, 14 related to early ($\leq$ 8 h) and 8 related to late ($\geq$ 24 h) plant responses to stress (Supplementary Table S3). To further assess the peroxisomal dependence of these TFs, we applied a new filter and compared our 22 TF list with DEGs in the triple knock-out mutant *cat1/2/3*, which is affected in the three peroxisomal catalase genes present in Arabidopsis (Su *et al.*, 2018). A total of 6 TFs were found in common, 5 related with early and 1 related with late plant responses to stress (Supplementary Fig. S1 A). To obtain an integrative regulatory network reporting interactions within our group of TFs we used the algorithm GeneMANIA. The 6 TFs (in the core of Supplementary Fig. S1 B) show a closely related co-expression network (around 60 %) and different interactors (located in the outer circumference of Supplementary Fig. S1 B), being more than 50 % TFs also. The analysis suggests that the selected TFs may be at the top of the plant response to the stress network. Interestingly, within the interactors we found two TFs, *AtERF109/AtRRTF1* and *AtERF018/AtORA47,* related previously with peroxisomal-dependent signaling (Terrón-Camero *et al.*, 2022; Rodríguez-Serrano *et al.*, 2016), thus completing the list of peroxisomal-dependent TFs with a total of 8 (selected TFs from now on; Table 1).

The regulation of the selected TFs for each of the experimental conditions described in Terrón-Camero *et al.* (2022) is represented in Fig. 1A. We obtained 2 gene cores, one encompassing *AtAGL3* and *AtERF56* and the other with the remaining TFs. The first cluster appears to be less responsive and when it does, it has an antagonist regulation with respect to the second cluster. This occurs in experiments with short high light treatments and the Arabidopsis mutants with an H_2O_2

Table 1
List of the *Arabidopsis thaliana* selected TFs and their respective orthologues in *Solanum lycopersicum*. Gene identifiers from the selected TF in Arabidopsis and their orthologues in *Solanum lycopersicum* are highlighted in bold. The gene names used for those identifiers in the literature are between brackets. Especially for tomato (*Solanum lycopersicum*), when no consensus name is found in literature, we proposed a name similar to that of Arabidopsis to facilitate the comparison between species. The gene name used across this manuscript is double underlined. Score: Gene order conservation score (ranged from 0 to 100 %). AP2/ERF: summarizes whether the TF belongs to APETALA2 superfamily (Y) or not (N).

Arabidopsis thaliana ID and known name	*Solanum lycopersicum* ID and known name	Sequence similarity/ Score	Read counts	AP2/ ERF
AT2G22200 (ERF56)	**SOLYC04G054910** (ERF.H10/ERF13/ ERF56-like)	39 %/-	20932	Y
AT2G03710 (AGL3/SEP4)	**SOLYC03G114840** (MADS1/EJ2)	58 %/-	56	N
	SOLYC04G005320 (CMB1/J2/LIN)	57,14 %/52,71 %	6	N
	SOLYC05G012020 (RIN)	33 %/50,78 %	1	N
AT1G22810 (ERF19)	**SOLYC01G057080** (ERF1-5_DREB/ERF20/ ERF19-like)	48,67 %/38,19 %	31	Y
AT5G59820 (RHL41/ ZAT12)	SOLYC03G093870 (-)	-	0	N
	SOLYC05G054650 (ZFP19/ZAT11-l/ZAT12-like)	-	35	N
AT1G80840 (WRKY40)	**SOLYC03G116890** (WRKY39)	44,57 %/51,66 %	7936	N
	SOLYC06G068460 (WRKY40)	43,06 %/51,32 %	4578	N
	SOLYC12G042590 (WRKY43)	45,24 %/37,75 %	37	N
AT1G74930 (ERF18/ ORA47)	**SOLYC12G009240** (ERF4/ERF16/ERF17)	37,5 %/47,69 %	10	Y
AT4G34410 (ERF109/ RRTF1)	**SOLYC01G108240** (SlERF.D3/RRTF1)	32,91 %/38,81 %	179	Y
	SOLYC10G050970 (SlERF.D4/RRTF1-like)	45,29 %/37,69 %	34	Y
AT2G44840 (ERF13)	SOLYC01G090370 (Rin/ JRE4/JRE5/ERF.B9/ ERF5)	-	0	Y
	SOLYC05G050790 (ERF.B11/JRE6/ERF1/ ERF13-like)	-	2	Y

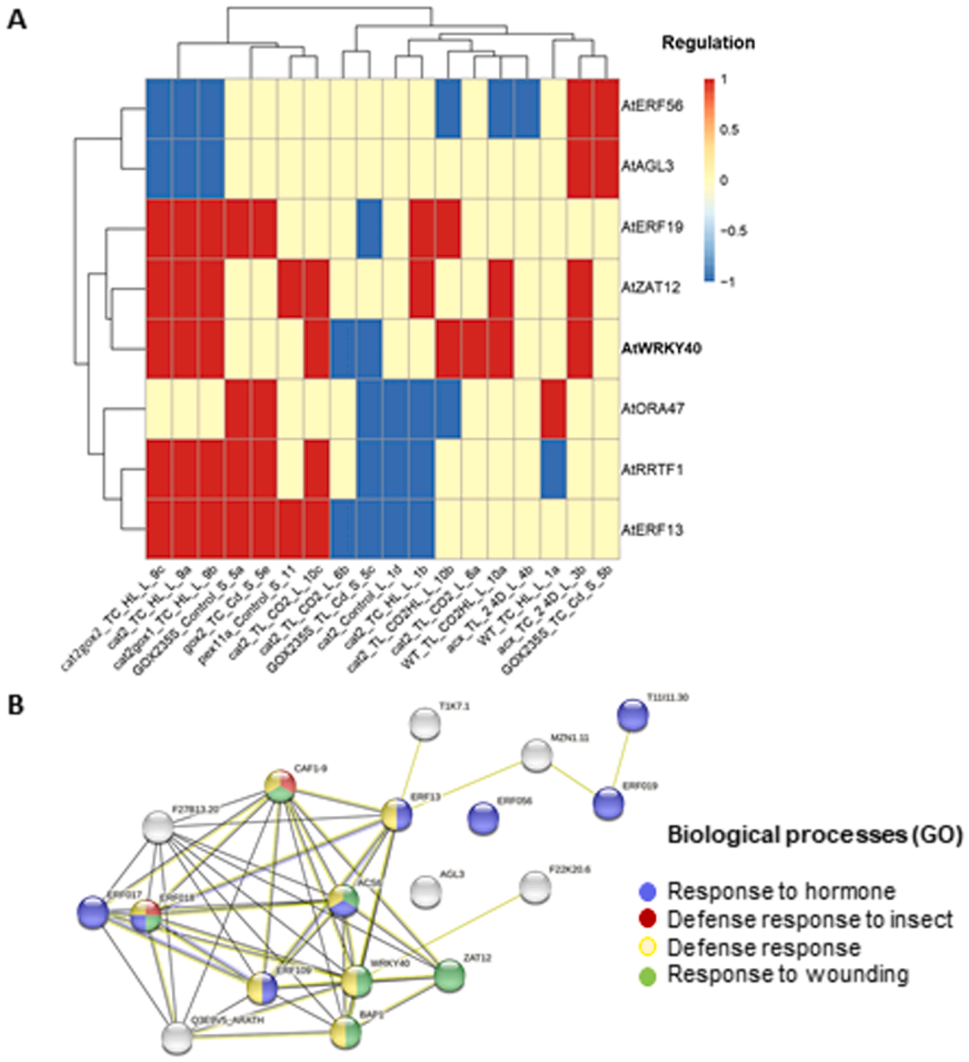

Fig. 1. Peroxisomal TFs regulation and network in Arabidopsis. A) Heatmap showing the regulation of the selected TFs under different experimental conditions (HL: high light, treatment with the herbicide 2,4-D, Cd or a shift from high CO_2 to air conditions) from the meta-analysis carried out by Terrón-Camero *et al.* (2022). Values are ranged between −1 (repression) and 1 (induction). The TF responsive to long-term treatments is highlighted in bold. B) StringDB analysis of the selected TFs showing 10 interactors in the first nutshell and assuming medium confidence in all available databases. The nodes were colored by the different biological process categories. In green: wounding response; in yellow: defence response; in red: defence response against insect and in blue: hormone response. ORA47 and RRTF1 correspond to ERF018 and ERF109 respectively.

impairment. This is also observed even in wild-type plants or in the peroxisomal ROS-altered mutant, *acx1*, under different stress conditions. On the other hand, the other gene core is generally upregulated in H_2O_2-impaired mutants under different stress conditions such as high light, heavy metals or changes in CO_2 concentration as well as in control conditions, but mostly during short stress exposures. In addition, there is another group of experiments in which the genes tend to be repressed when the *cat2* mutant is exposed to different stresses (Fig. 1A).

Interestingly, 5 of the selected peroxisomal-dependent TFs belong to the APETALA2/ethylene-responsive (AP2/ERF) superfamily which forms a large family of TFs predominantly found in plants (Table 1). These transcription factors play key regulatory roles in different biological and physiological processes, including plant morphogenesis, stress response mechanisms, hormone signaling, and metabolite regulation (Feng *et al.*, 2020). Furthermore, among the 8 selected TFs, 5 have been identified in the 124 ROS-related TFs extracted from the iGRN (integrated gene regulatory network; Supplementary Fig. S1 C; De Clercq *et al.*, 2021). This 124 TF list was extracted from the iGRN by identifying the TFs that entailed an enrichment for core ROS-responsive genes (ROS marker genes) within their target genes. Whether our selected TFs had been previously related to plant responses to ROS and/or ROS-inducing treatments is reflected in Supplementary Fig. S1 C. The remaining 3 uncommon genes have been described to have a function in plant development in which ROS are also involved (*AtAGL3*; Ditta et al., 2004; Liu et al., 2013), in hormone regulation and stress responses (*AtORA47*; Chen et al., 2016) and an unknown function (*AtERF56*). To further obtain information about the biological processes (GO categories) of the selected TFs and to interconnect molecular networks, we used the STRING database (Szklarczyk *et al.*, 2023). Therefore, a STRING-based network after adding 10 interactors in the first nutshell to an initial set with the selected TFs and assuming medium confidence in all available databases, was obtained (Fig. 1B). One main cluster with six of the eight selected TFs was obtained, being another TF (*AtERF19*) connected to this cluster through *AtERF13*. The selected TFs were enriched in the biological processes of "response to hormone", and remarkably, to "defence response" and in particular, "defence against insects" and "response to wounding" (Fig. 1B). Although the selected TFs were obtained from different data sets related with abiotic stress processes, the data support their involvement on biotic stress responses, and therefore, they may be interconnecting the responses to abiotic and

biotic responses.

To further assess whether the selected TFs could also be regulated by ROS produced in other organelles or cell compartments, we analysed their regulation in different transcriptomic datasets from *flu, aox1* and *apx1* mutants, related with chloroplastic-, mitochondrial- and cytosolic-ROS dependent signaling, respectively (Davletova *et al.*, 2005a; Lee *et al.*, 2007; Giraud *et al.*, 2008). Only *AtWRKY40* was found to be regulated in the dark to light swift in the *flu* mutants and in the *apx1* mutants under control and after short-term HL (high light) stress (Supplementary Fig. S2). It has been shown that *WRKY40* modulates the expression of stress-responsive nuclear genes encoding mitochondrial and chloroplast proteins (Van aken *et al.*, 2013). Furthermore, it has been suggested recently that the nuclear-encoded chloroplast proteins EXECUTER1 (EX1) and EX2 interact in the nucleus with AtWRKY40 and AtWRKY18 regulating singlet oxygen-dependent nuclear genes (Lee and Kim, 2024). These results suggest that *AtWRKY40* might be a common node in the ROS-dependent retrograde signaling from organelles. Similarly, *AtZAT12* is regulated in *apx1* mutants only after short-term HL stress (Supplementary Fig. S2). Although APX1 is located in the cytosol, the ROS flow from organelles, such as chloroplast and peroxisomes, into the cytosol cannot be discarded (Castro *et al.*, 2021), and therefore, signaling in *apx1* mutants could also be due to ROS coming from organelles. None of the other selected TFs showed regulation in the organelle mutants analysed, suggesting that their peroxisomal-dependent regulation may be specific.

3.2. Experimental validation of peroxisomal-dependent transcription factors

For experimental validation of the stress regulation of the selected TFs, we used Arabidopsis WT and loss of function *CAT2* plants (*cat2–2; cat2* from now on). Arabidopsis *cat2* plants are deficient in peroxisomal catalase and have been widely used as a model system to simulate elevated peroxisomal endogenous H_2O_2 levels in a non-invasive and physiologically relevant way (Mhamdi *et al.*, 2010a). To extend the knowledge of the regulation of the selected TFs, we analyzed their regulation under two abiotic stress conditions, salinity and heat stress, not included in the previous study by Terrón-Camero et al. (2022) to identify the PTF. Two early (1 and 3 h) and one late (24 h) time-points were analyzed after salinity (100 mM NaCl) or heat stress (33 °C) treatments (Fig. 2A). Although the specific regulation pattern differs for each of the TFs and stress applied, in the WT all of them were upregulated in response to the stresses except for *AtAGL3* and *AtERF56*, which are down-regulated after 3 and 24 h of heat stress, respectively. This regulation is similar to their profile under HL stress as shown in the previous heatmap (Fig. 1A), showing an opposite trend compared to the other TFs in response to heat stress. However, *AtAGL3* and *AtERF56* were up-regulated under salt stress, showing a similar pattern of regulation to the other TFs, supporting the stress specificity in the TF regulation pattern. In *cat2* mutants however, PTF expression changes are mainly altered or attenuated under both stress conditions. In particular, *AtAGL3* upregulation under salt stress and downregulation of *AtERF56* under heat stress were not observed in *cat2* mutants. This result supports the link of peroxisomal H_2O_2 to the regulation of both TFs, although it appears to be dependent on the specific stress applied (Fig. 2A).

The most responsive TFs are *AtWRKY40* and *AtRRTF1*, upregulated in WT in response to both short and long-term treatments with salt and heat stress, suggesting that these TFs are positive regulators of plant response to both stresses (Fig. 2B and Supplementary Fig. S3). In fact, *AtRRTF1* was reported to confer salt tolerance in Arabidopsis plants (Bahieldin *et al.*, 2016). Interestingly, Pandey et al. (2010) demonstrated the direct, in vivo physical interaction of *AtWRKY40* to the W box containing promoter regions of *AtRRTF1*, which could explain the similar regulation pattern observed. However, the regulation of *AtWRKY40* and *AtRRTF1* transcription under heat and salt stress that we observed in WT was impaired in *cat2* mutants (Fig. 2B, Fig. 2C and Supplementary Fig. S3) supporting that peroxisomal H_2O_2 is also involved in the regulation of these TFs.

AtZAT12 is also upregulated under salinity and heat shock stress in WT plants and in contrast, in the *cat2* mutant a downregulation by heat stress was observed (Fig. 2B and Supplementary Fig. S3). Again, the results suggest that peroxisomal ROS are involved in *AtZAT*12 regulation at least, after heat stress. *AtZAT12* expression is triggered by different stresses including light, low temperatures, wounding, osmotic and salinity stress, as well as oxidative stress. Moreover, plants with a loss-of-function mutation in *AtZAT12* showed increased sensitivity to light, H_2O_2, salinity, osmotic, and heat stress, while *AtZAT12* overexpression enhanced tolerance to high light, oxidative, osmotic, and cold stress (Davletova *et al.*, 2005b; Le *et al.*, 2016). Thus, the experimental data support that *AtZAT12* plays a central role in reactive oxygen and abiotic stress signaling in *Arabidopsis*. On the other hand, *AtORA47* and *AtERF19* are upregulated in WT response only to salt stress while upregulation in *cat2* mutants is weaker and only observed at the beginning of the treatment (Fig. 2B and Supplementary Fig. S3). An induction of *AtERF19* is observed in *cat2* mutants after 1 h of heat stress while no changes are observed in WT however. *AtERF19* has been proposed to enhance Arabidopsis tolerance to drought stress (Huang *et al.*, 2019). *AtORA47* has been shown to be gradually induced within 10 h of wounding (Wang *et al.*, 2008), and it is suggested to contribute to the biosynthesis of JA among other hormones (Chen *et al.*, 2016). JA signaling plays a crucial role in mediating defence mechanisms against biotic and abiotic stresses (Wasternack and Hause, 2013). Finally, *AtERF13* is upregulated only in WT response to heat stress, while in *cat2* mutants *AtERF13* expression did not change in any of the stresses applied (Fig. 2B and Supplementary Fig. S3). However, *AtERF13* has been previously shown to be upregulated after high salinity treatment by Lee et al. (2010).

3.3. Peroxisomal-dependent transcription factors regulation in plant-pathogen interactions

We found that GO categories associated with our selected TFs also involve plant defence, linking these TFs with responses to biotic stresses. Then, we further investigate the possible role of the peroxisomal-dependent selected TFs under different contexts related to biotic stresses. For that, we performed a web search for available Differential Expressed Genes (DEGs) related to biotic interactions and treatments with defence-related hormones in the GEO database (https://www.ncbi.nlm.nih.gov/geo/). We searched for our selected TFs within the lists of DEGs provided, obtained by the author's filters, and no additional filters were applied. The different datasets were organized in the following categories: damage (wounding and herbivory), pathogens (*Fusarium* and *Pseudomonas*), damage-associated molecular patterns (DAMP; oligogalacturonides, OGs) and microbe-associated molecular patterns (MAMP; flagellin- flg22 and chitin) and hormones (jasmonic acid, JA; salicylic acid, SA; auxins and ethylene; Supplementary Table S2). We found that all selected TFs were regulated by some of the experimental conditions and hormonal treatments related to biotic stresses, as shown by the heatmap illustrating the number of studies where they were found to be differentially regulated (Fig. 3). A wide-range of studies supported that these TFs can be involved also in plant-biotic interactions. It is well known that plant immune responses to pathogen recognition imply the accumulation of plant hormones, mainly JA and SA, and they activate signaling cascades playing a major role in the regulation of defence responses (Pieterse et al., 2012). In general, plant response to damage and herbivory is governed by JA, while SA is the main hormone orchestrating plant responses to biotrophic pathogens, although a spatiotemporal dynamic of the SA and JA regulation has been shown, with specific signal signatures depending on the pathogenic interaction (Pieterse *et al.*, 2012; Betsuyaku *et al.*, 2018). Interestingly, we observed a regulation of the selected TFs in most of these treatments suggesting that may play a role in the regulation of responses by the JA- and SA-dependent

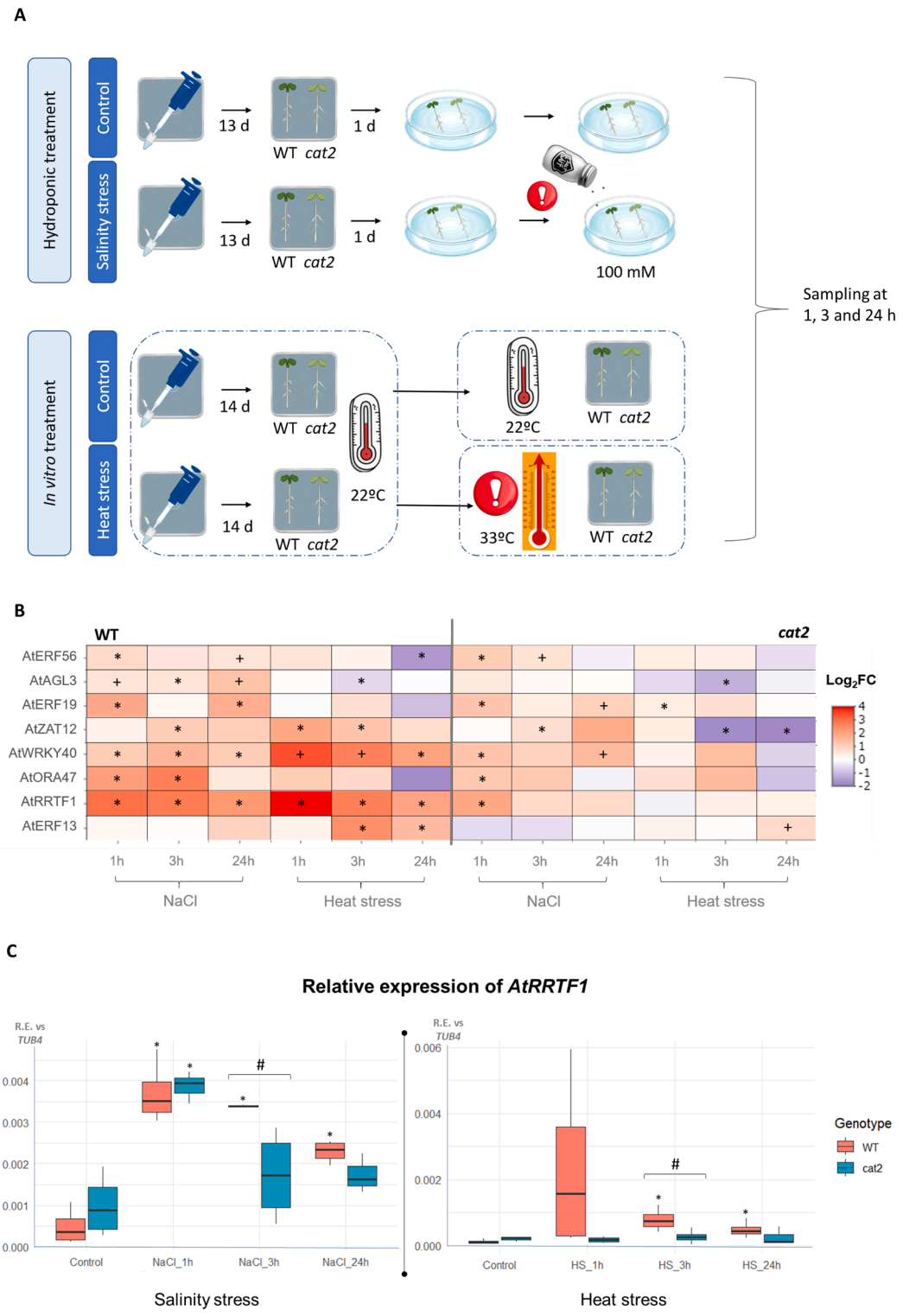

Fig. 2. Transcription factors (TFs) regulation during Arabidopsis response to salt and heat stress and its peroxisomal dependence. A) The scheme of the experimental design used to validate the regulation of the peroxisomal *Arabidopsis thaliana* selected TFs in abiotic stress. B) Heatmap representing the relative expression of the TFs shown on the left column in response to salt or heat stress. Gene expression levels in WT and *cat2* (left and right panels, respectively) are shown for early (1 and 3 hours) and late (24 hours) responses to salt or heat treatments. Asterisks represent significant differences between the treatments and their respective control conditions according to Student's *t*-test ($P < 0.05$). C) Box plot showing in detail the relative expression of one of the selected TFs, *AtRRTF1*. Box plots showing in detail the relative expression of all selected TFs are in Suppl. Fig. S3. Significant differences between genotypes under the same treatment are indicated with "#" according to Student's *t*-test ($P < 0.05$). R.E.: relative expression (arbitrary units).

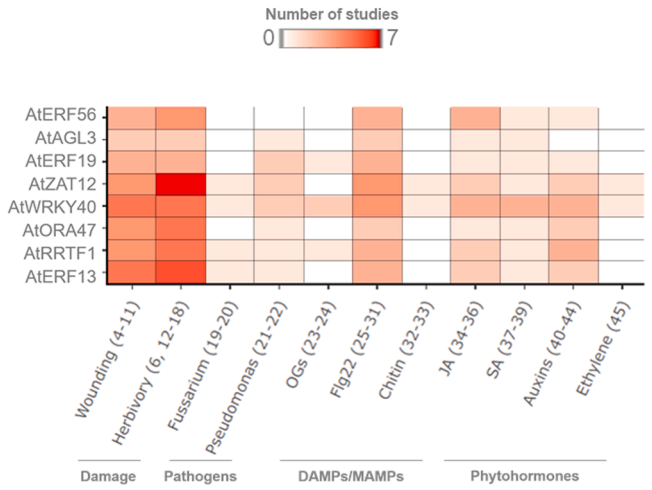

Fig. 3. Transcription factors (TFs) regulation in Arabidopsis response to biotic stress and hormones. Heatmap-type plotting an in-silico study of the Arabidopsis selected TFs genetic regulation related to biotic stress. The different studies analysed are categorized into: damage, pathogens, damage or microbe-associated molecular patterns (DAMP/MAMP) and hormones. The left column shows the selected TFs and the different available studies are grouped into columns. Numbers after the experimental conditions represent the experiments that were used to make the plot (detailed studies are described in Supplementary Table S2). Red intensity indicates the number of studies for each column in which each TF is regulated. Color range between white with no data published for the specific TF and the most intense red, representing seven studies. Flg22: flagellin; JA: jasmonic acid; OGs: oligogalacturonides; SA: salicylic acid.

signaling crosstalk. Interestingly, it has been shown that redox signaling is crucial for SA-dependent signaling and its crosstalk to the JA pathway, mediating its effect on the suppression of JA-dependent signaling (Spoel and Loake, 2011). Most of the TFs are also regulated by auxins, which are phytohormones mainly involved in plant development such as cell elongation and division (Gomes and Scortecci, 2021), but with a modulatory role in the regulation of defence responses, including effects on both pathogen and herbivore responses (Kazan and Manners, 2009; Machado *et al.*, 2016).

3.4. Selected transcription factors orthologs in tomato

We hypothesized that these genes, strongly responding to diverse stresses may play key roles in the regulation of plant stress responses and accordingly, their regulation should be conserved across plant species. We then aim to investigate potential orthologs of the selected TFs in tomato, of great economic importance. We used the information obtained in *Arabidopsis* as a basis for the identification of key regulators in plant response to stress in tomato. We look for *S. lycopersicum* orthologs of the selected TFs in Arabidopsis by using ePLANT, ENSEMBL plants and PANTHER databases and a total of 15 genes were proposed by at least one of the three bioinformatics tools (Table 1 and Supplementary Table S4). Sequence similarity parameters are also included in Table 1. We found one orthologs in tomato for the Arabidopsis *ORA47, ERF19* and *ERF56*; two orthologs for Arabidopsis *RRTF1, ERF13* and *ZAT12,* and three orthologs for *Arabidopsis AGL3* and *WRKY40* (Table 1). Despite the diversity of names in the bibliography for each tomato gene, most of them have been already reported to function in plant response to different stresses including both biotic and abiotic factors and/or in the regulation of hormone biosynthesis and dependent signaling pathways (Supplementary Table S4). Four TFs: *SlERF19-like, SlRRTF1-like*, the two orthologues of *AtZAT12* (*SlZAT12-like* and *SOLYC03G093870*) and one orthologs of *AtERF13* (*SlERF13-like*; Supplementary Table S4) had not been previously linked to plant stress responses. We further filtered the number of tomato orthologs by analyzing their expression levels in an in-house RNAseq (Lidoy *et al.*, 2024; Table 1). We maintained the TFs with only one orthologs but excluded those with no read counts. For TFs with more than one orthologs, we selected the ones with >10 read counts. Following these criteria, we finally selected 11 TFs in tomato for further analysis (Table 1).

3.5. Tomato transcription factors regulation in response to abiotic stress

To explore the potential transcriptional regulation of the orthologs during stress, we performed different bioassays challenging tomato with diverse biotic and abiotic stressors. To compare the responses to abiotic stress in both Arabidopsis and tomato, tomato plants were exposed to salinity (NaCl, 100 mM) or heat stress (35 °C) for 1, 3 and 24 hours and expression levels of the targeted genes were analyzed by quantitative RT-PCR. Most of the tomato TFs are upregulated during the early response to salinity stress (Fig. 4 and Supplementary Fig. S4), similar to the results in Arabidopsis (Fig. 2), although the induction in tomato (mostly at 3 h) seems delayed as compared to Arabidopsis, were the induction was already observed at 1 h, although this can be due to the different experimental systems (pots vs in vitro growth). Some other genes respond later, for example, *SlERF13-like* upregulation is observed at 24 h of salinity stress (Fig. 4 and Supplementary Fig. S4). Previous reports showed that *SlERF13-like* is regulated after 48 h of hypoxia treatment (Safavi-Rizi, *et al.*, 2020), supporting that they may be involved in the regulation of later responses. Although not significantly different, *SlRRTF1-like* and *SlERF56-like* were downregulated early upon salt stress (Fig. 4 and Supplementary Fig. S4) pointing to a differential regulation as that found in Arabidopsis (Fig. 2).

For those TF with several orthologs in tomato, we found differential regulation patterns among them. For example, while *SlWRKY39* is significantly upregulated only at 3 h of salt treatment, *SlWRKY43* is still induced after 24 h of salinity treatment, and *SlWRKY40* is repressed at 24 h of salinity stress. Similarly, *SlRRTF1* is induced after 3 h of salinity stress *while SlRRTF1-like* shows a downregulation tendency after 1 h (Fig. 4 and Supplementary Fig. S4). These different regulation patterns suggest a fine-tuned regulation of downstream responses to stress in tomato plants. In fact, gene duplication is proposed to provide greater and less-constrained chances for natural selection to shape novel functions or optimize existing ones, and is a major force in plants driving biological complexity, evolutionary novelty, and adaptation to specific conditions (Long *et al.*, 2003; Van de Peer *et al.*, 2009).

In response to heat stress, however, tomato showed a general downregulation trend at 1 h, followed by an upregulation after 3 h. In contrast, Arabidopsis showed a general upregulation in the early responses. The most striking differences between the two plants are found for *SlRRTF1* expression levels, as it is significantly downregulated after 3 and 24 h of heat stress, while *AtRRTF1* is significantly upregulated at these time points (Fig. 2). Similarly, while an upregulation is observed for *AtWRKY40*, a downregulation is observed for two of its orthologs, *SlWRKY43* and *SlWRKY40,* which are downregulated at different time points (1 and 24 h after stress, respectively), while *SlWRKY43* is then upregulated at 24 h supporting again a higher complexity of the response regulation in tomato than in Arabidopsis (Fig. 4 and Supplementary Fig. S4). The WRKY transcription factors represent a well-studied group of plant transcription factors involved in different biotic and abiotic stress responses. Previous research identified 81 WRKY genes in tomato, with several, including *SlWRKY39*, showing significant upregulation in response to salt and drought stress, abscisic acid, jasmonic acid and salicylic acid treatment, as well as to *Pst DC3000* infection. It was also reported that through *SlWRKY39* over-expression, the resistance to these multiple factors was enhanced (Sun *et al.*, 2015). However, their physiological roles in tomato plants remain largely unexplored. Although the tendency of *SlZAT12-like* is similar to that of *AtZAT12* at short time points after treatment (3 h), at a long time, is not (Fig. 4 and Supplementary Fig. S4). Interestingly, while *AtAGL3* and

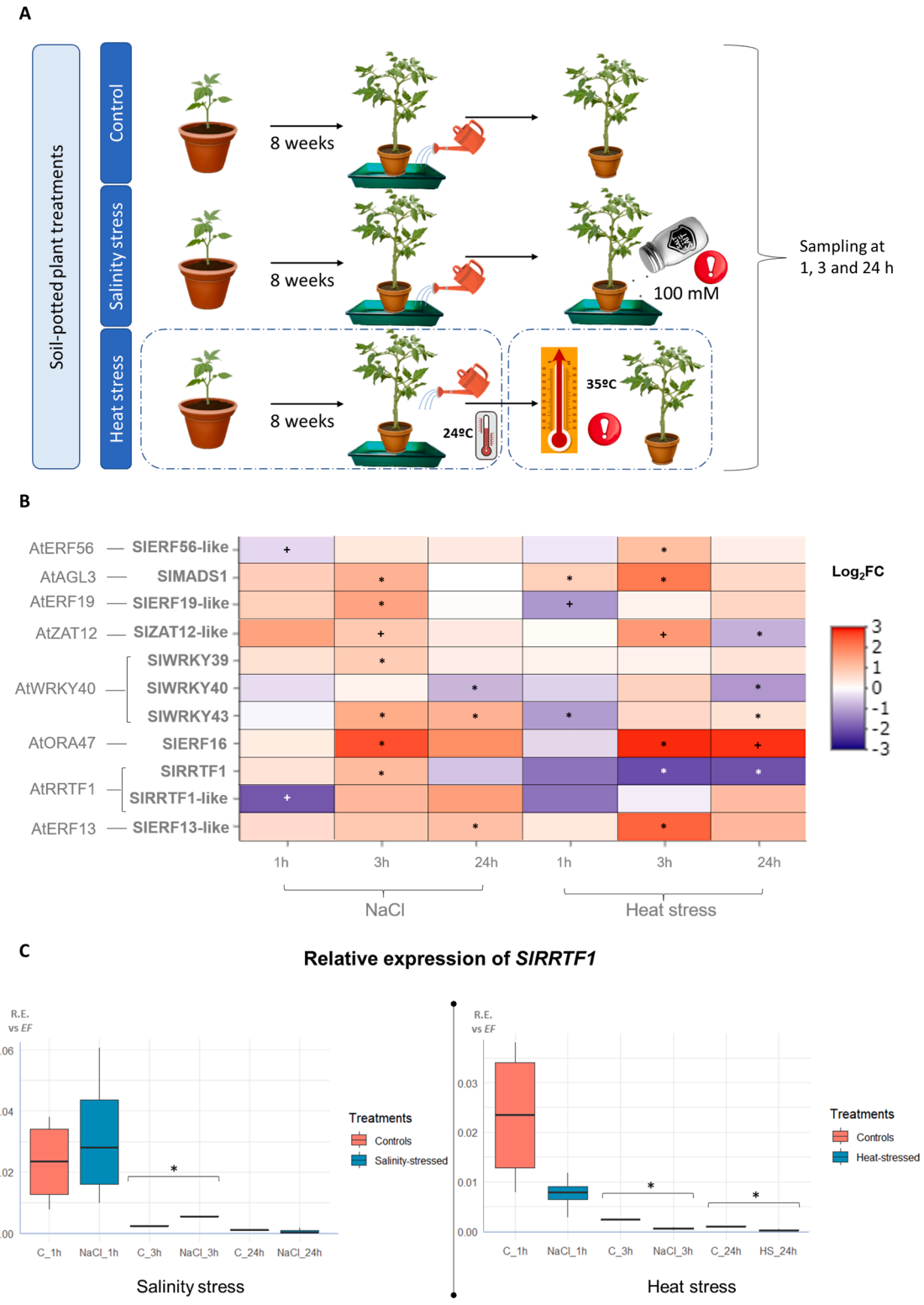

Fig. 4. Transcription factors (TFs) regulation in tomato response to abiotic stress. A) The scheme of the experimental design to check the regulation pattern of the *Solanum lycopersicum* selected TFs under abiotic stress. B) Heatmap representing the Log 2-fold change in the relative expression of the TFs from the left column. Gene expressions at the different time points after salt (left) and heat (right) treatments are shown. C) Box plot showing in detail the relative expression of one of the selected TFs, *SlRRTF1*. Box plots showing in detail the relative expression of all selected TFs are in Suppl. Fig. S4. Significant differences between treatments versus their controls are indicated with an asterisk, Student's *t*-test ($P < 0.05$). R.E.: relative expression (arbitrary units).

AtERF56 in *Arabidopsis* are repressed under heat stress (Fig. 2), their orthologues, *SlMADS1* and *SlERF56-like* are upregulated (Fig. 4). However, similar regulation patterns were observed for *SlERF13-like* and *AtERF13,* showing significant upregulation in plant response to heat stress (Fig. 4 and Fig. 2). In fact, *SlERF13-like* has been proposed to play a role in thermotolerance, showing Hu and collaborators (2020) a strong induction upon heat shock in tomato plants.

Taken together, our results support that the selected TFs are involved in the regulation of the responses to salinity and/or heat stress in both Arabidopsis and tomato. Regarding the differences in the regulation patterns, although salt stress tolerance has been described to be different in tomato and Arabidopsis plants (Kamanga *et al.*, 2020; Sanders *et al.*, 2000), the largest discrepancies in the expression trend of the analyzed TFs were found in response to heat stress. Tomato plants normally grow at a higher average temperature than Arabidopsis (Antoun and Ouellet, 2013; Alsamir et al., 2019), and plant responses to heat stress can be different between species that have adapted to different optima temperature (Zhang *et al.*, 2015). Moreover, the growth stage we analyzed in both plant species was also different, and it is known that age influences stress tolerance (Rankerberg *et al.*, 2021), so that differential dynamics in gene expression may be partly related to that. Nonetheless, our data suggest increased complexity in the stress response regulation in tomato, as illustrated by the different orthologs behavior in tomato plants.

3.6. Tomato transcription factors regulation in response to biotic stress

We aimed to explore if, as described in Arabidopsis, the orthologues in tomato are also regulated by biotic stress. For that, we used different attackers, including pathogens and chewing herbivores, and a damage-associated molecular pattern as oligogalacturonides (oligomers of alpha-1,4-linked galacturonosyl residues, OGs). For the biotic stressors, we challenged the plants with either the foliar necrotrophic pathogen *Botrytis cinerea*, or with chewing caterpillars, the generalist *Spodoptera exigua* and the Solanaceae specialist *Manduca sexta*, and we harvested the plants after 24 h. The response to herbivory seems to be more restricted, but there is a general upregulation trend in response to both herbivores. *SlZAT12-like* is significantly induced by both chewing caterpillars (Fig. 5 and Supplementary Fig. S5). *SlRRTF1, SlRRTF1-like* and *SlWRKY39* showed an upregulation trend although data are not significant. *AtZAT12* has been described previously as upregulated within minutes by wounding and herbivory (Takahashi *et al.*, 2011; Schweizer *et al.*, 2013). In this regard, transient upregulation of *AtRRTF1* was shown upon MeJA treatment, known to induce herbivore responses (Cai *et al.*, 2014). Although not significant, there is also an upregulation of *SlERF16* and *SlERF19* in tomato response to both caterpillars (Fig. 5). Both have been previously reported to respond to herbivory, but their regulation is likely to occur at earlier time points. Nonetheless, although our data correspond to 24 h from the initiation of the herbivory, the

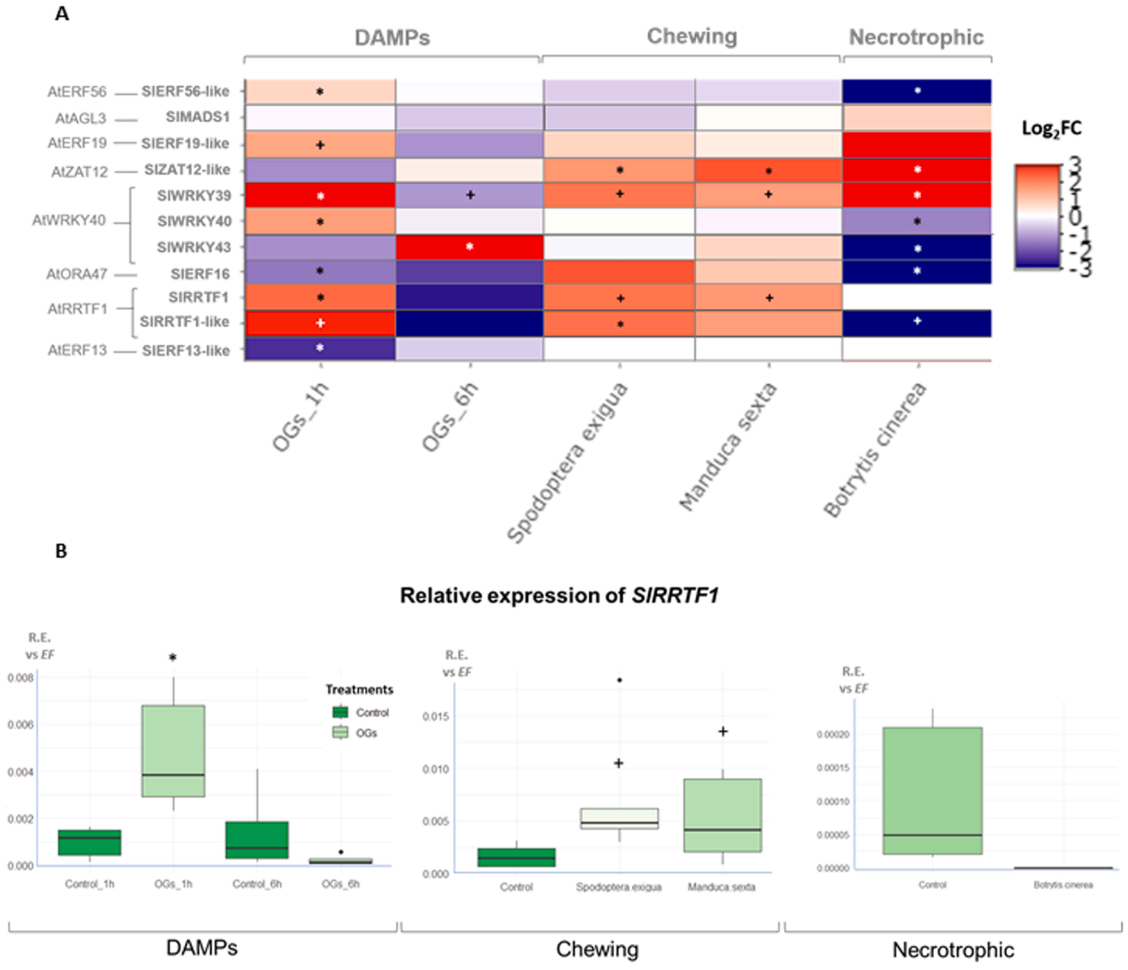

Fig. 5. Transcription factors (TFs) regulation in tomato response to biotic stress. A) Heatmap representing the Log 2-fold change of the tomato *Solanum lycopersicum* TFs, shown on the left column. Gene expressions of tomato TFs are shown from left to right respectively for early response to oligogalacturonides (1 and 6 hours) and late treatments (24 hours) with the pathogenic herbivores, *Spodoptera exigua* and *Manduca sexta*, and the fungus *Botrytis cinerea*. B) Box plot showing in detail the relative expression of *SlRRTF1*. Box plots showing in detail the relative expression of all selected TFs are in Suppl. Fig. S5. Along the figure, asterisks represent significant differences between the treatments and their respective control condition according to Student's *t*-test ($P < 0.05$). R.E.: relative expression (arbitrary units).

herbivore keeps feeding in the leaves, so that a continuous wounding stimulus can be considered. The role of *SlERF16* in regulating tomato responses has been previously shown in tomato challenged by the chewing caterpillar *Helicoverpa armigera* (Hu *et al.*, 2021). The authors demonstrated that ET signaling is involved in the rapid induction of the JA burst upon herbivory, and that *SlERF16* function as powerful transcriptional activator triggering the JA burst in response to herbivore attack. Similarly, Lidoy *et al.* (2024) reported the upregulation of *SlERF16*, in response to the herbivory by both *M. sexta* and *S. exigua*, and proposed that they connect ET and JA signaling in orchestrating mycorrhiza induced resistance against these pests.

Remarkably, while most TFs respond to both biotic and abiotic stress conditions, the expression of *SlMADS1* remains mostly unaltered in the biotic interactions. While it is up-regulated by both heat and salt stresses at short times (Fig. 4), this TF hardly changes its expression under the different biotic stress conditions (Fig. 5). These results are in line with

Fig. 6. TFs regulation under different stress conditions in WT *A. thaliana* and *S. lycopersicum* plants. Stresses are indicated in the top, including salinity, high temperature, herbivory and the cell wall sub-products oligogalacturonides, the microbe associated molecular pattern chitin and the fungi *Fusarium spp.* (only for *Arabidopsis*) and *Botrytis cinerea* (only for *S. lycopersicum*). Gene expression is summarized for each species as indicated by drawings. Blue and red arrows represent down or up regulation respectively, (at any of the time points analysed). When the regulation of the TF has been already described in the bibliography, according to data from Fig. 3, a grey colour Arabidopsis plant and an orange triangle are represented.

the so far described functions of both *SlMADS1* and its counterparts in *Arabidopsis* (Supplementary Table S4), mostly related to fruit ripening and the regulation of plant architecture (Zhang *et al.*, 2024). For the rest of TFs showing regulation by biotic stresses, the differential temporal dynamics of the regulation patterns, and the differences among the regulation profiles of the gene orthologs support the complexity of the transcriptional regulation of plant stress responses in tomato. For example, while several TFs showed a downregulation trend 6 h after OG treatment, Sl*WRKY43*, is significantly upregulated at this time point (Fig. 5 and Supplementary Fig. S5). In fact, we found that the three *AtWRKY40* orthologs were significantly upregulated in response to OGs although with differential timing, *SlWRKY39* and *SlWRKY40* at 1 h and *SlWRKY43* at 6 h. Most of the TFs responded also to the infection by the necrotrophic pathogen, with a diverse pattern, showing up or down regulation depending on the TF. Here, as we only have one time point it is difficult to establish if a temporal regulation is shaping the response. Interestingly, in relation to the three orthologs of *AtWRKY40*, only *SlWRKY39* is upregulated by *B. cinerea,* while *SlWRKY40* and *SlWRKY43* were repressed (Fig. 5 and Supplementary Fig. S5). *AtWRKY40* transcription was shown to be upregulated in Arabidopsis leaves infected with *Botrytis cinerea* (Wang *et al.*, 2024). Furthermore, constitutive co-expression of *AtWRKY40* and *AtWRKY18* resulted in enhanced susceptibility to *Botrytis cinerea* (Xu *et al.*, 2006), suggesting the complex regulation of the plant resistance to *Botrytis* disease, that may require repression of this transcription factor. The contrasting regulation pattern observed for the 3 orthologues in tomato (*SlWRKY39, SlWRKY40* and *SlWRKY43*) in response to OGs and Botrytis, support a fine-tuned regulation of the response to the pathogen in this species. Although not significant, *SlERF19-like* shows an upregulation after Botrytis infection and in Arabidopsis, *AtERF19* transcript levels are up-regulated within minutes of exposure to *Botrytis* spores or chitin, but then steadily decreased over time (Libault *et al.*, 2007; Huang *et al.*, 2019). Remarkably, overexpression of *AtERF19* increases the susceptibility of Arabidopsis to pathogens, including *Botrytis cinerea* (Huang *et al.*, 2019). Accordingly, a dual role in enhancing drought tolerance while suppressing immune responses has been proposed for *AtERF19*, suggesting a key role in balancing abiotic and biotic stress signaling (Huang *et al.*, 2019). Thus, the complex regulation patterns observed in the present study also support that the selected set of TFs, while responding to multiple stresses, may fine-tune and prioritize the response to both biotic and abiotic stresses both in Arabidopsis and tomato by following different temporal patterns (Fig. 2, Fig. 4 and Fig. 5).

The expression data are summarized in Fig. 6, allowing a comparison of the regulation trends among the two-plant species. The data reveal that the selected peroxisomal-dependent TFs respond to multiple stresses in both plant species, including both biotic and abiotic stress conditions, with some differences in their regulation profiles, suggesting their regulatory role in shaping the plant responses to cope with stress. The differential temporal dynamics suggest fine-tuned regulation of the downstream stress responses according to the specific stress encountered. In general, the presence of several orthologues in tomato for each *Arabidopsis* candidate, showing differential regulation upon some stresses, suggests a more complex regulation of the response in tomato plants.

4. Conclusion

Understanding signal transduction processes during the early stages of a plant's interaction with abiotic or biotic stressing factors, is essential to develop biotechnological strategies to improve crop resilience. Here, through in silico analysis we selected 8 TFs in Arabidopsis putatively dependent on peroxisomal H_2O_2 metabolism. We confirmed that the selected TFs were regulated in Arabidopsis response to different abiotic stress conditions, including salinity and heat stress. This response was compromised in the *cat2* mutants, altered in peroxisomal ROS metabolism, supporting peroxisomal ROS-dependence. Reported expression of the selected TFs supports that they are also regulated during Arabidopsis defence responses to biotic stressors, suggesting that they could be a key node in the plant response to biotic and abiotic crosstalk. We searched for the orthologues of these TFs in a phylogenetically distant species, tomato, and we analyzed their regulation in response to different biotic and abiotic stresses. The results revealed clear similarities in the regulation pattern of these TFs in both plants (Fig. 6), supporting the global relevance of peroxisome signaling in plant responses to stress. Our approach proves useful to identify key hubs in plant stress responses as suitable targets for future biotechnological applications. These strategies may contribute to the development of cultivars that are more resilient to harsh environments, especially in the context of the increasing adverse climate phenomena and the prevalence of pests associated with climate change.

SUPPLEMENTARY DATA

Supplementary Table S1. *Arabidopsis thaliana* and *Solanum lycopersicum* list of primers used for quantitative PCR.

Supplementary Table S2. *A. thaliana* transcriptomic studies used in Fig. 3 and Supplemental Fig. 2 which are available at Gene Expression Omnibus database and other repositories.

Supplementary Table S3. *A. thaliana* transcription factors extracted from the PTF (Terrón-Camero et al., 2022).

Supplementary Table S4. Classification and main functions of the *A. thaliana* TFs and their respective orthologues in *Solanum lycopersicum*.

Supplementary Fig. S1. A) Venn diagram, B) GeneMania representation and C) a table which summarizes the TFs selection, interconnection, and involvement in ROS metabolism of the *A. thaliana* transcription factors, respectively.

Supplementary Fig. S2. Heatmap-type plot representation of the *A. thaliana* selected TFs gene regulation by different subcellular ROS sources.

Supplementary Fig. S3. Box plots of the *A. thaliana* selected TFs gene regulation under salinity and heat stress.

Supplementary Fig. S4. Box plots of the *Solanum lycopersicum* selected TFs gene regulation under salinity and heat stress.

Supplementary Fig. S5. Box plots of the *Solanum lycopersicum* selected TFs gene regulation under oligogalacturonides treatment, *Spodoptera exigua, Manduca sexta* and *Botrytis cinerea* infection.

CRediT authorship contribution statement

Alejandro Rodríguez-González: Writing – original draft, Software, Methodology, Investigation, Formal analysis, Data curation. **Laura C. Terrón-Camero:** Software, Investigation, Formal analysis. **Zhivko Minchev:** Software, Investigation, Formal analysis, Data curation. **Luisa M. Sandalio:** Writing – review & editing, Funding acquisition. **María José Pozo:** Writing – review & editing, Supervision, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **María C. Romero-Puertas:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing interests that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.stress.2025.100874.

Data availability

Data will be made available on request.

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