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REVIEW ARTICLE

Exploring the Genetic and Molecular Mechanisms Underlying the Interaction Between Tomato and Endophytic Fungi: A Bioinformatic Analysis and Review of Key Genes and Pathways

Sepideh Ghaffari[1] | Ali Javadmanesh[1] | Ricardo Machado[2] | Stephan Jaronski[3] | Lukasz L. Stelinski[4] | Javad Karimi[1]

[1]Department of Plant Protection, Faculty of Agriculture, Ferdowsi University of Mashhad, Mashhad, Iran | [2]Experimental Biology Research Group, Institute of Biology, University of Neuchatel, Neuchâtel, Switzerland | [3]Jaronski Mycological Consulting LLC, Blacksburg, Virginia, USA | [4]Department of Entomology and Nematology, Citrus Research and Education Center, University of Florida, Lake Alfred, Florida, USA

Correspondence: Javad Karimi (jkb@um.ac.ir)

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ABSTRACT

Endophytic fungi are known to improve plant resistance to stress and enhance plant performance. A comprehensive understanding of the mechanisms underlying endophytic fungi-mediated systemic resistance is crucial for the widespread adoption of these fungi as beneficial biological control agents. To unravel the complex interactions between tomato and endophytic fungi, we compared the transcriptomic responses of tomato plants induced with *Trichoderma harzianum*, *T. afroharzianum*, *T. atroviride* and *Pochonia chlamydosporia*. RNA-seq datasets were used to assess the common expression patterns in defence-related pathways. Our analysis revealed that a group of common key genes were significantly induced in all investigations examined. Additionally, we observed that 20 transcripts related to anion transport, which is crucial for early plant immune responses, were consistently enriched in all the studies. These findings highlight the conserved and specific nature of plant–endophyte interactions and their potential for enhancing plant resistance through targeted genetic manipulation and breeding for long-lasting resistance.

1 | Introduction

In nature, plants are constantly exposed to a variety of abiotic and biotic stressors, such as herbivory, disease and low nutrient availability. Plants, as sessile organisms, have evolved multiple defence mechanisms to cope with these challenges, such as symbiotic partnerships with nonpathogenic microbes (Munir et al. 2022; Pathak et al. 2022; Soleimani et al. 2022). Endophytic fungi can colonise plants without causing symptoms, conferring enhanced resistance to biotic and abiotic stresses, promoting plant growth and development and stimulating the production of bioactive compounds (Díaz-Urbano et al. 2023; Wahab et al. 2023). In response to these fungal associations, plants undergo significant metabolic reconfigurations, involving the reprogramming of the transcriptome and regulation of gene expression (Janiak et al. 2018; Son and Park 2023). Transcriptome analysis offers a valuable approach for investigating the mechanisms underlying plant stress responses and the complex interactions between plants and their endophytic fungal symbionts.

Plants have developed complex, multilayered recognition and defence mechanisms to combat various types of invaders (Morales et al. 2022). As the host plant recognises commensal or beneficial microorganisms, it triggers numerous effective

TABLE 1 | Sources of raw data originally obtained from tomato plants infected by various species of endophytic fungi used in bioinformatic analyses conducted here.

Related article	Accession number	Endophytic fungus	Treated time	Samples (control/stress)
Coppola, Cascone, et al. (2019)	PRJNA532377	*Trichoderma harzianum*	20 days	12 (3/3)
Coppola, Diretto, et al. (2019)	PRJNA533559	*Trichoderma atroviride*	20 days	18 (2/2)
Juan et al. (2021)	PRJNA561218	*Trichoderma afroharzianum*	15 days	6 (3/3)
Pentimone et al. (2019)	PRJNA531604	*Pochonia chlamydosporia*	21 days	17 (4/4)

responses in distant regions of the plant, enabling it to deal with phytopathogens and herbivores (Gupta and Bar 2020; Cachapa et al. 2021). In general, plant innate immunity primarily consists of two defence systems: pattern-triggered immunity (PTI) and effector-triggered immunity (ETI) (Yuan et al. 2021). Mitogen-activated protein kinase (MAPK) cascades, reactive oxygen species (ROS), calcium (Ca^{2+}) and hormones such as ethylene (ET), abscisic acid (ABA), salicylic acid (SA) and jasmonic acid (JA) are among the signalling components that are engaged when PTI defence is triggered. These elements have the potential to reduce or prevent pathogen invasion, as well as increase the expression of defence genes, such as those encoding nucleotide-binding and leucine-rich repeat (NB-LRR), disease resistance proteins and pathogenesis-related proteins (Niehl et al. 2016; Glushkevich et al. 2022). The second line of plant defence, employed by species utilising ETI, is mediated by host resistance (R or N) genes that encode proteins that primarily belong to the nucleotide-binding leucine-rich repeat (NB-LRR) family. Upon interaction with pathogen-derived effectors, these R or N proteins initiate the sequential activation of intracellular signalling cascades, ultimately leading to disease resistance (Eitas and Dangl 2010; Lee and Yeom 2015; Glushkevich et al. 2022). Activation of the plant immune signalling network involves extensive signal transduction mediated by hormone signalling pathways and key plant signalling molecules, including ROS, Ca^{2+} and nitric oxide. These signalling entities play critical roles in inducing defence responses by modulating the cellular redox state, calcium homeostasis and nitric oxide production (Klessig et al. 2018; Turkan 2018; Khan et al. 2019).

Although the role of plant metabolism in immunity has been studied for many years, earlier metabolic analyses focused mostly on the production of individual metabolites or single metabolic genes. Importantly, plant defence responses involve numerous metabolic genes and pathways. Therefore, to obtain a deeper understanding of the mechanisms underlying plant immunity, it is essential to study genes at the pathway or genome level, rather than focusing on single genes. Although many studies have investigated the molecular mechanisms underlying plant responses to stress (Bolton 2009; Rojas et al. 2014), little is known about the effects of stress combinations (Mittler 2006; Atkinson and Urwin 2012). Understanding the interactions between diverse stresses is challenging because the complex relationships between these various forms of stress can obscure their cumulative effects. Advances in high-throughput sequencing have resulted in a wide and diverse variety of publicly available genomic data. By synthesising data from multiple prior studies, a more accurate and reliable understanding of plant defence responses can be obtained. Transcriptome data across differentially expressed genes (DEGs) can be integrated, making it easier to identify significant genes that are important for plant stress responses (Ashrafi-Dehkordi et al. 2018; Cohen and Leach 2019; Tahmasebi et al. 2019). These findings provide valuable insights into general plant responses and serve to corroborate individual transcriptome studies. Furthermore, by integrating plant responses to diverse infections, researchers can identify commonalities in plant-pathogen interactions, thereby elucidating the underlying mechanisms of these complex interactions (Atkinson et al. 2013).

In this comprehensive review and transcriptomic analysis, we leveraged publicly accessible gene expression data to elucidate the expression patterns of genes involved in the tomato response to beneficial endophytic fungi. Specifically, we examined the responses of tomato to *Trichoderma harzianum*, *T. afroharzianum*, *T. atroviride* and *Pochonia chlamydosporia* by analysing the transcriptomic profiles of genes associated with hormone biosynthesis signalling, MAPK cascades, plant-pathogen signalling and phenylpropanoid-related pathways. Our primary objective was not to perform a meta-analysis or directly compare gene expression levels across studies due to inherent variations in the experimental conditions. Rather, our goal was to identify the overarching genes, conserved signalling pathways and potential mechanisms underlying tomato-endophyte interactions. While this heterogeneity poses challenges, it also provides a unique opportunity to gain a broader understanding of how diverse tomato genotypes and tissues respond to different endophytic fungi species.

2 | Methods

2.1 | Search Strategy for the Selection of RNA-Seq Studies

Publications related to the response of tomato plants to endophytic fungi were selected from Scopus and PubMed if they met the following criteria: (i) included, in the title and abstract, at least one of the following fungal names: *Trichoderma*, *Pochonia*, *Tolypocladium*, *Hirsutella*, *Lecanicillium* (*Akanthomyces*), *Isaria* (*Cordyceps*), *Metarhizium* and *Beauveria*; (ii) included, in the title and abstract, RNA-seq analysis; and (iii) the raw data were publicly available in the EBI or NCBI. These keywords allowed us to select four articles that included 11 samples (Table 1). When a given study evaluated transcript levels at different time points,

the point closest to 20 days post inoculation (almost common in all studies) was chosen.

2.2 | Bioinformatic Analysis of RNA-Seq Data

With the SRA toolkit version 3.0.0, the raw data files in FASTQ format were obtained from NCBI SRA (https://www.ncbi.nlm.nih.gov/sra) and EMBL ArrayExpress (https://www.ebi.ac.uk/arrayexpress/) under the accession numbers provided in the original publications (Table 1). The quality of the raw reads was checked using FastQC v.0.11.9, using the default parameters (Andrews 2010). The Trimmomatic v.0.39 program removed adapter sequences and low-quality bases from paired reads (Bolger et al. 2014). High-quality reads were subsequently aligned to the tomato reference genome ITAG 2.4 (https://solgenomics.net) with HISAT2 v.2.2.1 using default parameters (Kim et al. 2015). For the downstream analysis, only uniquely mapped reads were used. The featureCounts tool v.2.0.0 was used to count the reads associated with each study and sample (Liao et al. 2014). After data normalisation using the trimmed mean of M-values (TMM) method with the Bioconductor edgeR package (v3.38.4) (Robinson et al. 2010), the DEGs corresponding to each experiment were separately identified according to log2-fold changes ≥ 1 and ≤ -1 with p-adj values of $0 < 0.05$, using the same R package, edgeR. A schematic workflow of this study is shown in Figure S1.

To investigate the co-occurrence of DEGs across the studies examined and to identify the pivotal genes that were effectively responsive to endophyte-plant interactions, a Venn diagram was employed in a two-stage approach using Venn diagram 2.0 (https://www.biotools.fr/misc/venny). First, a comparison was made between three studies involving *Trichoderma* sp. treatments. Second, a comprehensive comparison was conducted across all four studies, encompassing three *Trichoderma* species and one *Pochonia* species. The differentially expressed common genes that were detectable in all four experimental groups were subsequently visualised using a hierarchically clustered heatmap (Warnes et al. 2016).

2.3 | Gene Enrichment Analysis and Functional Analysis

The identified DEGs were uploaded to the Plant MetGenMAP (http://bioinfo.bti.cornell.edu/cgi-bin/MetGenMAP/home.cgi) system (Joung et al. 2009) for Gene Ontology (GO) term classification and enriched gene ontology (simulation-corrected $p \leq 0.05$) categories related to endophyte–plant interactions: cellular components, biological processes, and molecular functions. Pathway analysis of DEGs was conducted using the Kyoto Encyclopedia of Genes and Genomes (KEGG) mapper (https://www.genome.jp/kegg/mapper.html) and Plant MetGenMAP. To identify transcription factors (TFs) among the common DEGs, a list of *S. lycopersicum* TFs was generated from the iTAK database (http://itak.feilab.net/cgi-bin/itak/index.cgi; 16 June 2020).

Tomato phytohormone biosynthesis signalling, MAPK cascades, plant–pathogen signalling and phenylpropanoid-related pathways were identified using a gene-by-gene method. This analysis was performed by merging the expression data from our study with data from previously published literature (Falcone Ferreyra et al. 2012; Baldi et al. 2017; Jaiswal et al. 2020; Pott et al. 2020; Sadeghnezhad et al. 2020; Kumar et al. 2023) and using the Plant MetGenMAP and KEGG databases.

3 | Results

3.1 | Overview of the Tomato Transcriptome Response to Endophytic Fungi

To determine the genes and pathways induced by endophytic fungal infection in tomato plants, RNA-seq data from plants challenged with four endophytic fungi, *T. harzianum*, *T. afroharzianum*, *T. atroviride* or *P. chlamydosporia*, were retrieved from the SRA database (Table 1). For each experiment, we performed a comparative transcriptome analysis of fungal-colonised samples (plants treated with endophytic fungi) and control samples (untreated plants) (Table S1) independently. Differential expression analysis for each experiment was performed using edgeR (log2-fold change ≥ 1 and ≤ -1, and FDR corrected ≤ 0.05). In comparison to the control plants, the transcript abundance of the tomato plants was substantially altered in response to each of the endophytic fungi (Figure 1). A Venn diagram was used to compare the numbers of unique and common DEGs between the groups (Figure 2). A total of 71 DEGs were commonly regulated in response to *T. harzianum*, *T. afroharzianum*, and *T. atroviride* and among these DEGs, 30 DEGs were common to *P. chlamydosporia* treatment. The genes of interest included candidates that predominantly functioned in defence or immune pathways against endophytic fungi in tomatoes.

3.2 | GO Term Functional Classification and Enrichment Analysis

Only DEGs with log2-fold changes ≥ 1 and ≤ -1 and FDR corrected ≤ 0.05 were used for the GO term functional classification and enrichment analysis. The DEGs identified in the four

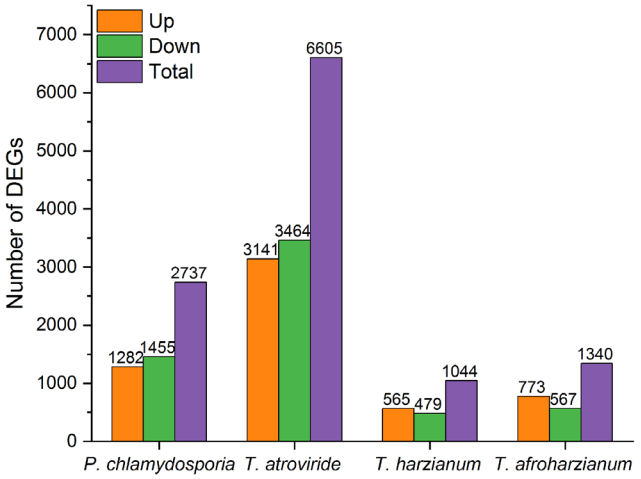

FIGURE 1 | Differentially expressed genes (DEGs) in tomato plants in response to four different endophytic fungi: *Trichoderma harzianum*, *T. afroharzianum*, *T. atroviride* and *Pochonia chlamydosporia*.

investigations involving tomato plants treated with the endophytic fungi *T. harzianum*, *T. afroharzianum*, *T. atroviride* and *P. chlamydosporia* exhibited a consistent pattern of GO term functional classification. In the biological process category, the most abundant DEGs were associated with cellular process (GO:0009987), response to stress (GO:0006950) and biosynthetic process (GO:0009058). In contrast, biotic stimulus (GO:0009607) and secondary metabolic process (GO:0019748) were less abundant (Figure 3). In the molecular function category, a high proportion of DEGs were associated with protein binding (GO:0005515), binding (GO:0005488) and catalytic activity (GO:0003824) (Figure 3). In the cellular component class, many DEGs were associated with membrane (GO:0016020) and nuclei (GO:0005634) (Figure 1,3).

GO enrichment analysis (simulation-corrected $p \leq 0.005$) of the biological processes was also performed for each investigation that was analysed (Tables S2–S5). In all four investigations,

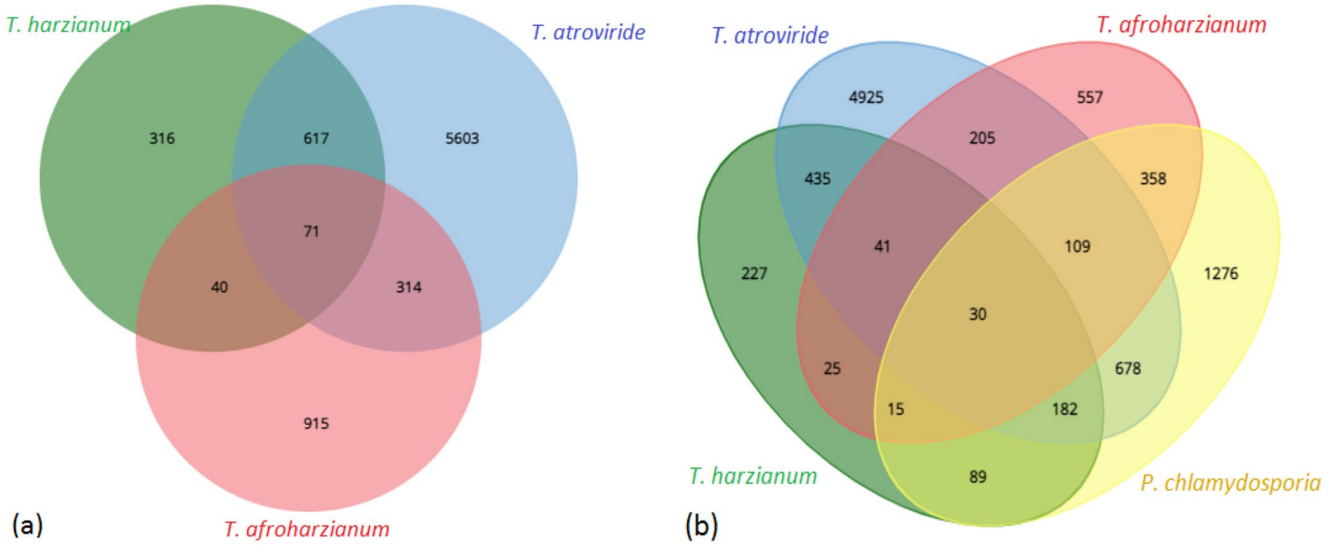

FIGURE 2 | Venn diagram illustrating the approach used to identify common stress genes. (a) Overlap of differentially expressed genes in three investigations involving *Trichoderma* sp. treatment. (b) Overlap of differentially expressed genes in all four investigations, including three *Trichoderma* sp. and one *Pochonia* sp. treatment. The numbers represent the number of differentially expressed genes.

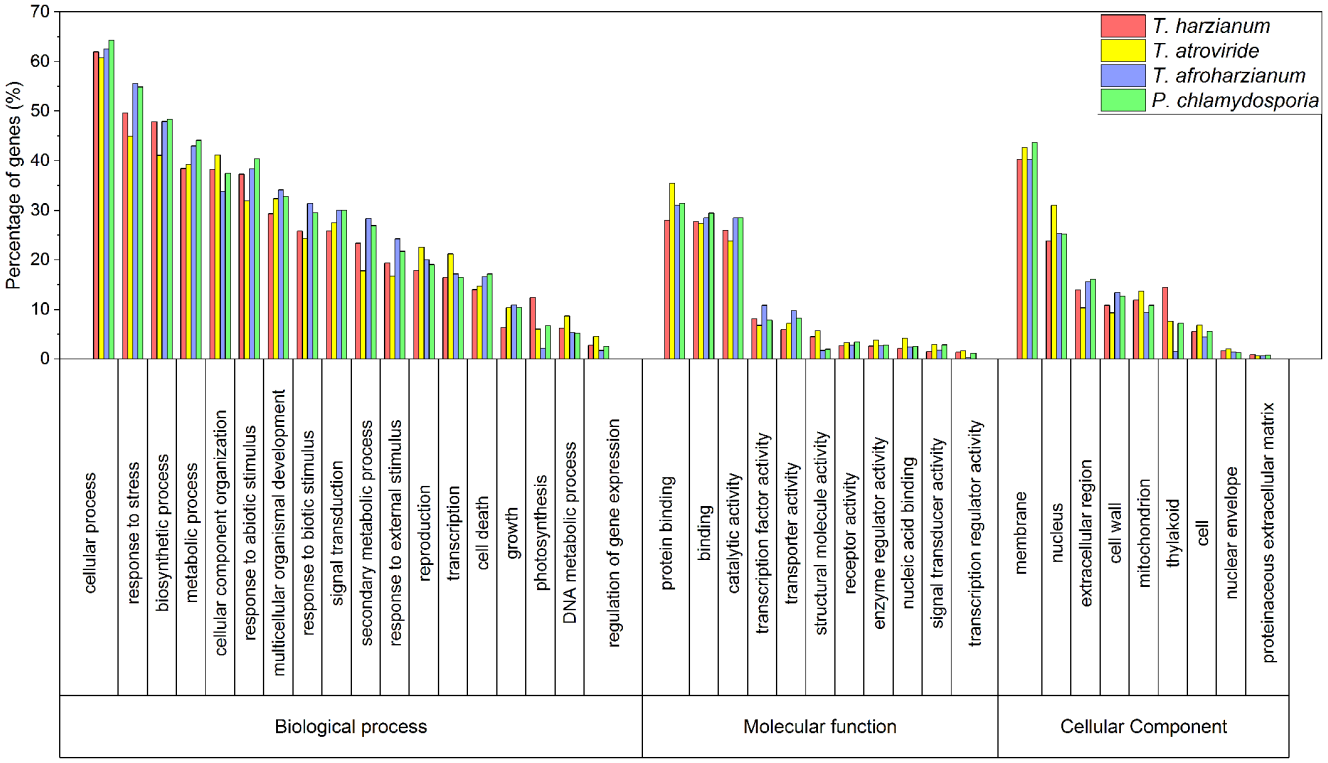

FIGURE 3 | Gene Ontology analysis of the differentially expressed genes. The percentages of genes assigned to each category were calculated for *Trichoderma harzianum*, *T. atroviride*, *T. afroharzianum* and *Pochonia chlamydosporia*.

the most significantly enriched GO terms in the biological process category were associated with defence, such as regulation of the defence response (GO:0031347) and response to chitin (GO:0010200). GO enrichment analysis indicated that the defence response to fungus (GO:0050832) was significantly enriched in tomatoes colonised by *T. afroharzianum*, *T. atroviride* or *P. chlamydosporia*. Moreover, in tomato plants colonised by these endophytic fungi, we observed significant enrichment of GO terms associated with plant immunity (GO:0045087 innate immune response, GO:0009627 systemic acquired resistance), hormone biosynthesis and signalling (GO:0009863 SA-mediated signalling pathway, GO:0009867 JA-mediated signalling pathway, GO:0009873 ethylene-mediated signalling pathway, GO:0009738 abscisic acid-mediated signalling) and programmed cell death (GO:0010363 regulation of plant-type hypersensitive response, GO:0043067 regulation of programmed cell death). Tomato plants colonised by *T. harzianum* exhibited significant overexpression of only the JA-mediated signalling pathway (GO:0009867) related to hormone biosynthesis and signalling. GO enrichment analysis also revealed that the DEGs associated with abiotic stress response (GO:0009699 response to abiotic stimulus, GO:0009611 response to wounding) and biotic stress response (GO:0002831 regulation of response to biotic stimulus, GO:0009595 detection of biotic stimulus, GO:0009620 response to fungus) were significantly enriched in tomato plants colonised by *T. afroharzianum*, *T. atroviride* or *P. chlamydosporia*. Analysis of the secondary metabolic process category revealed that tomato plants colonised by *T. harzianum*, *T. afroharzianum* or *P. chlamydosporia* exhibited significant enrichment of genes involved in phenylpropanoid biosynthetic processes (GO:0009699), flavonoid biosynthetic processes (GO:0009813) and terpenoid biosynthetic processes (GO:0016114). In contrast, tomato plants colonised by *T. atroviride* showed significant enrichment of genes related to terpenoid biosynthetic processes (GO:0016114).

We subsequently investigated the mechanisms of resistance in endophytically colonised tomatoes by examining several important gene categories, including plant MAPK signalling, plant-pathogen interactions, phytohormone signalling and phenylpropanoid biosynthesis.

3.3 | Mitogen-Activated Protein Kinase (MAPK) Signalling in Endophytically Colonised Tomato Plants

In the MAPK signalling pathway, we identified a total of 8, 22, 6 and 13 significantly induced genes in tomato plants colonised by *T. harzianum*, *T. atroviride*, *T. afroharzianum* and *P. chlamydosporia*, respectively. After pathogen infection, the genes induced in the MAPK signalling pathway were threonine-protein kinase FLS2 (*FLS2*), brassinosteroid insensitive 1-associated receptor kinase 1 (*BAK1*), pathogenesis-related protein 1 (*PR-1*), WRKY transcription factor 22 (*WRKY22*), MAP kinase substrate 1 (*MKS1*), 1-aminocyclopropane-1-carboxylate synthase 6 (*ACS6*), mitogen-activated protein kinase kinase 2 (*MKK2*) and mitogen-activated protein kinase kinase kinase 1 (*MEKK1*) (Table S6, Figure 4). Notably, the *PR-1* gene was consistently induced across all treatments, leading to a late defence response to pathogens.

Following pathogen attack, a set of genes exhibited significant activation in this pathway, including nucleoside-diphosphate kinase (*NDPK*), *PR-1*, *MEKK1*, mitogen-activated protein kinase 7/14 (*MPK1/2*) and *WRKY22* (Table S6; Figure 4). *PR-1* gene expression, which is linked to the induction of a pathogen defence response, was strongly upregulated after *P. chlamydosporia* and *T. afroharzianum* treatments, whereas its expression level decreased in response to *T. harzianum* treatment. In addition, *T. atroviride* treatment presented a complex expression pattern for *PR-1*.

Plant hormone signalling pathways linked to MAPK cascades, including those mediated by ethylene and abscisic acid (ABA), were elucidated and are summarised in Table S6, Figure 4. In the ethylene signalling pathway, a set of genes was significantly activated, including ethylene receptor (*ETR*), EIN3-binding F-box protein (*EBF*), basic endochitinase B (*ChiB*), ethylene-responsive transcription factor 1 (*ERF1*), serine/threonine-protein kinase CTR1 (*CTR1*) and P-type Cu^+ transporter (*RAN1*). Notably, *ChiB*, a gene involved in the activation of a defence response in all treatments, presented a complex and mixed expression pattern across *T. atroviride* and *P. chlamydosporia* treatment groups, and its transcriptional levels decreased in response to *T. harzianum* and *T. afroharzianum* treatments. In contrast, the ABA signalling pathway exhibited a distinct set of genes that were significantly activated due to MAPK cascades, including protein phosphatase 2C (*PP2C*), the ABA receptor PYR/PYL family (*PYL*), serine/threonine-protein kinase SRK2 (*SnRK2*), mitogen-activated protein kinase kinase kinase 17/18 (*MAPKKK17_18*), *MPK1_2* and catalase (*CAT*).

In the mitogen-activated protein kinase (MAPK) signalling pathway, we observed a significant plant response to wounding in tomato plants treated with *T. atroviride*, *T. afroharzianum*, or *P. chlamydosporia* (excluding *T. afroharzianum*) (Table S6; Figure 4). The most commonly induced gene in response to wounding was respiratory burst oxidase (*RbohD*), which plays a critical role in maintaining homeostasis of reactive oxygen species. Notably, the transcriptional levels of *RbohD* decreased in response to *T. atroviride* and *P. chlamydosporia* treatments, whereas they increased in response to *T. afroharzianum* treatment.

3.4 | Plant–Pathogen Interaction Signalling in Endophytically Colonised Tomato Plants

KEGG pathway analysis revealed distinct patterns of DEGs related to plant-pathogen interactions in tomato plants colonised by *T. harzianum*, *T. atroviride*, *T. afroharzianum* and *P. chlamydosporia* (Table S7, Figure S2). Specifically, 4, 16, 8 and 11 DEGs were identified in these pathways, respectively. The plant defence-related genes *PR-1*, calcium-binding protein CML (*CML*) and heat shock protein (*HSP90A-B*), which lead to defence-related gene induction, stomatal closure and hypersensitive response (HR), were consistently detected across all four investigations. In particular, the expression of *PR-1* was significantly upregulated in tomato plants colonised by *T. afroharzianum* and *P. chlamydosporia*, and to a lesser extent in those colonised by *T. atroviride*. In contrast, the expression of *PR-1* was downregulated in tomato plants

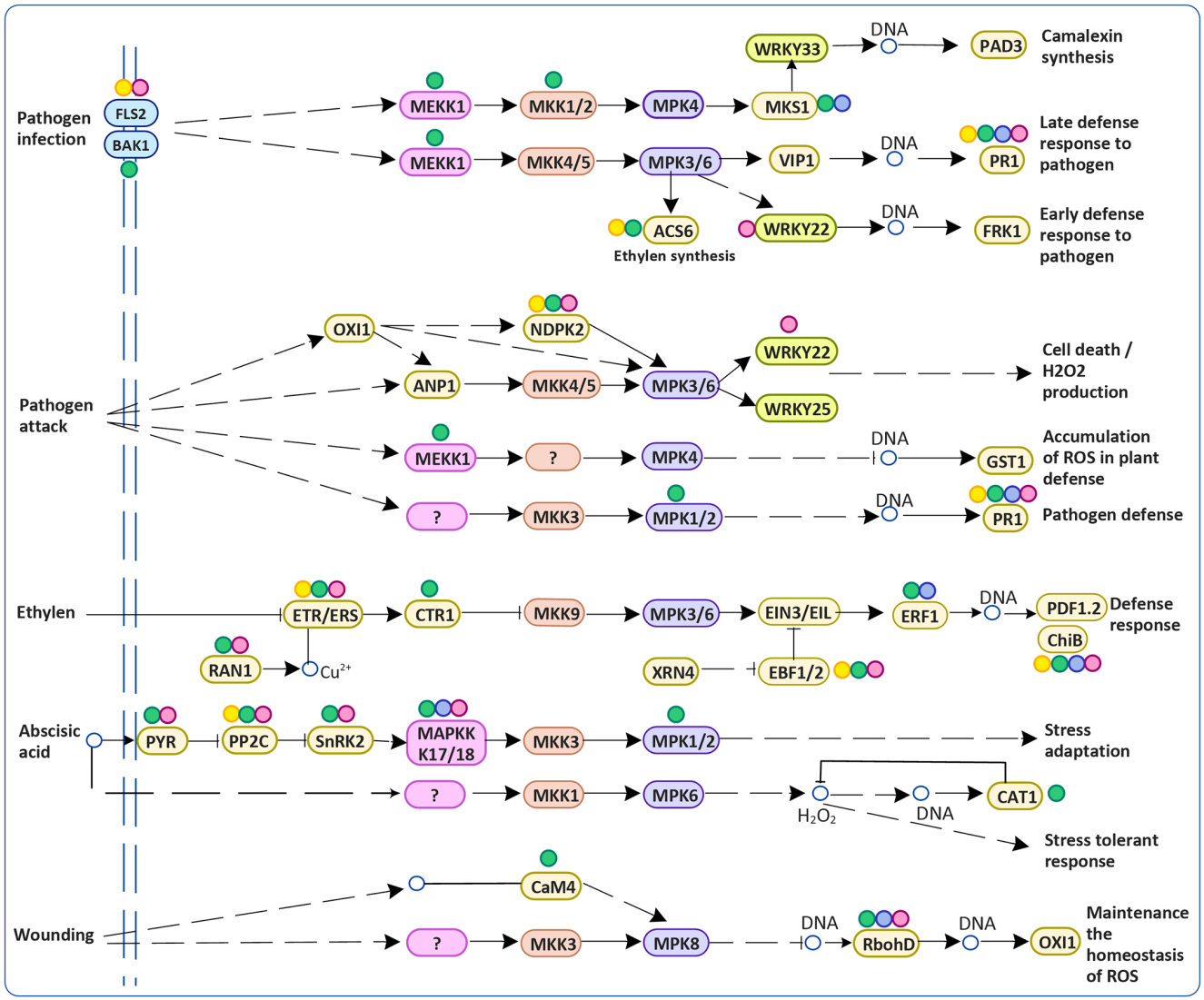

FIGURE 4 | MAPK signalling pathways induced in response to different endophytic fungi. The yellow, green, blue, and purple cycles represent differentially expressed transcripts in response to *Trichoderma harzianum*, *T. atroviride*, *T. afroharzianum* and *Pochonia chlamydosporia*, respectively. Abbreviations, transcript identification, expression profiles, and FDR values are described in Table S6. Pathway information adapted from the KEGG database.

colonised by *T. harzianum*. *HSP90A-B* gene expression was significantly altered in tomatoes colonised with different species of endophytic fungi. Specifically, in tomatoes colonised by *T. harzianum* and *T. afroharzianum*, *HSP90A-B* transcripts were upregulated, while in tomatoes colonised by *T. atroviride* and *P. chlamydosporia*, they were downregulated. In contrast, *CML* gene expression showed a more complex pattern, with upregulation in tomatoes colonised by *T. harzianum*, downregulation in those colonised by *T. afroharzianum* and a mixed expression pattern in those colonised by *T. atroviride* and *P. chlamydosporia*. Notably, a subset of genes, including cyclic nucleotide gated channel (*CNGC*), calcium-dependent protein kinase (*CDPK*), Rboh and 3-ketoacyl-CoA synthase (*KCS*), were commonly expressed in tomatoes colonised by *T. atroviride*, *T. afroharzianum* and *P. chlamydosporia*. Of these, *CNGC*, *CDPK* and *Rboh* were associated with the induction of hypersensitivity, cell wall reinforcement and stomatal closure, whereas *KCS* was found to suppress plant hypersensitivity and responses to endophytic fungal colonisation.

3.5 | Phytohormone Biosynthesis and Signalling in Endophytically Colonised Tomato Plants

In all four investigations analysed here, endophytic fungi significantly affected jasmonic acid (JA) biosynthesis and signalling pathways (Table S8, Figure 5). The genes associated with JA biosynthesis included phospholipase A1 (*PLA*), cytochrome P450 (*P450*), lipoxygenase (*LOX*), 12-oxophytodienoate reductase (*OPR*) and allene-oxide cyclase (*AOC*). Notably, the *LOX* gene was consistently induced across all colonised plants. *LOX* was strongly downregulated after T. *harzianum* and *T. atroviride* treatments, whereas its expression increased in response to *P. chlamydosporia* treatment and presented a complex expression pattern with *T. afroharzianum*. Furthermore, we observed a significant downregulation of genes related to JA signalling, including the jasmonate ZIM domain-containing protein (*JAZ*), in tomato plants colonised by *T. harzianum* or *T. atroviride*. In tomatoes colonised by *T. afroharzianum*, no significantly affected genes related to JA signalling were observed. However, in

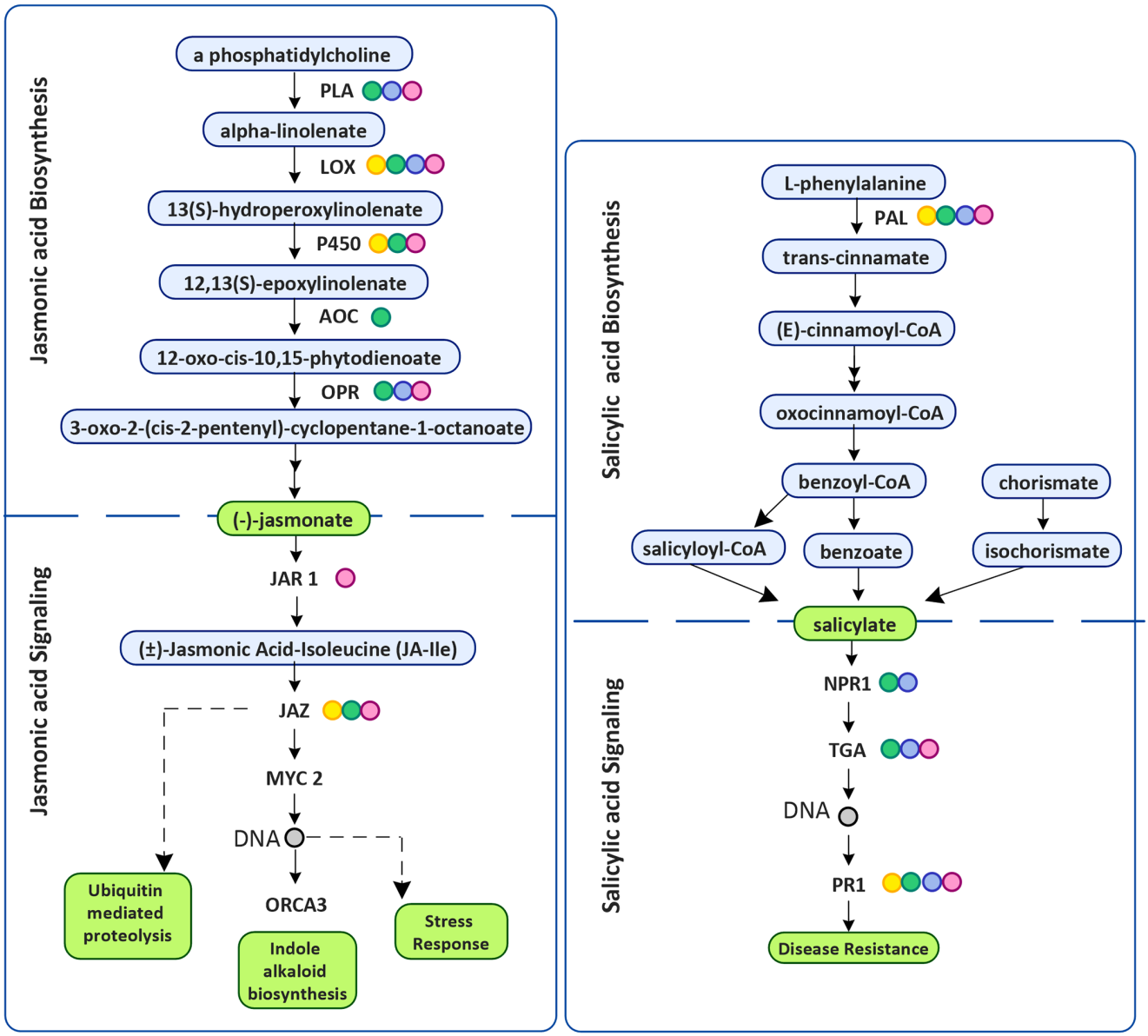

FIGURE 5 | Jasmonic acid (JA) and salicylic acid (SA) biosynthesis and signalling pathways are systemically induced in response to different endophytic fungi. The yellow, green, blue and purple cycles represent differentially expressed transcripts in response to *Trichoderma harzianum*, *T. atroviride*, *T. afroharzianum*, and *Pochonia chlamydosporia*, respectively. Abbreviations, transcript identification, expression profiles and FDR values are described in Table S8. Pathway information adapted from the Plant MetGenMAP and KEGG databases.

tomatoes colonised by *P. chlamydosporia*, we observed a mixed expression pattern of jasmonic acid-amino synthetase (*JAR 1*) and *JAZ*. Notably, several DEGs related to JA signalling were highly induced in tomatoes colonised with *P. chlamydosporia*, with the largest induction being up to 11.49-fold.

In the salicylic acid (SA) biosynthesis pathway, only phenylalanine ammonia-lyase (*PAL*) was significantly affected (Table S8, Figure 5). In the *T. harzianum*, *T. afroharzianum* and *P. chlamydosporia* treatments, all of the transcripts related to *PAL* (except two transcripts in the *P. chlamydosporia* treatment) were upregulated. However, the corresponding transcripts were downregulated in *T. atroviride*-colonised tomato plants. (8; Figure 5). *PR-1* was significantly induced in the SA signalling pathway in all four investigations analysed here. In tomatoes colonised by *T. afroharzianum* and *P. chlamydosporia*, the expression levels of *PR-1* transcripts were significantly upregulated, whereas in tomatoes colonised by *T. harzianum*, they were downregulated. Notably, the *P. chlamydosporia* treatment yielded a complex expression pattern. Furthermore, in the salicylic acid (SA) signalling pathways, the regulatory protein NPR1 and the transcription factor TGA were systemically regulated in response to colonisation by *T. afroharzianum*, *T. atroviride* and *P. chlamydosporia*.

In the ethylene biosynthesis pathway, the expression of genes encoding 1-aminocyclopropane-1-carboxylate oxidase (*ACO*) and 1-aminocyclopropane-1-carboxylate synthase (*ACS*) was exclusively observed in the four treatments and only the *Trichoderma* treatment, respectively (8; Figure S3). The majority of *ACO* transcripts were downregulated in the *T. harzianum*- and *T. atroviride*-treated groups, whereas these genes were significantly upregulated in response to *T. afroharzianum* and

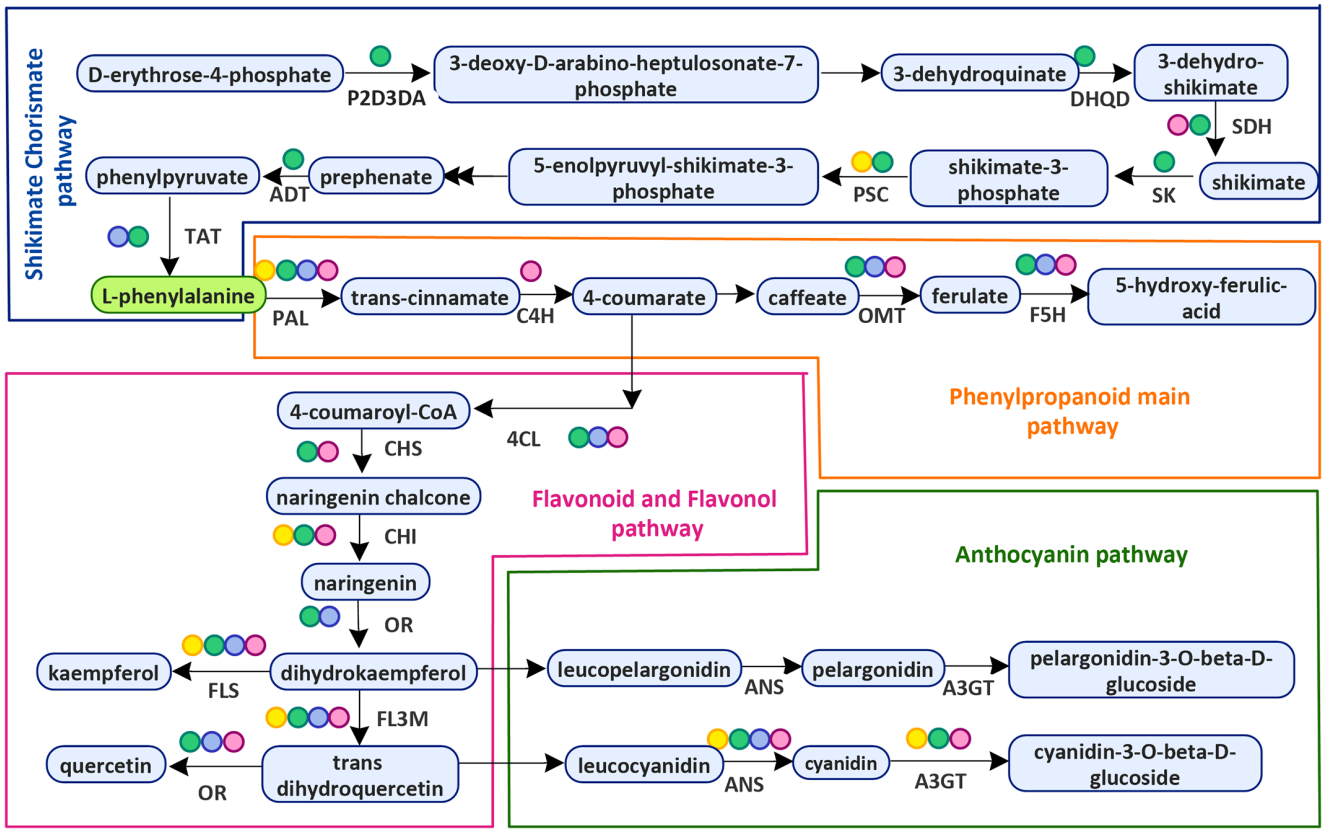

FIGURE 6 | Phenylpropanoid and related metabolite biosynthesis and signalling pathways systemically induced in response to different endophytic fungi. The yellow, green, blue and purple cycles represent differentially expressed transcripts in response to *Trichoderma harzianum*, *T. atroviride*, *T. afroharzianum* and *Pochonia chlamydosporia*, respectively. Abbreviations, transcript identification, expression profiles, and FDR values are described in Table S9. Pathway information adapted from the Plant MetGenMAP database.

P. chlamydosporia. Furthermore, genes involved in the ethylene signalling pathway, including *ETR*, *EBF*, *ERF1* and *CTR1*, were significantly downregulated in all of the investigations analysed here (8; Figure S3).

The number of significantly induced DEGs in the abscisic acid (ABA) biosynthesis pathway was found to be lower than that in other phytohormone pathways. The ABA biosynthesis pathway involves key enzymes such as carotenoid cleavage dioxygenase (*CCD*), xanthoxin dehydrogenase (*XanDH*) and aldehyde oxidase (*AOX*) (8; Figure S3), and the majority of these genes were upregulated across all four investigations analysed here. In contrast, the ABA signalling pathway (with the exception of *T. afroharzianum*, in which no induction was observed) comprised genes such as *PP2C*, ABA-responsive element binding factor (*ABF*), *PYL* and *SnRK2* (8; Figure S3). Notably, whereas the genes involved in the biosynthesis pathway predominantly exhibited upregulated expression patterns, the transcripts associated with ABA signalling genes presented a mixed pattern of upregulation and downregulation.

3.6 | Phenylpropanoid-Related Genes in Endophytically Colonised Tomato Plants

The genes that exhibited significant induction in the phenylalanine biosynthesis pathways, specifically the shikimate pathway leading to the biosynthesis of phenylpropanoid metabolites, included phospho-2-dehydro-3-deoxyheptonate aldolase 2 (*P2D3DA*), 3-dehydroquinate dehydratase (*DHQD*), shikimate dehydrogenase (*SDH*), shikimate kinase (SK), 3-phosphoshikimate 1-carboxyvinyltransferase (*PSC*), arogenate dehydratase (*ADT*) and tyrosine transaminase (*TAT*). All these genes were induced in response to *T. atroviride* treatment, shown in 9 and Figure 6.

The expression of cinnamate 4-hydroxylase (*C4H*), *PAL*, O-methyltransferase (*OMT*) and ferulate 5-hydroxylase (*F5H*) were induced in the phenylpropanoid pathway (9; Figure 6). *PAL*, which initiates the phenylpropanoid pathway, was consistently expressed in the four investigations analysed here. Specifically, all transcripts of this gene in tomatoes colonised by *T. harzianum* and *T. afroharzianum* exhibited upregulated expression, whereas those in tomatoes colonised by *T. atroviride* were downregulated. In contrast, the expression of *PAL* in tomatoes colonised by *P. chlamydosporia* was complex, with most genes showing upregulated expression.

During flavonoid biosynthesis, 4-coumarate CoA ligase (*4CL*), chalcone synthase (*CHS*), chalcone isomerase (*CHI*) and oxidoreductase (*OR*) were significantly activated (9; Figure 6). Furthermore, flavonoid 3-monooxygenase (*FL3M*), flavonol synthase (*FLS*) and *OR* were significantly induced during flavonol biosynthesis, with mixed expression patterns of upregulated and downregulated *FL3M* and *FLS* transcripts observed across all treatments (9; Figure 6).

Additionally, the anthocyanin biosynthesis pathway was characterised by the expression of anthocyanidin 3-O-glucosyltransferase (*A3GT*) and anthocyanidin synthase (*ANS*) (9; Figure 6). Notably, *ANS* was the most commonly expressed gene in this pathway, with upregulated expression observed in tomatoes treated with *T. afroharzianum* and *P. chlamydosporia*, and downregulated expression observed in those treated with *T. harzianum* and *T. atroviride* (9; Figure 6).

3.7 | Induced Overlapping Transcripts in Endophytically Colonised Tomato Plants

Concurrent analysis of the four transcriptomic datasets revealed a total of 71 DEGs that were commonly expressed in tomato plants colonised by *T. harzianum*, *T. afroharzianum* and *T. atroviride* (10; Figure 2). GO analysis of these genes, categorised by biological process, was performed to elucidate their functional relationships. GO analysis revealed a significant number of genes involved in stress response (GO:0006950), with 47 genes assigned to this category, followed by cellular processes (GO:0009987) with 45 genes, and biosynthetic processes (GO:0009058) with 36 genes. Furthermore, 27 and 25 genes were related to the response to abiotic and biotic stimuli, respectively, and ranked sixth and seventh, respectively (11). GO enrichment analysis (simulation-corrected $p \leq 0.005$) of the biological processes for the 71 common genes revealed two significantly enriched GO terms: response to stress (GO:0006950) and cellular aromatic compound metabolic processes (GO:0006725) (12), highlighting the key roles of these processes in the stress response of tomato plants colonised by these fungal species.

A comparison of the results obtained from investigations involving *P. chlamydosporia* treatment with those of the previously reported studies revealed a significant reduction in the number of shared genes, with only 30 DEGs common to both datasets (13; Figure 2). In terms of biological processes, GO analysis of the genes in the *P. chlamydosporia*-treated samples showed a distinct pattern, with stress response, cellular process and biosynthetic process ranking as the top three categories, with 20, 19 and 15 genes, respectively (14). Notably, responses to abiotic and biotic stimuli ranked seventh and eighth, respectively, indicating a reduced emphasis on these processes in *P. chlamydosporia*-treated samples. GO enrichment analysis (simulation-corrected $p \leq 0.005$) of the biological process category revealed that ion transport was the most enriched GO term among the DEGs, highlighting a key functional difference between the *P. chlamydosporia*-treated samples and the previously described dataset (15).

A heatmap of the normalised log2-fold changes in the 30 common DEGs identified in tomato plants endophytically colonised by *T. harzianum*, *T. afroharzianum*, *T. atroviride* or *P. chlamydosporia* was generated (Figure 7). The heatmap was divided into two distinct clusters. Treatments with *Trichoderma* species clustered together, suggesting a high degree of similarity in their gene expression profiles. In contrast, the *P. chlamydosporia* treatment was distinctly separated from the *Trichoderma* treatments, indicating a unique pattern of gene expression. Upon closer examination, our analysis

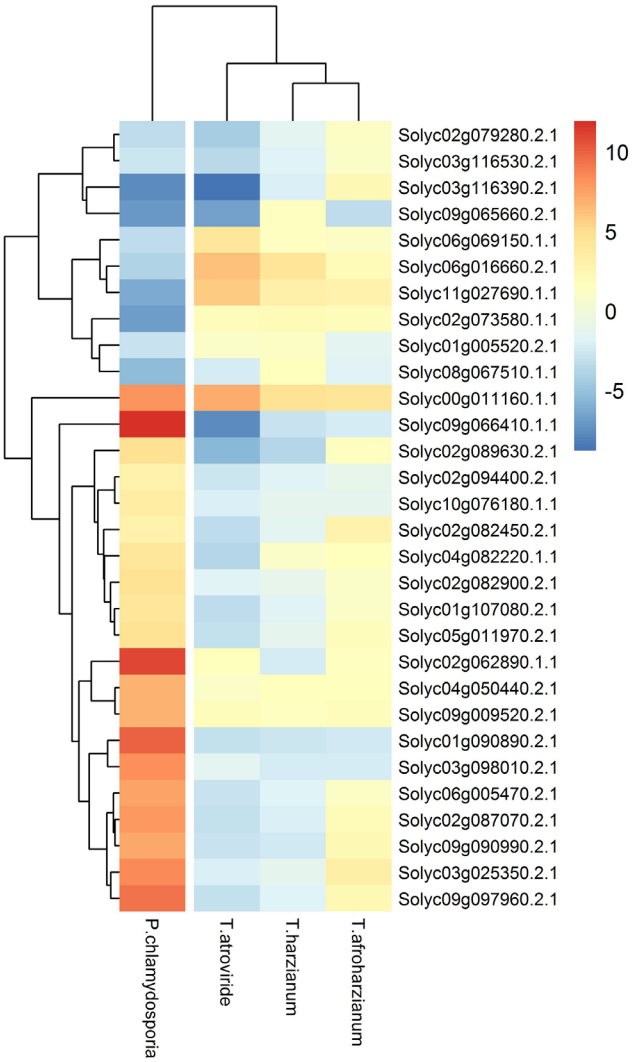

FIGURE 7 | Hierarchical clustering of the common differentially expressed genes identified in tomatoes endophytically colonised by *T. harzianum*, *T. afroharzianum*, *T. atroviride* or *P. chlamydosporia*, using normalised log2-fold changes (log2-fold changes ≥ 1 and ≤ -1 with *p*-adjusted values < 0.05). The blue bands indicate low gene expression, and the red bands represent high gene expression. The solgenomic ID (ITAG 2.4) is represented on the right.

revealed that the *P. chlamydosporia* treatment elicited a more pronounced response in certain genes, characterised by either significantly higher or lower gene expression levels compared to the *Trichoderma* treatments. This finding highlights the distinct functional responses of tomato plants to colonisation by different fungal species.

4 | Discussion

The immune responses of plants to various invaders and pathogens have been extensively studied, yet the immune reactions to beneficial endophytic organisms remain a relatively understudied area (Kumar and Nautiyal 2023). To elucidate the mechanisms underlying these interactions, it is essential to identify, isolate and characterise the genes involved in mutualistic associations between endophytes and host

plants. Recent fundamental research has demonstrated that endophytes can confer multiple benefits to their host, including enhanced biotic and abiotic resistance, increased metabolite production and improved growth by inducing systemic changes in plant gene expression (Kaul et al. 2016; Mishra et al. 2021; Chen et al. 2022). These effects are conserved across different species within the same fungal genus, highlighting the evolutionarily conserved nature of these interactions with host plants (Turner et al. 2013; Khare et al. 2018; Kumar and Nautiyal 2023).

Comparative studies of the differential expression profiles of endophyte host plants have provided valuable insights into these conserved interaction mechanisms, revealing commonalities in the gene expression and metabolic pathways induced by endophytes (Chen et al. 2022). To gain molecular insights into the different types of endophytic fungus-mediated resistance in tomato plants, we compared the transcriptomes of plants induced by three *Trichoderma* species and one *Pochonia* species. Given the variability in experimental conditions and transcriptome platforms used in different studies, the gene sets identified in transcriptome research often exhibit limited overlap. To increase the reliability of our analysis, the primary raw data were not merged, and each dataset was analysed independently. The outcomes of various transcriptome studies were then integrated to provide a comprehensive understanding of the underlying mechanisms. Our secondary analysis revealed that four main pathways were altered in response to endophytic fungi: plant mitogen-activated protein kinase (MAPK) signalling, phytohormone biosynthesis and signalling, plant-pathogen interaction and phenylpropanoid-related pathways.

In the MAPK signalling cascades, which play crucial roles in various plant physiological processes and stress adaptations, our analyses revealed that distinct gene sets were significantly induced across all treatment groups (tomato colonised by *T. harzianum*, *T. atroviride*, *T. afroharzianum* or *P. chlamydosporia*). One of the key components of plant defence mechanisms in MAPK cascades, which was conserved across all investigations, was *PR-1* expression (Joshi et al. 2021). *PR-1* is a critical regulator of plant defence responses and exhibits antifungal activity against several plant pathogenic fungi, including *Phytophthora infestans*, *Uromyces fabae* and *Erysiphe graminis* (Borad and Sriram 2008; Akbudak et al. 2020). Moreover, *PR-1* is a significant indicator of systemic acquired resistance (SAR) and suppresses viral activity in plants with SA-mediated resistance (Shaw et al. 2019; Dos Santos and Franco 2023). Another member of the *PR* gene family, *ChiB* (also known as *PR-3*), was consistently induced in all endophytically colonised tomato plants via MAPK cascades. *PR-3* exhibits enzymatic activity and acts as a chitinase in plant protection, confirming resistance against cell wall degradation by bacterial and fungal pathogens (Dos Santos and Franco 2023). *ChiB* is induced against chitin-containing fungi (Thomma et al. 1998) and has antifungal activity against several pathogenic fungi, including *Botrytis cinerea* (Finiti et al. 2014) and *Fusarium oxysporum* f. sp. *cucumerinum* (Xu et al. 2021). Our findings are consistent with those of previous studies demonstrating the changes in expression of endochitinase genes in response to pathogen infection (Santos et al. 2019). For instance, gene expression analysis has revealed that cabbage plants infected with *Xanthomonas campestris* pv. *campestris* overexpressed the endochitinase gene compared with uninoculated cabbage plants, highlighting the importance of this gene in plant defence against bacterial pathogens.

The release of reactive oxygen intermediates (ROIs) is one of the earliest responses triggered in plants upon detection of a microbial agent. *Rboh* proteins serve as the primary source of ROIs generated in response to microbial detection, as well as other stress-related processes (Torres and Dangl 2005). The *Rboh* gene family is transcriptionally regulated during plant-microbe interactions, allowing plants to modulate their defence responses accordingly. Our investigations revealed that the expression of *RbohD* transcripts in the MAPK signalling cascades was significantly changed in tomato plants colonised by *T. atroviride*, *T. afroharzianum* and *P. chlamydosporia* (with the exception of *T. harzianum*). This change can lead to variable effects on fungal growth and the HR, a characteristic feature of plant defence against pathogens (Torres and Dangl 2005). For instance, previous studies have shown that silencing the *Rboh* gene in *N. benthamiana* plants leads to decreased HR and increased susceptibility to avirulent *Phytophthora infestans* (Yoshioka et al. 2003). In contrast, the *Arabidopsis atrbohF* mutant exhibits enhanced HR and increased resistance to the a relatively virulent strain of the *Peronospora parasitica* fungus (Torres et al. 2002). These findings highlight the complex role of *Rboh* proteins in plant defence and their potential as targets for manipulating plant-microbe interactions.

In the plant-pathogen signalling cascade, three conserved genes were identified among the four endophytically colonised tomato plants. Notably, the *PR-1* gene, which plays a pivotal role in defence responses, was also detected in this pathway. Furthermore, the expression of two critical genes involved in environmental stress responses, pest and disease resistance and plant development, including calcium-modulated calmodulin-like (*CML*) and heat shock protein 90 (*HSP90*), was shared among these plants. CML is a plant-specific calcium-sensing protein that actively participates in signal perception and transmission by detecting changes in Ca^{2+} concentrations in the cell cytosol. It interacts with various effector regulatory proteins to establish a dependable network of signal transduction pathways (Cheval et al. 2013; Raina et al. 2021). Overexpression of *CML-APR134* in *Arabidopsis* has been shown to enhance HR to an avirulent strain of *Pseudomonas syringae* (Chiasson et al. 2005), whereas silencing of the *CML-APR134* gene in tomato plants suppresses HR (Zhang et al. 2022). Moreover, *SlCML55*-silenced tomato lines exhibited increased tolerance to the pathogen *P. capsici* due to the negative regulation of *PR* gene activation (Zhang et al. 2022). Another conserved gene, *HSP90*, is essential for cell death and *R*-gene-mediated HR resistance (Takabatake et al. 2007). The absence of functional *HSP90s* in plants can result in decreased immune receptor accumulation, decreased R protein-mediated immunity, and increased vulnerability to infection (Lu et al. 2022). Notably, experiments have demonstrated that cell death and *P. syringae* resistance genes were suppressed in *HSP90*-silenced *Arabidopsis* (Takahashi et al. 2003), highlighting the critical role of *HSP90* in plant defence against pathogens.

Phytohormones are small signalling molecules synthesised within plant cells that govern plant growth, development and

immunity. Plant hormone levels can fluctuate in response to pathogenic and beneficial microorganism infections. When a plant is colonised by an invading microorganism, the signalling molecules associated with plant hormones are often either suppressed or activated (Pieterse et al. 2012; Shigenaga et al. 2017). Moreover, crosstalk between different hormonal networks, especially between SA and JA, is often observed (Thaler et al. 2012; Shigenaga et al. 2017). JA and its associated metabolites are synthesised via the oxylipin biosynthesis pathway in response to various plant invaders, thereby mediating induced systemic resistance (ISR) (Pieterse et al. 2012). Many genes related to JA biosynthesis and signalling pathways were significantly induced in the four investigations examined here. For example, the *LOX* gene was consistently expressed across the four examined investigations. *LOX* plays an important role in various plant biological processes, including programmed degradation and cell death, defence responses to microbial agents, nematode infection, insect attack and wounding (Heitz et al. 1997; Veronico et al. 2006; Akram et al. 2008; Liu and Han 2010). Silencing the *tomloxD* gene in tomato plants has been shown to significantly reduce lipoxygenase activity and JA content, highlighting the importance of *LOX* in JA biosynthesis (Hu et al. 2015). Furthermore, *LOX1*, which encodes *LOX* and responds to JA, is expressed in guard cells in response to pathogen-associated molecular patterns (PAMPs). Its expression is necessary to initiate stomatal defence, indicating the involvement of the JA signalling pathway in regulating stomatal defence during microbial agent invasion (Montillet et al. 2013). In the JA signalling pathway, one of the most critical signalling molecules, *JAZ*, was induced in plants colonised by *T. harzianum*, *T. atroviride* or *P. chlamydosporia*. JAZ proteins regulate JA pathways by inhibiting and binding to the functions of transcription factors (TFs), such as MYC2, serving as a molecular link between the two steps in the JA pathway (Pauwels and Goossens 2011). Recent studies have demonstrated that *JAZ2* plays a role in controlling stomatal dynamics during microbial infection by regulating a specific transcriptional cascade that relies on the presence of MYC (Major et al. 2017).

One of the essential single molecules in SAR is SA. SA is a phenolic derivative that participates as a signalling molecule in plant responses to microbial agents and abiotic stresses, such as salt, temperature and oxidative conditions. In plants, SA is thought to originate from two possible pathways: the phenylalanine ammonia-lyase (PAL) and isochorismate synthase (ICS) pathways (Mishra and Baek 2021). Among the SA genes synthesised from the PAL pathway, *PAL* genes were common in all four investigations analysed here. PAL is an upstream enzyme involved in the biosynthesis of various aromatic secondary metabolites, such as SA, flavonoids, lignins and alkaloids (Tohge et al. 2013). Evidence from multiple studies indicates that high PAL activity plays an important role in SA production in response to microbial agents. For instance, Elkind et al. (1990) demonstrated that the amount of SA generated in tobacco leaves with a silenced *PAL* gene and those infected with the tobacco mosaic virus was both lower than that in control samples. Moreover, Mauch-Mani and Slusarenko (1996) reported that the primary function of PAL in enabling *Arabidopsis* to resist the downy mildew pathogen *Hyaloperonospora parasitica* is the generation of SA. Consistently, PAL-suppressed transgenic tobacco plants exhibited lower levels of SA in their leaves, as well as impaired systemic acquired resistance (Pallas et al. 1996). In the SA signalling pathway, the *PR-1* gene expression in tomato plants colonised by each of the four endophytic fungi examined in our analysis was similarly regulated to that observed in MAPK and plant-pathogen interaction cascades. Elucidating the precise mechanisms of action of PR proteins is challenging due to the complex interplay between stress response pathways and hormone signalling. SAR often leads to an increase in SA levels and the coordinated activation of *PR* genes, including *PR-1*, *PR-2* and *PR-5*. This process involves the transmission of one or more long-distance signals to amplify the immune response in unaffected plant tissues (Janda et al. 2020; Yu et al. 2022). Notably, the introduction of the nonpathogenic bacterium *Bacillus cereus* to *A. thaliana* resulted in the activation of *PR-1*, *PR-2* and *PR-5* genes, indicating that SAR was stimulated in the SA signalling pathway (Niu et al. 2011). Furthermore, Shi et al. (2019) confirmed that SA signalling increased the expression level of *PR-1* in tea plants resistant to anthracnose, highlighting the importance of SA signalling in plant defence responses.

Several essential transcripts related to phytohormones that are commonly expressed in tomato plants colonised by *T. atroviride*, *T. afroharzianum* or *P. chlamydosporia* are related to the *TGA* transcription factor. TGA transcription factors are a group of proteins involved in plant development and defence responses. These genes were grouped into five clades, some of which regulate JA- or SA-dependent gene expression (Fonseca et al. 2022; Tomaž et al. 2022). For example, in the immune response against microbial agents, TGAs from clade II play an essential role in SAR (SA responses) and produce long-lasting and broad-spectrum immune responses in plants. A remarkable function of clade II TGAs is that they negatively control SA accumulation under stress conditions, such as nonpathogenic *P. syringae* infection, which induces hormone production (Fonseca et al. 2022). Moreover, SA has transcriptional control over JA signalling with the help of *TGAs*. Rahman et al. (2012) reported that TGA1.a enhances grey mould development in tomato plants caused by *B. cinerea* (a necrotroph) by suppressing the expression of proteinase inhibitors I and II in the JA signalling pathway.

In addition to SA and JA, ethylene (ET) is a critical hormone associated with plant responses to biotic stress. In terms of ET biosynthesis, transcripts encoding *ACO* and *ACS* were significantly induced in the three *Trichoderma*-involved studies examined here. These genes are differentially expressed in plant tissues during development and in response to external stimuli. Research on various biotic (pathogenic infection) and abiotic (temperature, wounding and floods) treatments has revealed multiple cases of differential overexpression of *ACO* and *ACS* genes (Tatsuki and Mori 1999; Barry et al. 2000; Moeder et al. 2002). High accumulation of *ACO* transcripts has been noted in the hosts of *Colletotrichum destructivum* (Chen et al. 2003) and *Colletotrichum acutatum* (Lahey et al. 2004). Research on plants silenced by *NB-ACO1* has revealed that the *ACO* gene is not only triggered by pathogenic invasions but also has a significant effect on the development of necrotrophy as a result of fungal infections (Shan and Goodwin 2006). In addition, examination of the overall gene expression patterns in

plants infected with different microorganisms revealed significant interactions among the ethylene, SA, and JA signalling pathways within the immune signalling network. These findings demonstrate extensive crosstalk between these signalling pathways during plant responses to infection (Sato et al. 2010; Pieterse et al. 2012). For example, exogenously applied ethylene or ethylene produced during microbial infection can override the requirement of *NPR1* (a key regulator of SA signalling) to suppress the JA response caused by SA. These findings suggest that ethylene mediates antagonistic crosstalk between the SA and JA signalling pathways, influencing the outcome of plant defence responses (Leon-Reyes et al. 2009).

Among the different groups of plant-specific secondary metabolites, phenylpropanoids have been well described. In the first step of the phenylpropanoid pathway, the PAL enzyme (EC 4.3.1.5) catalyses cinnamic acid production, which is an important regulatory point between primary and secondary metabolism. PAL is a core enzyme in the phenylpropanoid pathway, and its metabolites are crucial for plant development, growth and resistance to both biotic and abiotic stressors (Huang et al. 2010; Zhang et al. 2023). *PAL* can be expressed differently in response to various of environmental stimuli, such as pathogen infection, nutritional deficiency, wounding, UV irradiation, and temperature variations (Fukasawa-Akada et al. 1996; Huang et al. 2010). Elkind et al. (1990) reported that tobacco plants with heterologous *PAL* genes exhibit localised fluorescent lesions, reduced xylem lignification, slowed growth, decreased pollen viability and abnormal floral morphology and leaf shape. Rohde et al. (2004) reported phenotypic changes in the *Arabidopsis* double mutant of *pal1* and *pal2*, including a significant decrease in lignin content, modification of secondary cell wall structure, and fertility issues.

Flavonoids derived from the phenylpropanoid pathway are classified into different subgroups based on their structural characteristics, including flavones, flavanones, flavanols, chalcones, anthocyanidins and catechins (Sugiyama and Yazaki 2014). Flavonoid derivatives with antioxidant properties can protect plants against various abiotic and biotic stresses and act as allelochemical agents, detoxifying agents, phytoalexins and pollinator attractants (Samanta et al. 2011; Zhang et al. 2020). The expression of genes encoding flavonols (*FL3M*) and flavonoids (*FLS*), as well as dose involved in the anthocyanidin pathway (*ANS*), exhibited differential expression patterns across the four studies examined in this analysis. The FLS enzyme (EC 1.14.20.6), responsible for the conversion of dihydroflavonols to flavonols, and the FL3M enzyme (EC 1.14.14.82), involved in the hydroxylation of dihydroflavonol, were identified as key enzymes in the flavonoid biosynthesis pathway. Notably, kaempferol is synthesised by FLS but degraded by FL3M (Kumari et al. 2023). The ANS enzyme, which is essential for anthocyanin synthesis, converts colourless leucoanthocyanins into coloured anthocyanins (Zhang et al. 2020). Zhang et al. (2020) reported that overexpression of *StANS* may promote the synthesis of anthocyanins in potato tubers. These findings suggest that *Trichoderma* and *Pochonia* species may influence tomato resistance by modulating the biosynthesis of phenylpropanoids and flavonoid derivatives.

Despite the presence of common genes in key pathways associated with the immune response in tomato, we identified 30 transcripts that were consistently induced by the fungi analysed. The most significantly enriched GO term in the biological processes of these genes was related to anion transport (GO:0006820). Ion efflux is among the first identifiable signalling events in cells treated with elicitors. Activation of anion flux in the context of innate immunity has been primarily reported as one of the initial reactions caused by plant-pathogen interactions (De Angeli et al. 2007). Anion transporters/channels appear to be key players in signalling pathways, leading to a wide range of physiological functions in plants, such as cell signalling, adaptation to environmental stresses in plant cells, and plant nutrition (Barbier-Brygoo et al. 2011). These anion channels are essential for mediating pathogen- and elicitor-induced processes, including oxidative bursts, MAPK cascades and differential expression of defence genes (Garcia-Brugger et al. 2006). These data also provide important evidence that anion channel activity is a necessary early precondition for the HR (Wendehenne et al. 2002). When cryptogein and *P. syringae* pv. *glycinea* are added to tobacco and soybean leaves, respectively, anion channel blockers significantly reduce HR and the development of cell death (Wendehenne et al. 2002). Using heatmap clustering to analyse plant-endophyte interactions, we observed that endophytes from the same genus but different species induced similar gene expression patterns in tomato. This phenomenon implies a conserved mechanism by which these fungi interact with host plants, underscoring the specificity and predictability of plant-endophytic relationships. Notably, despite potential variations in the genetic makeup of different species within a genus, fungi from the same genus trigger a consistent set of plant responses, highlighting a specific mode of communication and adaptation between the two. This uniformity in gene expression supports the notion of an evolutionarily conserved mechanism of plant interaction within specific fungal genera (Genre et al. 2020; Chen et al. 2022; Kumar and Nautiyal 2023).

5 | Conclusion

Interactions between endophytes and their hosts facilitate plant vigour and health, which requires a better understanding of the molecular mechanisms underlying endophyte-mediated systemic resistance. In this study, we re-examined the transcriptomic profiles of tomato plants colonised by the endophytic fungi *Trichoderma* spp. and *P. chlamydosporia* to elucidate the molecular mechanisms underlying tomato growth and defence response. Our comprehensive analysis revealed significant transcriptomic changes in various gene pathways associated with plant defence and development, following fungal inoculation. Notably, we identified 30 genes that specifically responded to the four endophytic fungi and 71 genes that responded to only three *Trichoderma* species, which were predominantly involved in defence signalling pathways. Furthermore, our analysis revealed conserved gene expression following the colonisation of tomatoes by several different species of endophytic fungi. Our findings should facilitate future investigations of endophyte-host interactions, focusing on the development of genetically modified fungus-resistant plants, as well as traditional breeding programmes for long-lasting fungal resistance.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Peer Review

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** jph70172-sup-0001-FigureS1.docx. **Table S2:** jph70172-sup-0002-TableS1.xlsx.