

RESEARCH

Open Access



Volatile organic compound-induced metabolic and biochemical reprogramming in *Zingiber officinale* for resistance to *Pythium myriotylum*

Sinoy Johnson¹, Sachin Philip², Nandana Unni¹, Devika Vimal¹, P. P. Shandev¹ and Sayuj Koyyappurath^{1*}

*Correspondence:

Sayuj Koyyappurath
sayujcusat@gmail.com

¹Department of Biotechnology,
Cochin University of Science and
Technology, Kochi 682022, Kerala,
India

²Department of Applied Chemistry,
Cochin University of Science and
Technology, Kochi 682022, Kerala,
India

Abstract

Rhizome rot, caused by *Pythium myriotylum* (*P. myriotylum*), is a significant constraint on ginger cultivation, necessitating the development of sustainable defense strategies. The present study, therefore, evaluated the capacity of the monoterpenes Geraniol, Eugenol, and Linalool to function as priming agents for resistance induction in cultivated ginger. Our comprehensive evaluation of the defense response, employing biochemical and metabolomics approaches, revealed that Geraniol emerged as the most effective candidate, significantly reducing disease severity in infected plants. Biochemical analysis demonstrated that Geraniol-primed infected plants exhibited a notable enhancement in defense-related compounds and enzymatic activities compared to infected plants. Geraniol primed plants showed elevated levels of phenolics, flavonoids, anthocyanin, and lignin, with increased activities of Phenylalanine Ammonia Lyase (PAL) enzyme. Metabolomics profiling studies identified significant shifts in secondary metabolism, highlighting the accumulation of key defense-related metabolites in primed plants. The findings of the study strongly suggests that Geraniol effectively primed the ginger defense system, leading to a faster and stronger induction of both constitutive and induced defenses upon *P. myriotylum* challenge. Geraniol priming proved to be a promising, eco-friendly strategy for managing *P. myriotylum*-induced rhizome rot in ginger.

Keywords Defense priming, Metabolomics, Rhizome rot, VOC, *Zingiber officinale*

1 Introduction

Ginger (*Zingiber officinale* Roscoe) is an economically vital spice crop worldwide, celebrated for its extensive culinary, medicinal, and industrial applications [64]. The sustained production of ginger is continually challenged by soil-borne pathogens, often leading to significant economic and yield losses reaching up to 90% in India [103]. Among these, *Pythium myriotylum* is recognized as the dominant etiological agent responsible for devastating rhizome soft rot. Kumar, [46]. This devastating disease does not just lead to significant yield losses; it also contributes to substantial pre- and post-harvest spoilage, posing a constant threat to ginger producers worldwide [61].



© The Author(s) 2026. **Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

Conventional disease management strategies have historically relied heavily on chemical fungicides. In addition, current strategies integrate cultural practices like proper soil drainage and crop rotation with biological control agents such as *Trichoderma* species and *Pseudomonas fluorescens*, which offer a more sustainable alternative to traditional soil solarization and chemical drenching [3, 8]. While these offer immediate solutions, they come with a growing list of concerns, including the risk of residual toxicity in the crop, the development of fungicide resistance in pathogen populations, and inevitable environmental contamination [28]. These drawbacks underscore the critical need for more sustainable and environmentally benign approaches to crop protection.

In light of these escalating challenges, alternative and sustainable disease management approaches, such as induced resistance, have gained considerable prominence in plant pathology and agricultural research [108]. Among these, Induced Systemic Resistance (ISR) and Systemic Acquired Resistance (SAR) represent sophisticated, plant-intrinsic defense mechanisms. These mechanisms are not constantly active, but “switched on” or amplified in plants following exposure to specific biological or chemical elicitors [107]. A crucial concept within induced resistance is priming, which describes a state of enhanced defense capacity induced by a prior, often non-damaging, stimulus. This “primed” state enables the plant to respond significantly more rapidly and intensely to subsequent pathogen attacks, effectively preparing its immune system without expending excessive energy prematurely [5].

This study investigated the efficacy of the volatile monoterpenes Geraniol, Eugenol, and Linalool as potential priming agents in combating *Pythium* Soft Rot. These compounds are naturally occurring components of various essential oils and have attracted scientific interest due to their diverse biological activities [66]. For instance, Geraniol has been extensively documented for its antimicrobial and insecticidal properties [13]. Furthermore, these monoterpenes are increasingly recognized for their roles in plant-plant communication and their direct influence on plant-pathogen interactions, suggesting they can act as signaling molecules [16]. While recent studies have suggested that Geraniol, in particular, might trigger defense responses in various crops (Shuning [11, 37, 79, 91]), the comparative efficacy of these specific monoterpenes as priming agents for inducing resistance against *Pythium* in ginger had, until now, remained largely underexplored. This knowledge gap represents a significant opportunity to identify novel, eco-friendly elicitors for ginger defense against the soft rot pathogen.

A profound understanding of the molecular and cellular mechanisms underpinning induced resistance is absolutely crucial for developing truly effective and durable crop protection strategies especially for ginger [38]. Plant defense responses are highly complex, involving intricate biochemical pathways such as the Jasmonic acid pathway, phenylpropanoid pathway, which collectively synthesize a diverse array of protective secondary metabolites (Simardeep [40]). These pathways lead to the orchestrated accumulation of various protective compounds, including phytoalexins, phenolics, and flavonoids, which possess direct antimicrobial properties or act as signaling molecules [67, 80]. Simultaneously, defense responses involve the rapid reinforcement of physical barriers, such as cell wall components, through processes like lignification and callose deposition [63], which will ultimately impede pathogen progression. Building upon these structural reinforcements, the intricate network of plant metabolites played a critical role in orchestrating a comprehensive defense response. To comprehensively capture

the dynamic changes within the plant's metabolic state during these defense responses, metabolomics provides an invaluable tool [95]. Gas Chromatography-Mass Spectrometry (GC-MS)-based metabolomics enables the identification and quantification of a wide array of metabolites, providing a holistic snapshot of the plant's metabolic adjustments in response to priming and pathogen challenge [21].

Therefore, the primary aim of this study was to rigorously evaluate the effectiveness of Geraniol, Eugenol, and Linalool in priming *Z. officinale* for enhanced resistance against the devastating rhizome rot caused by *P. myriotylum*. To achieve this, we employed a robust multifaceted approach. This integrated methodology combined detailed biochemical analysis of key defense markers with advanced GC-MS-based metabolomics profiling to comprehensively map shifts in the plant's metabolic landscape. This holistic approach was designed not only to identify the most effective monoterpene priming agent among the candidates but also to provide profound insights into the intricate underlying molecular and cellular mechanisms by which these compounds activate and modulate ginger's defense system. The findings from this research could pave the way for novel, sustainable, and eco-friendly strategies to protect ginger crops.

2 Materials and methods

2.1 Plant materials and treatments

Healthy rhizomes of the ginger cultivar 'Athira' (*Zingiber officinale* Roscoe), a commonly cultivated variety in South India, were purchased from the authorized institutional center of the Kerala Agricultural University (KAU), Mannuthy, Thrissur, Kerala, India (10.53° N, 76.24° E). The rhizomes were sprouted and maintained in the shade house facility under natural conditions at the Department of Biotechnology, Cochin University of Science and Technology, Kochi. To ensure environmental clarity, the plants were grown under a natural photoperiod (approximately 12/12 h light/dark) with an average ambient temperature of 28 ± 3 °C and a relative humidity ranging between 70% and 85%, reflecting the typical tropical climate of the region. A highly pathogenic in-house culture of *P. myriotylum* was used for this study and maintained on Potato Dextrose Agar (PDA). Geraniol, Eugenol, and Linalool (analytical grade, > 98% purity) were purchased from Tokyo Chemical Industry (TCI) Co., Ltd., Japan, and prepared as 150, 200, and 200 µM solutions, respectively, in distilled water based on a pre-optimized study. Our study used a foliar-based priming strategy to prime the aerial parts of ginger plants with the help of a standard spray bottle, ensuring a uniform spray. The ginger plants selected for the study were systematically divided into distinct treatment groups to investigate the effects of priming with volatile organic compounds (VOCs) and subsequent infection with *P. myriotylum*. The experimental design comprised unprimed control plants and plants primed with Geraniol, Eugenol, or Linalool. Specifically, the groups comprised: Unprimed (C), consisting of healthy plants treated solely with water; *P. myriotylum* infected (P), in which C was inoculated with a *P. myriotylum* spore suspension; Geraniol-primed (G), involving plants treated with a Geraniol; Geraniol-primed + *P. myriotylum* infected (G + P), where plants received Geraniol treatment followed by *P. myriotylum* inoculation 48 h post priming; Eugenol-primed (E), for plants primed with an Eugenol; Eugenol-primed + *P. myriotylum* infected (E + P), indicating Eugenol treatment followed by *P. myriotylum* inoculation 48 h post priming; Linalool-primed (L), for plants treated with a Linalool; and Linalool-primed + *P. myriotylum* infected (L + P),

representing Linalool treatment followed by *P. myriotylum* inoculation 48 h post priming. Each treatment group consisted of six biological replicates, with each replicate comprising one plant per pot to ensure statistical validity and account for biological variation. This comprehensive setup enabled assessment of both direct VOC effects and their role in enhancing resistance to *P. myriotylum*. Ginger plants were challenged with inoculation at the collar region with *P. myriotylum* [27]. The mycelial discs of 10 mm in diameter, were excised from the actively growing margins of a 48-hour-old *P. myriotylum* culture maintained on Potato Dextrose Agar (PDA). These discs were then aseptically applied to the collar region of each plant. To maintain high humidity and promote infection, the inoculated area was covered with sterile wet cotton. Control plants were mock-inoculated with sterile PDA discs. The leaf and collar region samples were harvested on the 5th and 7th days post-inoculation for subsequent analyses. Disease severity was assessed using a visual scale based on symptom progression. Disease severity was scored on a 0–3 scale, where 0 indicated green, healthy plants; 1 indicated discoloration of the leaf sheath collar and yellowing of lower leaves; 2 represented plants with entirely yellow or dead shoots despite still being alive; and 3 was assigned when all shoots were dead [84]. The ratings were conducted at regular intervals post-inoculation to track disease progression.

3 Physiological parameters

The physiological parameters of the plants under post-priming and post-infection conditions were assessed by harvesting samples from each treatment set at respective time points. The physiological responses to defense-priming and subsequent infection were quantified through comprehensive assessments including biochemical and metabolomic profiling, conducted on the 5th and 7th days post-pathogen inoculation.

The total carotenoids in the leaf samples were evaluated as described earlier [36]. Solvent extraction was carried out by homogenizing approximately 500 mg of leaf samples with 4 mL of 80% acetone (SRL, Maharashtra, India) using a standard mortar and pestle. The absorbance values of the supernatant obtained after centrifugation were estimated using the Spark multimode microplate reader (TECAN, Zurich, Switzerland) and final values were calculated following established equations [86].

$$\text{Chl } a \text{ (}\mu\text{g/g FW)} = (12.25 \cdot A_{663}) - (2.79 \cdot A_{647}).$$

$$\text{Chl } b \text{ (}\mu\text{g/g FW)} = (21.5 \cdot A_{648}) - (5.1 \cdot A_{663}).$$

$$\text{Total Carotenoids (}\mu\text{g/g FW)} = ((1000 \cdot A_{470} - 1.82 \cdot \text{Chl } a) - (85.02 \cdot \text{Chl } b))/198.$$

To quantify other stress-related biomarkers, ginger plant leaf samples were analyzed for total flavonoids, anthocyanins, total phenolics, soluble lignin, and malondialdehyde (MDA) content. Total flavonoid content was determined spectrophotometrically via the Aluminum Chloride (AlCl_3) colorimetric method, measuring absorbance at 420 nm and expressed as quercetin equivalents based on a calibration curve [4]. Similarly, anthocyanin content was determined after homogenizing 100 mg of ground tissue in 2 ml of ethanol with 2% HCl. The supernatant's absorbance was read at 530 nm and 657 nm [96]. Total phenolic content was quantified using the Folin-Ciocalteu method, in which methanolic extracts reacted with the Folin-Ciocalteu reagent and sodium carbonate, and absorbance was measured at 765 nm against a gallic acid standard curve [6]. The lignin content was determined following an established protocol, involving an acid-catalyzed reaction to generate a colored, soluble lignin-thioglycolate complex. The concentration

of lignin was calculated from a lignin standard calibration curve based on absorbance values at 340 nm [78]. Finally, malondialdehyde (MDA) content, indicating lipid peroxidation, was determined spectrophotometrically after homogenizing fruit peel in Trichloro Acetic Acid (TCA), reacting the extract with Thiobarbituric acid (TBA), and measuring absorbance at 532 nm, 600 nm, and 450 nm. The final MDA content was calculated using a specific formula based on these absorbance readings and reaction volumes [31].

As a pivotal enzyme in the phenylpropanoid pathway, Phenylalanine Ammonia-Lyase (PAL) activity was also measured to elucidate the biochemical defense mechanisms contributing to the plant's physiological responses. The PAL activity was determined by preparing a reaction mixture consisting of an enzyme solution, 20 mmol/L phenylalanine, and a 50 mmol/L borate buffer (pH 8.8) with additives. The reaction was incubated at 37 °C for 60 min and subsequently terminated by the addition of 6 mol/L HCl. The resulting absorbance was then measured at 290 nm to quantify the activity (Yanzheng Sun et al., 2023). Detailed procedural information, including reagent preparation, calibration curves, and calculation formulae, is provided in the Supplementary Materials.

4 GC-MS analysis

A Gas Chromatography-Mass Spectrometry (GC-MS) approach was conducted to identify volatile metabolites, enabling a comprehensive evaluation of the plant's metabolic shifts in response to the different priming agents. The analysis was carried out at the Department of Applied Chemistry, Cochin University of Science and Technology. Organic compounds were extracted by homogenizing leaf samples in methanol at a concentration of 100 mg/ml. The resulting homogenate was centrifuged at 4000 xg for 5 min to separate the supernatant, which contained the extracted metabolites. GC-MS analysis was performed using an Agilent 7890 A instrument (California, USA) equipped with an HP-5MS capillary column. Compound identification was achieved by comparing the obtained mass spectra against the comprehensive National Institute of Standards and Technology (NIST) database [98]. The resulting data were then tabulated, sorted, and filtered for visualization using Venn diagrams generated with the ggVennDiagram (v1.5.2) package in the R statistical environment (v4.4.2)(C.-H. Gao et al., [25]).

5 Experimental design and statistical analysis

The experiment was conducted in a randomized complete block design and repeated to ensure repeatability. The corresponding results are represented as the mean $\pm$ Standard Deviation (SD). The R Statistical Programming language (v4.4.1) was employed to conduct variance of analysis (ANOVA) and Tukey's Honestly Significant Difference (HSD) test using the stats package (v4.4.1). All the analyses were subjected to a p-value cut-off of 0.05.

6 Results and discussion

6.1 Plant material and treatment

The study was conducted using healthy Athira ginger rhizomes, which are a common cultivated ginger variety in South India (Fig. 1). The virulent *P. myriotylum* isolate effectively established characteristic disease symptoms, providing a robust and reliable



Fig. 1 Ginger plants used in study. The image represents 3-month-old healthy ginger (KAU Athira variety) plants used in the assays for priming, pathogenicity and GCMS analysis. The plants were maintained in a greenhouse facility at the premises of the Department of Biotechnology, CUSAT

pathosystem for the investigation. Clear-cut differences were observed between primed and unprimed plants with varying disease indices.

7 VOC priming significantly mitigated disease severity

Disease severity, visually assessed on a 0–3 scale, showed distinct differences in progression among the treatment groups, consistent with previous studies on plant-pathogen interactions. Unprimed plants inoculated with *P. myriotylum* exhibited severe disease progression, characterized by progressive chlorosis, wilting, and significant plant collapse (scores 2–3), key symptoms of soft rot in ginger. This observation confirmed the pathogenicity of the *P. myriotylum* isolate and established a baseline for disease development, consistent with typical disease curves observed in susceptible plant varieties [84].

Critically, plants primed with Geraniol, Eugenol, or Linalool prior to inoculation consistently showed significantly reduced disease symptoms and lower severity scores than unprimed infected controls. The mean Area Under Disease Progress Curve (AUDPC) for the control group (P) (11.5) was higher than that for the VOC-treated groups (E + P: approximately 2.0, L + P: approximately 0.5, G + P: approximately 0.1) (Fig. 2a). This outcome strongly suggested an induced resistance effect, echoing findings where volatile organic compounds have been shown to prime plant defenses against various pathogens [32, 53, 53]).

Among the VOCs, G + P plants consistently demonstrated the most significant reduction in disease severity, indicating their superior defense efficacy (Fig. 2e). The G + P plants appeared considerably healthier and exhibited negligible disease symptoms compared to the unprimed group (P) (Fig. 2b). This optimal performance of Geraniol aligns with recent research highlighting its potent elicitor properties in plant defense responses

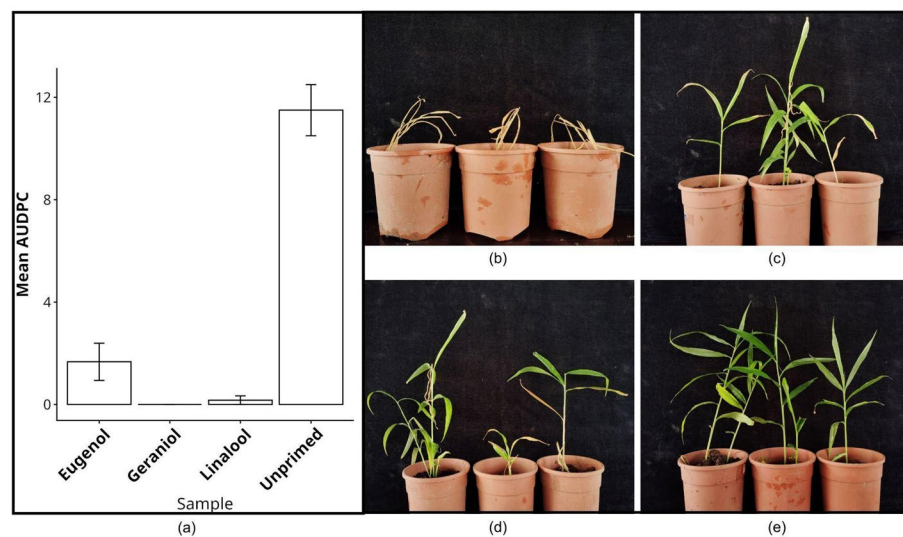


Fig. 2 Effect of VOCs Treatments on Plant Disease Progression. **a** represents the mean Area Under Disease Progress Curve (AUDPC) for different treatments (mean $\pm$ SD, $n=3$). **b**, **c**, **d**, and **e** show the visual representation of the plants under various conditions. (b) depict the unprimed control group exhibiting severe disease symptoms, while (c), (d), and (e) showed the plants treated with Linalool, Eugenol and Geraniol, respectively, indicating reduced disease progression compared to the control

which were reported in rice and citrus [44, 99]. L + P plants also showed considerable disease suppression, performing better than E + P plants, although less effectively than G + P. L + P plants (Fig. 2c) exhibited better health compared to E + P plants (Fig. 2d). The observed efficacy of linalool in suppressing disease corroborated findings from prior research that reported its antimicrobial properties and its capacity to induce defense responses in various plant systems such as *Arabidopsis-Pseudomonas*, *Berry-Alternaria* pathosystems ([20, 110], suggesting a common yet less potent activation of signaling or metabolic pathways when compared to geraniol. The Eugenol priming, while still offering some protection compared to the unprimed infected control, exhibited the least pronounced effect among the three VOCs (Fig. 2d). This ranking suggested a hierarchical effectiveness of the VOCs in inducing resistance, with Geraniol > Linalool > Eugenol. This hierarchy was clearly supported by the AUDPC values with Geraniol having the lowest AUDPC, followed by Linalool, and then Eugenol (Fig. 2a). These results resonated with studies indicating varying degrees of effectiveness among different VOCs in triggering plant defense mechanisms, often dependent on their chemical structure and specific plant-pathogen interactions [82].

This strong evidence indicates that VOC priming conferred resistance against *P. myriotylum* infection in ginger, likely by activating defense mechanisms that mitigate disease development. Such a reduction in disease severity following volatile organic compound treatment aligns with previous research highlighting the eliciting capabilities of these compounds in various plant-pathogen interactions [9]. The absence of symptoms in uninfected control plants (P) further validated the experimental setup, confirming that disease progression in the infected groups was solely attributable to *P. myriotylum* infection. The significant differences observed between primed and unprimed infected plants underscored the potential of VOCs as sustainable strategies for disease management in ginger cultivation.

8 Physiological parameters

Analysis of various physiological parameters on the 5th and 7th days post-inoculation provided more profound insights into the plant's responses, clearly supporting the observed hierarchy in disease suppression, which are listed below.

8.1 Enhanced carotenoid content as a marker of defense response upon VOC priming

Carotenoids play a crucial role in plant defense and health, acting as essential photosynthetic pigments and antioxidants. An elevated concentration of plant carotenoids generally indicates enhanced physiological well-being and fortified defensive capabilities. The levels of carotenoid on day 5 in *P. myriotylum* infected leaf samples displayed a slight increase in carotenoid content across all treatment groups in comparison with uninfected controls, indicating a normal stress-induced defense response (Fig. 3a). This increase in carotenoid content reflected the immediate impact of the pathogen on the plant's photosynthetic machinery and its overall physiological state, suggesting a role for carotenoids in the plant defense response [87]. However, G + P plants showed significantly higher carotenoid levels compared to the other infected groups, even surpassing their unprimed infected counterparts. This observation reiterated the geraniol's ability to bolster the plant's defense mechanisms, potentially by enhancing antioxidant capacity or reducing oxidative damage [83]. Similarly, L + P plants also maintained higher carotenoid levels than E + P, indicating differential protective effects among the priming agents.

This trend was significantly altered and became even more pronounced on day 7. Infected plants across all groups continued to exhibit lower carotenoid content than their uninfected controls, reinforcing the sustained stress imposed by the infection (Fig. 4a). However, Geraniol-primed infected plants consistently maintained the highest carotenoid levels among all infected groups, significantly exceeding those of the C, E + P, and L + P plants. This suggested that Geraniol has a superior ability to mitigate oxidative stress and protect the photosynthetic apparatus during infection, possibly through

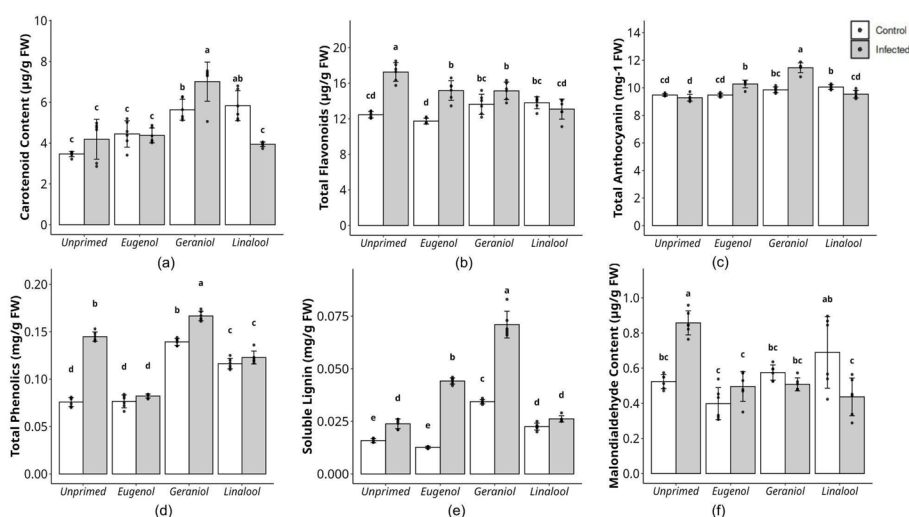


Fig. 3 Physiological parameters of samples at 5 days post infection. The bar graphs represent: **a** Carotenoid content, **b** Total Flavonoids, **c** Total Anthocyanin, **d** Total Phenolics, **e** Soluble Lignin and **f** Malondialdehyde content. Different lowercase letters indicate significant differences among treatments according to Tukey's Honestly Significant Difference (HSD) test ($p < 0.05$) (mean $\pm$ SD, $n = 6$)

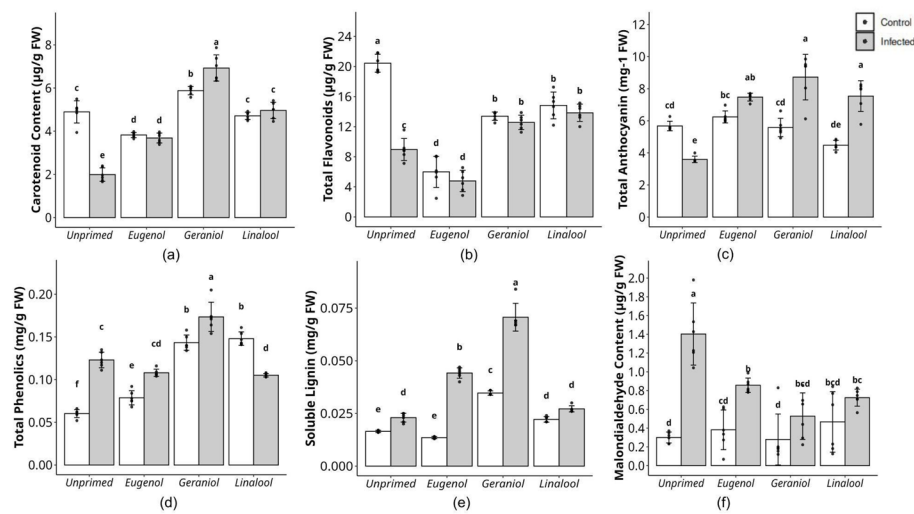


Fig. 4 Physiological parameters of samples at 7 days post infection. The bar graphs represent: **a** Carotenoid content, **b** Total Flavonoids, **c** Total Anthocyanin, **d** Total Phenolics, **e** Soluble Lignin and **f** Malondialdehyde content. Different lowercase letters indicate significant differences among treatments according to Tukey's Honestly Significant Difference (HSD) test ($p < 0.05$) (mean $\pm$ SD, $n = 6$)

the modulation of Reactive Oxygen Species (ROS) scavenging pathways [19]. The L + P plants also showed better carotenoid retention than E + P plants at Day 7, reinforcing the hierarchy of protection observed earlier. These findings collectively demonstrate the potential of priming agents, particularly Geraniol, to preserve vital photosynthetic pigments under pathogenic stress, thereby enhancing plant resilience.

8.2 Stress-related biomarkers

The quantification of other stress-related biomarkers provided direct evidence of the biochemical changes underpinning the observed physiological and resistance phenotypes, further substantiating the effectiveness hierarchy of the VOCs.

8.3 VOC priming modulated total flavonoid content for antioxidant defense

The flavonoid content was evaluated to assess the plant's antioxidant response and its ability to mitigate oxidative stress caused by the *P. myriotylum* infection. Flavonoids played a crucial role in plant defense by acting as antioxidants to mitigate oxidative stress and by exhibiting direct antimicrobial activity against pathogens [72]. The data in this study revealed a dynamic response modulated by the applied priming treatments. On Day 5, a rapid defense response was evident across all treatment groups (Fig. 3b). The *P. myriotylum* infection led to a significant increase in total flavonoid content in the P and E + P plants compared to their respective uninfected controls. In contrast, the Geraniol and Linalool-primed plants did not show a significant difference between infected and uninfected samples, with both groups maintaining flavonoid levels around 14–15 µg/g FW.

By Day 7, the pattern was strikingly different, highlighting the sustained impact of both the pathogen and the priming agents (Fig. 4b). In the P and E + P groups, the pathogen's effect appeared to overwhelm the plant's initial defense. The total flavonoid content in the P plants dropped dramatically to approximately 9 µg/g FW, a significant reduction from C, which had the highest flavonoid levels at around 20 µg/g FW. The E + P plants

also showed a decrease in flavonoid levels compared to their controls. In marked contrast, the Geraniol and Linalool plants demonstrated a robust and sustained defense response. The flavonoid levels in their infected samples remained high and comparable to their uninfected counterparts, at approximately 13 and 14 $\mu\text{g/g}$ FW, respectively. This indicated that priming with Geraniol and Linalool enabled the plants to maintain production of these critical antioxidant compounds, thereby resisting the detrimental effects of the pathogen over a longer period [81]. This sustained production of flavonoids likely contributed to enhanced plant resistance by mitigating pathogen-induced oxidative stress and potentially through direct antimicrobial activity, which were crucial for long-term defense [47, 69, 106]. The results hence demonstrated the superior efficacy of these priming agents in fortifying the plant's defense mechanisms.

8.4 Priming-induced anthocyanin accumulation mitigated stress

Anthocyanins play a significant role in plant defense by accumulating in response to environmental and biotic stresses and by acting as potent antioxidants to mitigate cellular damage [39]. Anthocyanins and their breakdown products can exhibit direct antimicrobial properties, to help plants defend against certain phytopathogens such as *Erwinia amylovora*, *Pseudomonas syringae* etc. Lucas-Bautista et al., [57], Sánchez-Hernández, [77]. In our study, on Day 5, *P. myriotylum* infection did not significantly alter total anthocyanin content across most groups compared to their controls, with slight variations (Fig. 3c). Interestingly, on Day 7, a notable increase in total anthocyanin content was observed in infected plants across all priming treatments, indicating an oxidative stress response (Fig. 4c). On the contrary, anthocyanin was significantly reduced in the P plants, suggesting the detrimental effects of the pathogen on disease progression. Among the various treatment groups, G + P plants showed the highest levels of total anthocyanins, significantly higher than those in the P, E + P, and L + P infected groups. The L + P infected plants also had higher anthocyanin content than E + P plants. This pronounced anthocyanin accumulation in Geraniol-primed plants suggests an enhanced antioxidant defense capacity or a more robust stress response. This sustained accumulation of anthocyanins in the G + P and L + P plants likely contributed to enhanced disease tolerance by mitigating oxidative stress, a finding that was consistent with previous studies on plant defense priming where anthocyanins were demonstrated to function as potent scavengers of Reactive Oxygen Species (ROS), thus protecting cellular components from damage and enhancing stress tolerance [34, 48, 54]. The ability of these priming agents to maintain high anthocyanin levels suggested a successful activation of defense mechanisms that conferred prolonged protection against the pathogen.

8.5 Priming-induced phenolic accumulation for broad-spectrum defense

Phenolics play a critical role in plant defense by functioning as structural barriers, signal molecules, and antimicrobial compounds that protect against pathogens and herbivores [94]. There are several studies that highlight the crucial role of phenolics in regulating lignin and suberin formation and in inducing antioxidant activity during pathogen invasion. The total phenolic content was significantly increased in the P group following *P. myriotylum* infection, a difference clearly observed on Day 5 itself (Fig. 3d). Similarly, G + P plants showed a significant increase in total phenolics compared to their uninfected controls and other infected groups. The L + P plants also exhibited elevated phenolic

levels, though less pronounced than Geraniol. The E + P plants showed only a modest increase. By Day 7, total phenolic content remained significantly elevated in infected plants across all priming treatments compared to their controls (Fig. 4d). The G + P plants continued to exhibit the highest total phenolic content, significantly surpassing all other groups, including unprimed infected controls. L + P plants maintained higher phenolic levels than E + P plants. This consistent and strong induction of phenolics by Geraniol highlights its ability to activate the phenylpropanoid pathway for broad-spectrum defense. The elevated phenolic levels indicate an enhanced capacity to scavenge for reactive oxygen species generated during the infection, could have caused significant cellular damage [14, 30, 76]. This observation was consistent with previous research studies conducted on other crops where phenolic compounds were reported to function as key secondary metabolites in plant defense, acting as antimicrobial agents and contributing to physical barriers like lignin deposition, linking an intense and prolonged phenolic response to improved disease resistance in plants [1, 81, 85].

8.6 Soluble lignin accumulation for structural defense upon priming

Lignin plays a crucial role in plant defense by forming a rigid, physical barrier in cell walls that provides a mechanical shield against pathogen invasion and spread [93]. To elucidate the dynamics of lignin accumulation in primed ginger plants post-pathogen inoculation, lignin was quantified in samples, and on Day 5, soluble lignin content generally increased in infected plants compared to their controls (Fig. 3e). The G + P plants displayed a marked and significant increase in soluble lignin, indicating an early and strong response towards cell wall reinforcement. L + P plants also showed an increase, while E + P plants had a lesser effect. On Day 7 (Fig. 4e), the increase in soluble lignin continued in infected plants, with G + P plants showing the highest and most significant soluble lignin content, indicative of robust lignification for structural defense against pathogen spread. L + P plants maintained higher soluble lignin levels than E + P plants. The high levels of soluble lignin precursors indicated an active lignification process, which was crucial for forming a rigid physical barrier to impede pathogen spread [58]. This robust lignification likely served as a key mechanism for the primed plants to resist the pathogen's assault, and this finding was consistent with previous research that linked enhanced lignification to improved mechanical strength and increased resistance against pathogens [24, 60, 70].

8.7 Priming reduced malondialdehyde (MDA) content to mitigate cellular damage

Malondialdehyde (MDA) plays a role in plant defense as a key biomarker of oxidative stress and cellular damage, with its accumulation indicating the extent of lipid peroxidation in response to a pathogen challenge [23]. On Day 5, *P. myriotylum* infection significantly increased MDA content (indicating lipid peroxidation and oxidative stress) in the P group (Fig. 3f). In the present study it was observed that all primed infected groups, particularly G + P plants, showed significantly lower MDA levels than the P plant. The L + P plants also had lower MDA than the E + P plants. This trend continued and became more pronounced on Day 7 (Fig. 4f). While MDA levels remained elevated in the P group, G + P plants consistently exhibited the lowest MDA content among all infected treatments, indicating superior mitigation of oxidative damage. L + P plants maintained lower MDA levels than E + P plants. This consistent reduction in MDA levels indicates a

significant decrease in lipid peroxidation and membrane damage, suggesting that these plants maintained better cellular integrity during *P. myriotylum* infection. This consistent reduction in MDA by Geraniol strongly suggests an enhanced antioxidant defense system, that protects cellular membranes from pathogen-induced oxidative stress and correlates directly with superior disease resistance. Significantly higher levels of MDA observed in the P and E + P plants, indicate that their defense mechanisms were overwhelmed by the pathogen's assault. This led to substantial oxidative stress and a breakdown of cell membrane integrity, which were both clear signs of disease progression. The low MDA content provided strong evidence that these priming agents conferred enhanced disease tolerance, consistent with previous studies correlating reduced MDA accumulation with increased stress resistance [29, 41, 109].

The physiological and biochemical data for stress-related biomarkers consistently indicated that the most effective defense responses, characterized by robust and sustained induction of defense compounds and a significant reduction in oxidative stress, were observed in G + P and L + P plants. These treatments led to a persistent accumulation of key defense molecules, including flavonoids, anthocyanins, phenolics, and soluble lignin, which collectively contributed to a multifaceted and resilient defense system [7, 37, 52]. While an initial defense response was observed in unprimed groups at Day 5, the trend was not visible in the later days. By Day 7, the P and E + P plants showed a decline in their defense mechanisms and a corresponding increase in cellular damage, as evidenced by elevated malondialdehyde content. This demonstrated the superior efficacy of Geraniol and Linalool priming, resulting in sustained disease tolerance throughout the experimental period. Overall, the findings highlighted that these priming agents conferred enhanced disease tolerance by activating and maintaining a long-term defense system that effectively counteracted the pathogen's assault.

8.8 Priming elevated PAL activity to enhance defense responses

The experiment investigated how the different VOCs affected phenylalanine ammonia-lyase (PAL) activity in infected plants, a key enzyme in the plant's defense response. The PAL is a primary enzyme that catalyzes the conversion of L-phenylalanine into trans-cinnamic acid, initiating the phenylpropanoid pathway that produces vital defense compounds such as lignin and phenolic compounds [18]. During 5 days of post-infection, all infected plants showed a significant increase in PAL activity compared with their uninfected controls, which was a typical defense response (Fig. 5a). However, the most potent effect was observed in the G + P plants, which exhibited the highest PAL activity among all treatments. L + P also induced a notable increase, but it was less pronounced than G + P. In contrast, Eugenol's priming effect on PAL activity was minimal, showing a much smaller increase.

This indicated that Geraniol was particularly effective in rapidly activating the plant's defense system. By 7 days post-infection, the initial surge in PAL activity had declined in both the P and E + P groups, suggesting that their defense responses were short-lived (Fig. 5b). This trend contrasted sharply with the G + P plants, which maintained a high level of PAL activity, comparable to day 5. Similarly, L + P plants also sustained a high PAL activity at this later time point. The sustained PAL activity in Geraniol and Linalool-primed plants provided strong enzymatic evidence that these VOCs effectively primed the plant's defense machinery for a more durable, prolonged response to the pathogen,

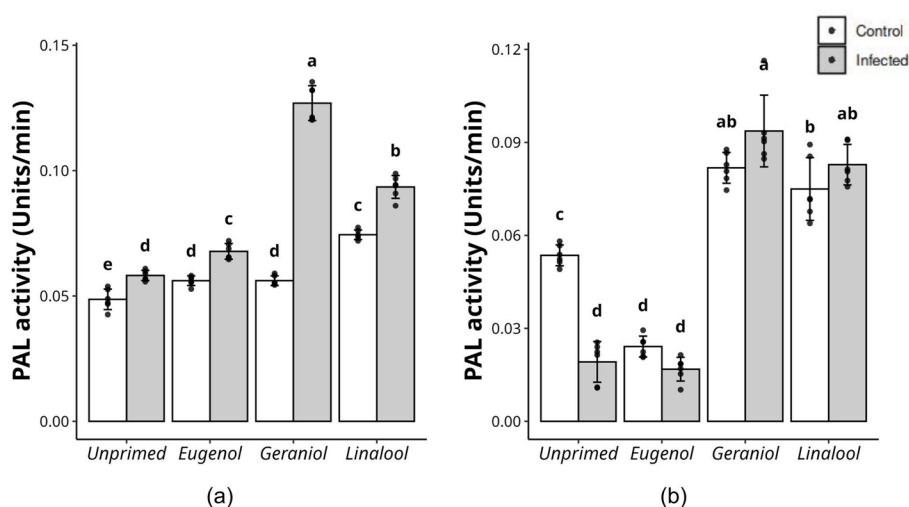


Fig. 5 Phenylalanine Ammonia-Lyase (PAL) activity of primed and unprimed samples: **a** 5 days post-infection and **b** 7 days post-infection, highlighting the enhanced defense enzyme activity upon priming. Different lowercase letters indicate significant differences among treatments according to Tukey's Honestly Significant Difference (HSD) test ($p < 0.05$) (mean $\pm$ SD, $n = 6$)

which is one of the critical findings of our study. The existing literature demonstrates that an increase in PAL activity is a key indicator of a plant's robust defense response, leading to the accumulation of various protective phenolic compounds and lignin [2, 71, 73, 92].

8.9 Metabolomic profiling revealed priming-induced changes in defense compounds

Metabolomic profiling of ginger rhizome samples using GC-MS provided a broad overview of changes in the plant's chemical landscape. The objective of this comprehensive analysis was to characterize the dynamic shifts in the ginger metabolome and identify key metabolic pathways—such as the phenylpropanoid pathway—that are significantly modulated by priming. The study aimed to correlate specific metabolite accumulation with the enhancement of physiological defense, thereby providing a more robust biochemical basis for the efficacy of geraniol-induced resistance. The identification of various organic compounds by comparing mass spectra against the NIST database revealed distinct metabolic shifts in response to VOC priming and *P. myriotylum* infection. These shifts included changes in both primary and secondary metabolites, providing a molecular foundation for the observed physiological and biochemical responses. The heatmaps, which illustrate the presence or absence of identified compounds across various treatment groups at Day 5 and Day 7 post-priming/infection, provide critical insights into the dynamic metabolic shifts underlying the plant's defense responses (Fig. 6).

At Day 5 post-treatment, significant metabolic differences were evident between the control and *P. myriotylum* infected plants. Pathogen infection generally resulted in the induction or elevated accumulation of several compounds not readily detected or present at lower levels in healthy control plants. These compounds likely represented the ginger plant's initial, basal defense response to pathogen challenge. Concurrently, individual VOC priming with geraniol (G), eugenol (E), and linalool (L) induced distinct metabolic profiles even in the absence of pathogen challenge, suggesting a pre-activation or “priming” of specific defense mechanisms. The G plants at Day 5 showed the presence

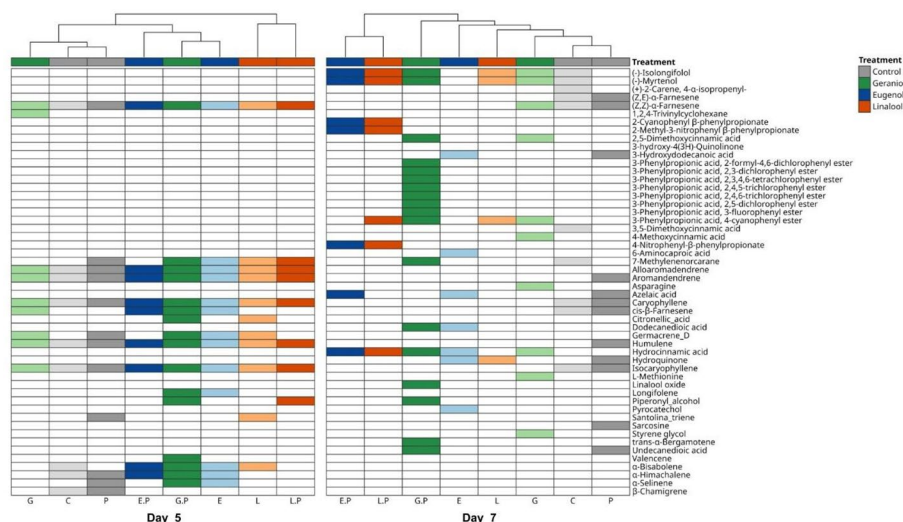


Fig. 6 Heat map illustrating the presence (colors) or absence (white) of various defense related compounds in plant samples. These samples were categorized by treatment: Control (C), *P. myriotylum* infected (P), Geraniol-primed (G), Geraniol-primed + *P. myriotylum* infected (G + P), Eugenol-primed (E), Eugenol-primed + *P. myriotylum* infected (E + P), Linalool-primed (L), and Linalool-primed + *P. myriotylum* infected (L + P). Data were collected on Days 5 and 7 post-inoculations

of compounds like Humulene and Alloaromadendrene, which were largely absent in the unprimed control, indicating an early metabolic shift. Upon subsequent challenge with *P. myriotylum* (G + P, E + P, L + P), the metabolic landscape was profoundly altered. The treatments often resulted in greater diversity and, implicitly, a higher concentration of defense-related compounds than in comparison with P or G, E and L. This synergistic or additive effect suggested that priming pre-conditioned the plant, enabling it to mount a more robust, rapid, and comprehensive defense response upon subsequent pathogen attack. These differences became even more pronounced by Day 7, highlighting the long-term metabolic adjustments associated with effective priming.

A wide array of compounds with established or hypothesized roles in plant defense was identified, providing crucial insights into the underlying mechanisms. Terpenoids constituted a major group of compounds that were significantly altered by priming and infection, serving as both direct defensive compounds and signaling molecules. Monoterpenoids such as (-)-Myrtenol and (+)-2-Carene showed differential accumulation patterns. Notably, (-)-Myrtenol, often recognized for its antimicrobial properties [112], was induced and sustained in Geraniol-primed (G and G + P) plants at Day 7, suggesting its role in bolstering systemic immunity. Sesquiterpenes, including various Farnesene isomers, Alloaromadendrene, Aromadendrene, Caryophyllene, cis- β -Farnesene, Germacrene D, Humulene, Isocaryophyllene, Longifolene, trans- α -Bergamotene, Valencene, α -Bisabolene, α -Himachalene, α -Selinene, and β -Chamigrene, were particularly abundant and responsive. Many of these sesquiterpenes are well-documented for their roles as direct antimicrobials, antifeedants, as volatile signaling molecules that attract natural enemies of herbivores [11, 26, 75, 114]. While P set generally induced some sesquiterpenes, the G + P group consistently demonstrated a broader and more sustained array of these compounds, including Alloaromadendrene, Caryophyllene, Germacrene_D, and Humulene, at both Day 5 and Day 7 compared to other primed or unprimed infected groups. For instance, Germacrene D, a common volatile emitted upon herbivore attack,

was strongly and persistently detected in G + P at Day 7, indicating a robust signaling response. Similarly, Caryophyllene and Humulene, known for their direct antimicrobial and insecticidal properties, were consistently present in G + P, further strengthening the defense profile and suggesting a broad-spectrum protective mechanism.

Phenylpropanoids and phenolic compounds, which are indispensable for plant defense by contributing to structural integrity, antioxidant activity, and direct antimicrobial effects (Naoumkina et al., 2010), also showed significant changes. Cinnamic acid derivatives (e.g., 2,5-Dimethoxycinnamic acid, 4-Methoxycinnamic acid) and a multitude of 3-Phenylpropionic acid esters were consistently identified. These compounds are pivotal precursors to a vast array of phenolics, including flavonoids and lignans, which play crucial roles in defense against pathogens and herbivores, as well as providing UV protection [45, 62, 89]. Their presence was notably elevated in primed and challenged plants, particularly within the Geraniol-primed groups, signifying an active and augmented phenylpropanoid pathway. A diverse group of 3-Phenylpropionic acid esters (e.g., 2-formyl-4,6-dichlorophenyl ester, 2,3-dichlorophenyl ester, etc.) and related compounds like 2-Cyanophenyl β -phenylpropionate and 4-Nitrophenyl- β -phenylpropionate were observed. These esters can act as feeding deterrents or exhibit direct toxic effects against pathogens and pests [53, 100, 101]. Their increased and sustained presence in primed and challenged plants indicated robust activation of the phenylpropanoid pathway contributing to enhanced defense. The G + P group consistently demonstrated a particularly strong presence of these compounds, indicating that geraniol priming was highly effective in upregulating this crucial metabolic route. Simple phenols such as Hydroquinone and Pyrocatechol, common phenolic compounds involved in oxidative defense responses, also exhibited differential patterns [43, 59, 74]. Furthermore, the modulation of fatty acid derivatives (e.g., 3-Hydroxydodecanoic acid) suggested alterations in lipid metabolism supporting defense. In contrast, changes in amino acids like L-Methionine, a precursor to ethylene, a key plant defense hormone, indicated metabolic shifts toward defense-related secondary metabolite production [56, 90, 105].

The observed metabolic shifts provided comprehensive insights into the potential molecular and biochemical mechanisms by which VOCs, particularly geraniol, prime ginger plants against *P. myriotylum* infection. The broad and robust upregulation of terpenoids and phenylpropanoids in primed plants, primarily upon subsequent pathogen infection, strongly suggested that VOCs like geraniol did not merely induce a basal defense state but rather primed the plant for a more rapid, stronger, and sustained immune response. This pre-activation likely involved the sensitization of specific defense genes, making the plant's immune system more "alert" and ready to respond quickly and efficiently to pathogen recognition [5, 15]. The pronounced and widespread induction of various sesquiterpenes (e.g., Farnesene, Germacrene D, Caryophyllene) in the primed-and-challenged groups unequivocally pointed towards a significant activation of the Jasmonate (JA) signaling pathway, a central regulator of defense responses against necrotrophic pathogens like *Pythium myriotylum* and many insect herbivores [22, 35, 55, 102]. Priming with geraniol appeared to sensitize the JA pathway, leading to faster and stronger production of JA-mediated defense compounds upon infection, potentially through enhanced perception of JA signals or more efficient downstream gene activation. While the primary focus based on the metabolite profile, leaned towards JA-mediated responses, some phenolic compounds can also be part of Salicylic Acid

(SA)-mediated defense responses, typically against biotrophic pathogens. The fine-tuned cross-talk between JA and SA pathways is crucial for effective plant immunity [52], and priming might modulate this intricate balance. Moreover, changes in L-Methionine, a precursor of ethylene, indicated the involvement of ethylene signaling, which often acts synergistically with JA in defense responses [10,], Cox, [17, 113].

The induction of defense enzymes and metabolic shifts observed in ginger aligns with broader findings where VOC treatment “primes” diverse plant species against various pathogens. For instance, the application of monoterpenes like linalool has been shown to enhance resistance in *Arabidopsis* against the hemibiotrophic *Pseudomonas syringae* by augmenting the defense response pathway, similar to the defense priming seen in this study [20, 66]. Furthermore, in woody perennials and fruit crops, treatment with geraniol or eugenol has been reported to trigger a robust oxidative burst and the accumulation of phenylpropanoid-derived compounds, effectively limiting the spread of necrotrophic fungi such as *Botrytis cinerea* (Shuning [11, 33, 79]). This comparative evidence suggests that while the specific metabolite profile is host-specific, the underlying mechanism of VOC-induced resistance remains a highly conserved strategy for modulating plant immunity against soil-borne and foliar pathogens alike.

The consistent upregulation of the phenylpropanoid pathway further indicated reinforcement of the plant’s physical and chemical barriers. This pathway is critical for the production of lignin monomers, which strengthen cell walls and form a robust physical barrier against pathogen penetration and spread [42, 65, 93, 104, 110]. Additionally, many phenolic compounds derived from this pathway possess direct antimicrobial properties, inhibiting pathogen growth, while also acting as powerful antioxidants mitigate oxidative stress induced by the defense response itself [68]. This comprehensive metabolic reprogramming, in which resources were efficiently shifted towards defense compound synthesis, highlighted a key aspect of Induced Systemic Resistance (ISR) and Systemic Acquired Resistance (SAR), enabling the plant to swiftly mobilize its resources to counteract infection without significant growth penalties [97].

Based on detailed GC-MS data, geraniol emerged as the most effective priming compound for enhancing ginger’s defense against *P. myriotylum* infection. The G + P group consistently exhibited a more comprehensive, robust, and sustained defense metabolite profile compared to all other treatments, including E + P, L + P, and especially the unprimed infected control. Geraniol’s superior performance was evident through a broader spectrum and often higher abundance of key sesquiterpenes (e.g., Alloaromadendrene, Caryophyllene, Germacrene D, Humulene) and monoterpenoids (e.g., Myrtenol) that are known for their direct antimicrobial activity or their roles as signaling molecules in plant defense. Furthermore, the phenylpropanoid pathway appeared to be more consistently and effectively induced in the G + P group, leading to more substantial chemical and physical barriers. The sustained defence metabolite profile in the G + P group from Day 5 to Day 7 also suggested a durable, long-lasting priming effect, providing extended protection against the pathogen. The overall metabolite patterns in the G + P group indicated a more harmonious and effective integration of various defense pathways, particularly the JA-mediated terpenoid synthesis and the phenylpropanoid pathway, leading to a synergistic defense response. This implied that geraniol’s specific molecular structure might be particularly recognized by ginger’s defense perception machinery, potentially binding to specific receptors or modulating key signal

transduction pathways, such as the JA pathway, more efficiently than eugenol or linalool. This superior recognition and activation would lead to more potent pre-activation of defense genes and a subsequent rapid and high-level production of a broad spectrum of defense metabolites upon pathogen challenge. Consequently, geraniol is a highly promising natural priming agent for enhancing ginger's resistance to *Pythium myriotylum*.

9 Conclusion

This comprehensive study strongly suggests the efficacy of VOC priming in enhancing the defense responses of ginger plants against the soft rot disease caused by *Pythium myriotylum*. The findings highlighted a clear hierarchy of effectiveness among the tested VOCs, with Geraniol (specifically at 150 μ M) consistently inducing the most robust defense mechanisms, followed by Linalool (200 μ M), and Eugenol (200 μ M). This superior protection was evidenced by significant reductions in visual disease severity and a better maintenance of photosynthetic pigments, alongside a pronounced upregulation of various stress-related biomarkers including total flavonoids, anthocyanins, phenolics, and lignin content. Crucially, priming with these VOCs, particularly Geraniol, significantly mitigated oxidative stress as indicated by markedly lower MDA levels in infected plants. The activation of the key defense enzyme PAL further substantiated these biochemical changes, indicating a primed state that enabled a faster and stronger defense response upon pathogen challenge. The metabolomic analysis corroborated these findings, revealing distinct defense-related metabolic shifts in primed plants. Importantly, the most pronounced and effective defense responses, particularly in early biochemical activation and oxidative stress mitigation, were consistently observed at Day 5 post-infection rather than at Day 7, suggesting a rapid and efficient priming effect.

Despite the significant insights gained, this study had certain limitations. The study focused on only three specific VOCs and their pre-optimized concentrations under controlled conditions, suggesting a need for broader exploration of compounds, doses, and validation in diverse field environments, which involve more complex interactions. Future research should prioritize investigating the molecular basis of VOC-induced priming through transcriptomic and proteomic analyses to identify specific genes and proteins involved. Exploring practical application methods and formulations of these VOCs for field deployment, including dose optimization, combinations, timing, and potential synergistic effects with other sustainable agricultural practices, is critical. Furthermore, assessing the long-term impacts of priming on ginger growth, yield, and quality under various environmental stresses would be beneficial.

The findings of this study hold significant societal relevance, particularly for the agricultural sector in South India and globally. Ginger is a major cash crop, and its cultivation is severely affected by PSR, resulting in substantial economic losses for farmers. The demonstration that Geraniol at 150 μ M can be effectively used as a priming agent to combat PSR in ginger offers a sustainable and eco-friendly alternative or supplement to conventional chemical fungicides. This approach aligns with the growing demand to reduce chemical inputs in agriculture, promote safer food production, and minimize environmental pollution. By providing farmers with a natural and effective disease management tool, this research contributes to improved crop yields, enhanced food security, and increased economic stability for ginger cultivators. It exemplifies a sustainable

strategy for plant protection, fostering more resilient agricultural systems in the face of evolving disease pressures and climate change challenges.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1007/s44372-026-00585-1>.

Supplementary Material 1

Supplementary Material 2

Acknowledgements

The authors gratefully acknowledged the Department of Biotechnology for providing the necessary Laboratory facilities and supportive environment that aided in the successful completion of this work. We would also like to thank the Department of Applied Chemistry, CUSAT, for their generous assistance in providing the GC-MS analysis. Their expertise in this technique was crucial for identifying organic compounds in our samples. The authors would also like to acknowledge the Kerala Agricultural University, Thrissur, for providing the high-quality planting materials.

Author contributions

****SJ**** : *Writing – original draft, Writing - review & editing, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. ****SP**** : *Methodology, Formal analysis, Data curation. ****NU**** : *Methodology, Formal analysis. ****DV**** : *Methodology, Formal analysis. ****SPP**** : *Methodology, Writing – review & editing. ****SKP**** : Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization, Validation.

Funding

We would like to thank Cochin University of Science and Technology (CUSAT) for Junior Research Fellowship (Order No. CUSAT/AC(C).C1/2133/2022) and Senior Research Fellowship (Order No. CUSAT/AC(C).C1/1403/2024), Seed Money for New Research Initiatives (SMNRI) grant (Order No. CUSAT/PL(UGC).A5/2624/2022) and Kerala State Council for Science, Technology and Environment (KSCSTE) (Order No. 307/2023/KSCSTE dated 29-10-2023) for the financial support. We would also like to extend our gratitude to DST-PURSE, MoES, RUSA, and DST-FIST funding sources for their support in the successful completion of this project.

Data availability

The detailed methodology for the estimation of Physiological parameters is available in the supplementary file. All data generated or analysed during this study are available from the corresponding author on reasonable request.

Declarations

Competing interests

The authors declare no competing interests.

Ethical approval

The plant material used in this study was the ginger cultivar 'Athira' (*Zingiber officinale Roscoe*). The rhizomes of this widely cultivated and released variety were purchased from the authorized institutional center of the Kerala Agricultural University (KAU), Mannuthy, Thrissur, Kerala, India (10.53° N, 76.24° E). As the material was obtained from a registered, cultivated source, no specific permits or licenses for collection from wild or protected areas were required. The use of this plant material adheres to all relevant institutional and national guidelines. It complies with the principles outlined in the International Union for Conservation of Nature (IUCN) Policy Statement on the responsible utilization of plant resources.

Consent to participate

Not applicable.

Consent to publish

Not applicable.

Received: 17 October 2025 / Accepted: 9 April 2026

Published online: 29 April 2026

References

1. Adss S, Liu B, Beerhues L, Hahn V, Heuer H, Elhady A. Priming Soybean cv. Primus Leads to Successful Systemic Defense Against the Root-Lesion Nematode, *Pratylenchus penetrans*. *Front Plant Sci.* 2021;12:651943.
2. Al-Ameri HA. Estimation of phenyl alanine ammonialyase (PAL) and some phytoalexins in *Vicia faba* plants infected with spot disease caused by *Alternaria alternata*. *J Appl Nat Sci.* 2023. <https://doi.org/10.31018/jans.v15i4.4811>.
3. Alarjani KM, Elshikh MS. (2024). Plant growth-promoting and biocontrol traits of endophytic *Bacillus licheniformis* against soft rot causing *Pythium myriotylum* in ginger plant. *J Basic Microbiol*, 64(7), e2300643.
4. Ali AMA, El-Nour MEAM, Yagi SM. Total phenolic and flavonoid contents and antioxidant activity of ginger (*Zingiber officinale Rosc.*) rhizome, callus and callus treated with some elicitors. *J Genetic Eng Biotechnol.* 2018;16(2):677–82.

5. Aranega-Bou P, de la Leyva O, Finiti M, García-Agustín I, P, Gonzalez-Bosch C. (2014). Priming of plant resistance by natural compounds. Hexanoic acid as a model. In *Frontiers in Plant Science* (Vol. 5, Issue OCT). Frontiers Media S.A. <https://doi.org/10.3389/fpls.2014.00488>
6. Augustine L, Varghese L, Kappachery S, Ramaswami VM, Surendrababu SP, Sakuntala M, Thomas G. Comparative analyses reveal a phenylalanine ammonia lyase dependent and salicylic acid mediated host resistance in *Zingiber zerumbet* against the necrotrophic soft rot pathogen *Pythium myriotylum*. *Plant Science: Int J Experimental Plant Biology*. 2024;340. <https://doi.org/10.1016/j.plantsci.2023.111972>.
7. Avesani S, Lazazzara V, Robatscher P, Oberhuber M, Perazzolli M. Volatile linalool activates grapevine resistance against downy mildew with changes in the leaf metabolome. *Curr Plant Biology*. 2023;35–36(100298):100298.
8. Banik S, Srivastava JN. (2022). Diseases of Ginger (*Zingiber Officinale* Rosc.) and Their Management. In *Diseases of Horticultural Crops: Diagnosis and Management* (Vol. 4, pp. 225–256).
9. Brosset A, Blande JD. Volatile-mediated plant–plant interactions: volatile organic compounds as modulators of receiver plant defence, growth, and reproduction. *J Exp Bot*. 2022;73(2):511–28.
10. Chen C-L, Yuan F, Li X-Y, Ma R-C, Xie H. Jasmonic acid and ethylene signaling pathways participate in the defense response of Chinese cabbage to *Pectobacterium carotovorum* infection. *J Integr Agric*. 2021;20(5):1314–26.
11. Chen S, Kinani A, Horyn S, Galliano O, Srivastava C, Rowley E, Ramsey DC, Mathur KM, D., Bertin MJ. Specialization of sesquiterpene lactone metabolites in *Liriodendron* plant defense. *J Nat Prod*. 2025;88(7):1811–8.
12. Chen S, Yuan A, Wang H, Yang D, Cui L, Hao F, Yan X, Yuan H. Enhancing agrochemical delivery in citrus leaves with geraniol: a promising strategy for controlling huanglongbing (HLB). *Pest Manag Sci*. 2025;81(3):1274–85.
13. Chen W, Viljoen AM. Geraniol — A review of a commercially important fragrance material. *Suid-Afrikaanse Tydskrif Vir Plantkunde [South Afr J Botany]*. 2010;76(4):643–51.
14. Chowdhary V, Alooparampil S, Pandya V, R, Tank G, J. Physiological function of phenolic compounds in plant defense system. In: Badria FA, editor. *Phenolic Compounds - Chemistry, Synthesis, Diversity, Non-Conventional Industrial, Pharmaceutical and Therapeutic Applications*. IntechOpen; 2022.
15. Conrath U. Molecular aspects of defence priming. *Trends Plant Sci*. 2011;16(10):524–31.
16. Conrath U, Pieterse CMJ, Mauch-Mani B. Priming in plant-pathogen interactions. *Trends Plant Sci*. 2002;7(5):210–6.
17. Cox KL. (2022). Stronger together: Ethylene, jasmonic acid, and MAPK signaling pathways synergistically induce camalexin synthesis for plant disease resistance [Review of *Stronger together: Ethylene, jasmonic acid, and MAPK signaling pathways synergistically induce camalexin synthesis for plant disease resistance*]. *The Plant Cell*, 34(8), 2829–2830. Oxford University Press (OUP).
18. Deng Y, Lu S. Biosynthesis and regulation of phenylpropanoids in plants. *CRC Crit Rev Plant Sci*. 2017;36(4):257–90.
19. Dewanjee S, Bhattacharjee N, Chakraborty P, Bhattacharjee S. Carotenoids as antioxidants. *Carotenoids: Structure and Function in the Human Body*. Springer International Publishing; 2021. pp. 447–73.
20. Dong Y, Wei Z, Zhang W, Li J, Han M, Bai H, Li H, Shi L. LaMYC7, a positive regulator of linalool and caryophyllene biosynthesis, confers plant resistance to *Pseudomonas syringae*. *Hortic Res*. 2024;11(4):uhae044.
21. Farhat H, Urooj F, Sohail N, Ullah S, Ali MS. Plant disease management with amelioration of systemic resistance in soybean by endophytic fungi associated with GC-MS metabolic profiling of *Chaetomium* sp. *Physiol Mol Plant Pathol*. 2023;126(102049):102049.
22. Frank L, Wenig M, Ghirardo A, van der Krol A, Vlot AC, Schnitzler JP, Rosenkranz M. Isoprene and β -caryophyllene confer plant resistance via different plant internal signalling pathways. *Plant Cell Environ*. 2021;44(4):1151–64.
23. Fujita M, Hasanuzzaman M. Approaches to enhancing antioxidant defense in plants. *Antioxid (Basel Switzerland)*. 2022;11. <https://doi.org/10.3390/antiox11050925>.
24. Gallego-Giraldo L, Posé S, Pattathil S, Peralta AG, Hahn MG, Ayre BG, Sunuwar J, Hernandez J, Patel M, Shah J, Rao X, Knox JP, Dixon RA. Elicitors and defense gene induction in plants with altered lignin compositions. *New Phytol*. 2018;219(4):1235–51.
25. Gao C-H, Chen C, Akyol T, Dusa A, Yu G, Cao B, Cai P. (2024). ggVennDiagram: Intuitive Venn diagram software extended. *IMeta*, 3(1), e177.
26. Gao J, Li T, Jiao L, Jiang C, Chen S, Huang L, Liu J. Metabolome and transcriptome analyses identify the plant immunity systems that facilitate sesquiterpene and lignan biosynthesis in *Syringa pinnatifolia* Hemsl. *BMC Plant Biol*. 2022;22(1):132.
27. Geetha KA, Koyyappurath S, Augustine L, Thomas G. Transcriptional analysis and histochemistry reveal a dominant role for cell wall signaling in mediating *Pythium myriotylum* resistance in *Zingiber zerumbet*. *Physiol Mol Plant Pathol*. 2019;106:7–15.
28. Gopi R, Kalita H, Avasthe RK. Organic management of soft rot of ginger (*Zingiber officinale*) in Sikkim Himalayan region. *Indian J Agric Sci*. 2016;86(12):1586–90.
29. Goswami A, Banerjee R, Raha S. Drought resistance in rice seedlings conferred by seed priming: role of the anti-oxidant defense mechanisms: Role of the anti-oxidant defense mechanisms. *Protoplasma*. 2013;250(5):1115–29.
30. Goura K, Legrifi I, Kallali NS, Taoussi M, Kenfaoui J, Meddich A, Esmaeel Q, Barka A, E., Lahlali R. Beyond survival: The role of secondary metabolites in plant defense mechanisms. *J Crop Health*. 2025;77(4). <https://doi.org/10.1007/s10343-025-01183-z>.
31. Habibi F, Ramezani A, Rahemi M, Eshghi S, Guillén F, Serrano M, Valero D. Postharvest treatments with γ -aminobutyric acid, methyl jasmonate, or methyl salicylate enhance chilling tolerance of blood orange fruit at prolonged cold storage. *J Sci Food Agric*. 2019;99(14):6408–17.
32. Harsha K, Aswati Nair R. (2020). Volatile metabolites of endophytic *Klebsiella aerogenes* from *Zingiber zerumbet* rhizome and its antagonistic effect on soft rot causative *Pythium myriotylum*. *J Spices Aromatic Crops*, 122–32.
33. Hirose S, Horiyama S, Morikami A, Fujiwara K, Tsukagoshi H. Eugenol and basil essential oil as priming agents for enhancing Arabidopsis immune response. *Biosci Biotechnol Biochem*. 2024;89(1):41–50.
34. Ishtiaq M, Mazhar MW, Maqbool M, Hussain T, Hussain SA, Casini R, Abd-ElGawad AM, Elansary H. Seed priming with the selenium nanoparticles maintains the redox status in the water stressed tomato plants by modulating the antioxidant defense enzymes. *Plants*. 2023;12. <https://doi.org/10.3390/plants12071556>.
35. Jin W, Yang Z, Xu K, Liu Q, Luo Q, Li L, Xiang X. A comprehensive review of plant volatile terpenoids, elucidating interactions with surroundings, systematic synthesis, regulation, and targeted engineering production. *Biology*. 2025;14. <https://doi.org/10.3390/biology14050466>.

36. Johnson S, Philip S, Shandev, Koyyappurath S. PEG seed priming enhances drought tolerance in ginger through physiological and molecular modulation. *J Crop Sci Biotechnol*. 2025. <https://doi.org/10.1007/s12892-025-00299-y>.
37. Ju J-M, Lee H-L, Jang Y-S, Byeon J. Geraniol treatment enhances sulforaphane content through modulation of the glucosinolate biosynthetic pathway in kale (*Brassica oleracea*). *Appl Biol Chem*. 2025;68(1). <https://doi.org/10.1186/s13765-025-01053-2>.
38. Kamle M, Borah R, Bora H, Jaiswal AK, Singh RK, Kumar P. (2020). *Systemic Acquired Resistance (SAR) and Induced Systemic Resistance (ISR): Role and Mechanism of Action Against Phytopathogens* (pp. 457–470).
39. Kaur S, Tiwari V, Kumari A, Choudhary E, Sharma A, Ali U, Garg M. Protective and defensive role of anthocyanins under plant abiotic and biotic stresses: An emerging application in sustainable agriculture. *J Biotechnol*. 2023;361:12–29.
40. Kaur S, Samota MK, Choudhary M, Choudhary M, Pandey AK, Sharma A, Thakur J. (2022). How do plants defend themselves against pathogens-Biochemical mechanisms and genetic interventions. In *Physiology and Molecular Biology of Plants* (Vol. 28, Issue 2, pp. 485–504). Springer. <https://doi.org/10.1007/s12298-022-01146-y>
41. Khaled JM, Alobaidi AS. Priming effect of chitosan on induces protection against tomato root wilt disease mediated through upregulation of defense enzymes. *Physiol Mol Plant Pathol*. 2023;127(102118):102118.
42. Khan P, Tong L, Khan S, Zhang C, Wang W. Lignin: A defensive shield halting the environmental stresses – a review. *Appl Ecol Environ Res*. 2022;20(3). https://doi.org/10.15666/aer/2003_19912015.
43. Khanday AH, Badroo IA, Wagay NA, Rafiq S. Role of phenolic compounds in disease resistance to plants. *Plant Phenolics in Biotic Stress Management*. Springer Nature Singapore; 2024. pp. 455–79.
44. Kiyama H, Matsunaga A, Suzuki G, Gomi K. Monoterpene geraniol produced by rice terpene synthase 21 suppresses the expression of cell-division related genes in the rice bacterial pathogen, *Xanthomonas oryzae* pv. *oryzae*. *Physiol Mol Plant Pathol*. 2021;115(101673):101673.
45. Korkut A, Özkaya Gül S, Aydemir E, Er H, Odabaş Köse E. Cinnamic acid compounds (p-coumaric, ferulic, and p-methoxycinnamic acid) as effective antibacterial agents against colistin-resistant *Acinetobacter baumannii*. *Antibiot* (Basel Switzerland). 2025;14(1):71.
46. Kumar A. Diseases of ginger and turmeric. *Handbook of Spices in India: 75 Years of Research and Development*. Springer Nature Singapore; 2024. pp. 3675–707.
47. Kumar AP, Bhasker K, K., N. B. S., Srinivas P. Role of phenylpropanoids and flavonoids in plant defense mechanism. *Int J Environ Clim Change*. 2023;13(9):2951–60.
48. Li C, Wang K, Lei C, Cao S, Huang Y, Ji N, Xu F, Zheng Y. Alterations in Sucrose and Phenylpropanoid Metabolism Affected by BABA-Primed Defense in Postharvest Grapes and the Associated Transcriptional Mechanism. *Mol Plant-Microbe Interactions: MPMI*. 2021;34(11):1250–66.
49. Li J, Chen L, Ding X, Fan W, Liu J. Transcriptome analysis reveals crosstalk between the abscisic acid and jasmonic acid signaling pathways in rice-mediated defense against *Nilaparvata lugens*. *Int J Mol Sci*. 2022;23(11):6319.
50. Li M, Zhang X, Li J, Ali M, Wang Y, Liu X, Li F, Li X. GABA primes defense responses against *Botrytis cinerea* in tomato fruit by modulating ethylene and JA signaling pathways. *Postharvest Biol Technol*. 2024;208(112665):112665.
51. Li Q, Xu M, Wu F, Guo Z, Yang N, Li L, Wen W, Xu D. Integrated transcriptomics and metabolomics provide insights into the biosynthesis of militarine in the cell suspension culture system of *Bletilla striata*. *Adv Biotechnol*. 2024;2(3):25.
52. Li X, Wang Q, Li H, Wang X, Zhang R, Yang X, Jiang Q, Shi Q. Revealing the mechanisms for linalool antifungal activity against *Fusarium oxysporum* and its efficient control of *Fusarium* wilt in tomato plants. *Int J Mol Sci*. 2022;24(1):458.
53. Li Z, Jing S, Wang D, Song Z, An B, Wang S, Liu F, Di N, Aradottir GI, Sun J, Tan X, Qu C, Kang Z. Plant volatile methyl salicylate primes wheat defense against the grain aphid by altering the synthesis of defense metabolites. *Plant Cell Environ*. 2024. <https://doi.org/10.1111/pce.15351>.
54. Lin Y, Fan L, He J, Wang Z, Yin Y, Cheng Y, Li Z. Anthocyanins contribute to fruit defense against postharvest green mold. *Postharvest Biol Technol*. 2021;181(111661):111661.
55. Ling S, Rizvi SAH, Xiong T, Liu J, Gu Y, Wang S, Zeng X. Volatile signals from guava plants prime defense signaling and increase jasmonate-dependent herbivore resistance in neighboring citrus plants. *Front Plant Sci*. 2022;13:833562.
56. Liu Y, Lei X, Deng B, Chen O, Deng L, Zeng K. Methionine enhances disease resistance of jujube fruit against postharvest black spot rot by activating lignin biosynthesis. *Postharvest Biol Technol*. 2022;190(111935):111935.
57. Lucas-Bautista JA, Cárdenas-Valdovinos JG, Mena-Violante HG, Pacheco-Aguilar JR, Mendoza S. (2025). Antimicrobial activity of berries anthocyanin extracts against phytopathogenic bacteria. *J Mex Chem Soc*, 542–54.
58. Ma Q-H. Lignin biosynthesis and its diversified roles in disease resistance. *Genes*. 2024;15(3):295.
59. Mahatma MK, Thawait LK, Jadon KS, Thirumalaisamy PP, Bishi SK, Rathod KJ, Verma A, Kumar N, Golakiya BA. Metabolic profiling for dissection of late leaf spot disease resistance mechanism in groundnut. *Physiol Mol Biology Plants: Int J Funct Plant Biology*. 2021;27(5):1027–41.
60. Malinská HA, Vaněk M, Nebeská D, Šubrt D, Brestič M, Trögl J. Plant priming changes physiological properties and lignin content in *Miscanthus x giganteus*. *Ind Crops Prod*. 2021;174(114185):114185.
61. Meenu G, Jebasingh T. (2020). Diseases of ginger. In *Ginger Cultivation and Its Antimicrobial and Pharmacological Potentials*. IntechOpen.
62. Moreira-Vilar FC, da Silva HA, Marchiosi R, Siqueira-Soares R, de Finger-Teixeira C, da Silva A, Contesoto KG, de Constantin I, dos Santos RP, W. D., Ferrarese-Filho O. (2022). *p*-Methoxycinnamic acid disturbs cellular respiration and increases the lignification of *Euphorbia heterophylla* roots. *Plant Biosystems*, 1–12.
63. Munzert KS, Engelsdorf T. Plant cell wall structure and dynamics in plant-pathogen interactions and pathogen defence. *J Exp Bot*. 2024. <https://doi.org/10.1093/jxb/erae442>.
64. Nair KP. The agronomy and economy of ginger. *Turmeric (Curcuma longa L.) and Ginger (Zingiber officinale Rosc.) - World's Invaluable Medicinal Spices*. Springer International Publishing; 2019. pp. 245–315.
65. Ninkuu V, Yan J, Fu Z, Yang T, Ziemah J, Ullrich M, Kuhnert N, Zeng H. Lignin and its pathway-associated phytoalexins modulate plant defense against fungi. *J Fungi* (Basel Switzerland). 2022;9. <https://doi.org/10.3390/jof9010052>.
66. Ninkuu V, Zhang L, Yan J, Fu Z, Yang T, Zeng H. Biochemistry of terpenes and recent advances in plant protection. *Int J Mol Sci*. 2021;22(11):5710.
67. Noel JP, Austin MB, Bomati EK. Structure-function relationships in plant phenylpropanoid biosynthesis. *Curr Opin Plant Biol*. 2005;8(3):249–53.

68. Ortiz A, Sansinenea E. Phenylpropanoid derivatives and their role in plants' health and as antimicrobials. *Curr Microbiol*. 2023;80(12):380.
69. Patil JR, Mhatre KJ, Yadav K, Yadav LS, Srivastava S, Nikalje GC. Flavonoids in plant-environment interactions and stress responses. *Discover Plants*. 2024;1(1). <https://doi.org/10.1007/s44372-024-00063-6>.
70. Patil SV, Kumudini BS. Seed priming induced blast disease resistance in finger millet plants through phenylpropanoid metabolic pathway. *Physiol Mol Plant Pathol*. 2019;108(101428):101428.
71. Qin Y, Li Q, An Q, Li D, Huang S, Zhao Y, Chen W, Zhou J, Liao H. A phenylalanine ammonia lyase from *Fritillaria unibracteata* promotes drought tolerance by regulating lignin biosynthesis and SA signaling pathway. *Int J Biol Macromol*. 2022;213:574–88.
72. Ramaroson M-L, Koutouan C, Helesbeux J, Le Clerc V, Hamama L, Geoffriau E, Briard M. Role of phenylpropanoids and flavonoids in plant resistance to pests and diseases. *Molecules*. 2022;27. <https://doi.org/10.3390/molecules27238371>.
73. Rasool F, Uzair M, Naeem MK, Rehman N, Afroz A, Shah H, Khan MR. Phenylalanine ammonia-lyase (PAL) genes family in wheat (*Triticum aestivum* L.): Genome-wide characterization and expression profiling. *Agron (Basel Switzerland)*. 2021. <https://doi.org/10.3390/agronomy11122511>.
74. Richter A, Schroeder AF, Marcon C, Hochholdinger F, Jander G, Negin B. Catechol acetylglucose: a newly identified benzoxazinoid-regulated defensive metabolite in maize. *New Phytol*. 2024;244(6):2474–88.
75. Rosenkranz M, Chen Y, Zhu P, Vlot AC. Volatile terpenes - mediators of plant-to-plant communication. *Plant Journal: Cell Mol Biology*. 2021;108(3):617–31.
76. Saini N, Anmol A, Kumar S, Wani AW, Bakshi M, Dhiman Z. Exploring phenolic compounds as natural stress alleviators in plants- a comprehensive review. *Physiol Mol Plant Pathol*. 2024;133(102383):102383.
77. Sánchez-Hernández E, Buzón-Durán L, Lorenzo-Vidal B, Martín-Gil J, Martín-Ramos P. Physicochemical Characterization and Antimicrobial Activity against *Erwinia amylovora*, *Erwinia vitivora*, and *Diplodia seriata* of a Light Purple Hibiscus *syriacus* L. Cultivar. *Plants*. 2021;10. <https://doi.org/10.3390/plants10091876>.
78. Schenk S, Schikora A. Lignin Extraction and Quantification, a Tool to Monitor Defense Reaction at the Plant Cell Wall Level. *Bio-Protocol*. 2015;5(6). <https://doi.org/10.21769/bioprotoc.1430>.
79. Shao B, Diao Y-D, Yang Q-L, Zhao F-Y, Ju J. Geraniol causes apoptosis in *Colletotrichum gloeosporioides* by inducing a burst of ROS. *Food Health*. 2025;7(1):2.
80. Sharma A, Sharma A, Sharma A, Kumar Y, Sharma P, Bhardwaj R, Sharma I. Polyphenol phytoalexins as the determinants of plant disease resistance. *Plant Phenolics in Biotic Stress Management*. Springer Nature Singapore; 2024. pp. 243–74.
81. Sheteiwy MS, Ulhassan Z, Qi W, Lu H, Abdelgawad H, Minkina T, Sushkova S, Rajput VD, El-Keblawy A, Joško I, Suleiman S, El-Esawi MA, El-Tarabily KA, AbuQamar SF, Yang H, Dawood M. Association of jasmonic acid priming with multiple defense mechanisms in wheat plants under high salt stress. *Front Plant Sci*. 2022;13:886862.
82. Shulaev V, Cortes D, Miller G, Mittler R. Metabolomics for plant stress response. *Physiol Plant*. 2008;132(2):199–208.
83. Sierra J, McQuinn R, León P. The role of carotenoids as a source of retrograde signals that impact plant development and stress responses. *J Exp Bot*. 2022. <https://doi.org/10.1093/jxb/erac292>.
84. Stirling GR, Turaganivalu U, Stirling AM, Lomavatu MF, Smith MK. Rhizome rot of ginger (*Zingiber officinale*) caused by *Pythium myriophyllum* Fiji and Australia. *Australasian Plant Pathology: APP*. 2009;38(5):453.
85. Striganavičiūtė G, Žiauka J, Sirgedaitė-Šežienė V, Vaitiekūnaitė D. (2021). Priming of resistance-related phenolics: A study of plant-associated bacteria and *Hymenoscyphus fraxineus*. *Microorganisms*, 9. <https://doi.org/10.3390/microorganisms9122504>
86. Sumanta N, Haque CI, Nishika J, Suprakash R. Spectrophotometric Analysis of Chlorophylls and Carotenoids from Commonly Grown Fern Species by Using Various Extracting Solvents. *Res J Chem Sci Res J Chem Sci*. 2014;4(9):2231–606.
87. Sun T, Rao S, Zhou X, Li L. Plant carotenoids: recent advances and future perspectives. *Mol Hortic*. 2022;2(1):3.
88. Sun, Yanzheng, Shuai L, Luo D, Ba L-J. The inhibitory mechanism of eugenol on *Lasioidiplodia theobromae* and its induced disease resistance of passion fruit. *Agron (Basel Switzerland)*. 2023. <https://doi.org/10.3390/agronomy13051408>.
89. Sun Y, Wang X, Huang Z, Zhao X, Qiao L, Wu C, Xue Z, Kou X. Phenylpropanoids for the control of fungal diseases of post-harvest fruit. *Plant Mol Biol*. 2025;115(2):39.
90. Tanaka T, Fujita M, Kusajima M, Narita F, Asami T, Maruyama-Nakashita A, Nakajima M, Nakashita H. Priming of immune system in tomato by treatment with low concentration of L-methionine. *Int J Mol Sci*. 2024;25(12):6315.
91. Tian J, Hong H, Mo S, Mo S, Shi H, Shi J, Zhou Y. Effects of Geraniol on Survival, Reproduction, Endophytes, and Transcriptome of Tea Green Leafhoppers (*Empoasca onukii*). *Agron (Basel Switzerland)*. 2025. <https://doi.org/10.3390/agronomy15040782>.
92. Timofeeva TA, Bubnova AN, Shagdarova BT. (2024). Phenylalanine ammonia-lyase-mediated differential response of tomato (*Solanum lycopersicum* L.) cultivars with different stress tolerance to treatment ... *Agronomy*. <https://www.mdpi.com/2073-4395/14/2/386>
93. Tiwari RK, Goswami SK, Gujjar RS, Kumar R, Kumar R, Lal MK, Kumari M. Mechanistic insights on lignin-mediated plant defense against pathogen infection. *Plant Physiol Biochem*. 2025;228(110224):110224.
94. Tuladhar P, Sasidharan S, Saudagar P. Role of phenols and polyphenols in plant defense response to biotic and abiotic stresses. In: Jogaiah S, editor. *Biocontrol Agents and Secondary Metabolites*. Elsevier; 2021. pp. 419–41.
95. Upadhyay R, Saini R, Shukla PK, Tiwari KN. Role of secondary metabolites in plant defense mechanisms: a molecular and biotechnological insights. *Phytochemistry Reviews: Proc Phytochemical Soc Europe*. 2024. <https://doi.org/10.1007/s11101-024-09976-2>.
96. Varghese L, Thomas G. Chitosan triggers tolerance to *Pythium myriophyllum* infection in ginger (*Zingiber officinale*) by modulating multiple defense signaling pathways. *Physiol Mol Plant Pathol*. 2023;125:101983.
97. Vlot AC, Sales JH, Lenk M, Bauer K, Brambilla A, Sommer A, Chen Y, Wenig M, Nayem S. Systemic propagation of immunity in plants. *New Phytol*. 2021;229(3):1234–50.
98. Wallace W. (2023). *National Institute of Standards and Technology (NIST)*. Mass Spectrometry Data Center. <https://chemdata.nist.gov/dokuwiki/doku.php?id=chemdata:start>
99. Weng T, Wang Y-Q, Long C. (2023). *Inhibitory mechanism of geraniol against Geotrichum citri-aurantii in citrus*. <https://doi.org/10.5555/2023005107>
100. Wu L, Sun M, Chen X, Si D, Si J. Hormonal and Metabolomic Responses of *Dendrobium catenatum* to Infection with the Southern Blight Pathogen *Sclerotium delphinii*. *Phytopathology*. 2023;113(1):70–9.

101. Xie J, Yang F, Xu X, Peng Y, Ji H. Salicylic acid, jasmonate, and ethylene contribute to rice defense against white tip nematodes *Aphelenchoides besseyi*. *Front Plant Sci.* 2021;12:755802.
102. Xu R, Gao H, Wang S, Ye H, Li J, Wu C, Zhong F. Volatile organic compounds accumulation and *Bemisia tabaci* resistance in tomato leaves treated with different caryophyllene concentrations. *Sci Hort.* 2024;334(113262):113262.
103. Yadav D, Gaurav H, Yadav R, Waris R, Afzal K, Shukla C, A. A comprehensive review on soft rot disease management in ginger (*Zingiber officinale*) for enhancing its pharmaceutical and industrial values. *Heliyon.* 2023;9(7):e18337.
104. Yadav S, Chattopadhyay D. Lignin: The building block of defense responses to stress in plants. *J Plant Growth Regul.* 2023;42(10):6652–66.
105. Yang C, Wu P, Yao X, Sheng Y, Zhang C, Lin P, Wang K. Integrated transcriptome and metabolome analysis reveals key metabolites involved in camellia oleifera defense against anthracnose. *Int J Mol Sci.* 2022;23(1):536.
106. Yang F, Shen H, Huang T, Yao Q, Hu J, Tang J, Zhang R, Tong H, Wu Q, Zhang Y, Su Q. Flavonoid production in tomato mediates both direct and indirect plant defences against whiteflies in tritrophic interactions. *Pest Manag Sci.* 2023;79(11):4644–54.
107. Younus Wani M, Rani S, Mir MR, Kamili AS, Wani Y, Mehraj CM, Rather S, Hajam R, Ganie O, N., Baqual MF. (2018). Systemic acquired resistance (SAR): A novel strategy for plant protection with reference to mulberry. *Int J Chem Stud.* 6(2). <https://www.researchgate.net/publication/326988502>
108. Yu Y, Gui Y, Li Z, Jiang C, Guo J, Niu D. Induced Systemic Resistance for Improving Plant Immunity by Beneficial Microbes. *Plants.* 2022;11(3). <https://doi.org/10.3390/plants11030386>.
109. Zehra A, Meena M, Dubey MK, Aamir M, Upadhyay RS. Synergistic effects of plant defense elicitors and *Trichoderma harzianum* on enhanced induction of antioxidant defense system in tomato against *Fusarium wilt* disease. *Bot Stud (Taipei Taiwan).* 2017;58(1):44.
110. Zhang C, Jian L, Guan T, Wang Y, Pang H, Xu Y, Xing Y, Wang J, Kang Z, Zhao J. Coordinated transcriptomic and metabolomic responses in rice reveal lignin-based physical barriers as key mechanisms of nonhost resistance to rust fungi. *PLoS Genet.* 2025;21(5):e1011679.
111. Zhang H, Zhou Y, Yang Y, Zhao L, Li H, Long L, Wang J, Wu X, Wei Z-J. The role of linalool in managing *Alternaria alternata* infection and delaying black mold rot in goji berry. *Postharvest Biol Technol.* 2025;219(113240):113240.
112. Zhao M, Liu B, Sun Y, Wang Y, Dai L, Chen H. Presence and roles of myrtenol, myrtanol and myrtenal in *Dendroctonus armandi* (Coleoptera: Curculionidae: Scolytinae) and *Pinus armandi* (Pinales: Pinaceae: Pinoideae). *Pest Manag Sci.* 2020;76(1):188–97.
113. Zhou J, Mu Q, Wang X, Zhang J, Yu H, Huang T, He Y, Dai S, Meng X. Multilayered synergistic regulation of phytoalexin biosynthesis by ethylene, jasmonate, and MAPK signaling pathways in *Arabidopsis*. *Plant Cell.* 2022;34(8):3066–87.
114. Zhou S, Zhan C, Zhu J, Yang C, Zhao Q, Sun Y, Zhou J, Shen S, Luo J. Molecular and biochemical evolution of casbene-type diterpene and sesquiterpene biosynthesis in rice. *J Integr Plant Biol.* 2025;67(4):1105–18.

Publisher's note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.