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Essential Oils and Plant Extracts for Postharvest Control of *Monilinia fructicola* in Peaches: Direct Antifungal Activity and Defence Induction

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ABSTRACT

This study evaluated the antifungal potential of essential oils and plant extracts for the control of *Monilinia fructicola*, the causal agent of brown rot in peaches, under in vitro and postharvest conditions. Essential oils and cold aqueous, hot aqueous, and hydroalcoholic extracts of *Allium sativum*, *Syzygium aromaticum*, *Origanum vulgare*, *Rosmarinus officinalis*, *Artemisia absinthium* and *Eugenia uniflora* were evaluated using direct and indirect contact assays. In vitro assays showed complete inhibition of mycelial growth by the essential oils of *A. sativum*, *S. aromaticum* and *O. vulgare*, comparable to the chemical control (captan). The essential oil of *A. sativum* exhibited the lowest minimum inhibitory concentration (0.04%), whereas essential oils of *S. aromaticum* and *O. vulgare* showed minimum inhibitory concentrations of 0.16%. Plant extracts exhibited predominantly fungistatic effects. Scanning electron microscopy revealed structural damage to fungal hyphae induced by the essential oils, confirming their fungitoxic activity. In postharvest assays, only the essential oil of *O. vulgare* and the chemical treatment, when applied by direct contact, completely suppressed disease incidence and severity over 7 days of storage. Although the essential oils of *A. sativum* and *S. aromaticum* reduced disease development at early stages, their efficacy decreased over time, particularly under indirect contact. Biochemical analyses indicated that essential oil treatments, particularly *O. vulgare*, induced defence responses in the host fruit, as evidenced by increased protein content and enhanced phenylalanine ammonia-lyase and chitinase activity. These results indicate that essential oils—particularly that of oregano—act through a dual mechanism involving direct antifungal activity and induction of fruit defence responses. These findings highlight their potential as sustainable alternatives for postharvest management of brown rot in peaches.

1 | Introduction

Brown rot, caused by *Monilinia fructicola*, is one of the most important diseases in peach production and remains difficult to manage. This disease also affects other fruit tree species, including plum, nectarine, apricot, sweet cherry and sour cherry. Alternative products are being evaluated to reduce reliance on synthetic chemicals for disease management while maintaining fruit quality and minimising risks to human health and the environment (Fabiane et al. 2020). In addition to the genus *Monilinia fructicola*, species such as *Monilinia laxa* and *Monilinia fructigena* cause brown rot in stone fruits, manifesting as fruit rot, flower blight and cankers on branches (Wagner Júnior et al. 2011).

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This disease begins during the flowering period and persists into the postharvest phase (Baseggio et al. 2019). The fungal inoculum remains primarily in mummified fruits in the orchard, and its conidia are disseminated by wind, rain, insects or hail (May-De-Mio et al. 2008). Consequently, disease management is challenging, as no commercial cultivar exhibits complete resistance to brown rot (Fabiane et al. 2020).

Synthetic fungicides remain the most widely used approach to mitigate damage caused by the pathogen (Cristofoli et al. 2025) and are applied both pre- and postharvest (Pavanello et al. 2015). However, isolates of the pathogen resistant to certain fungicide active ingredients have already been reported, indicating reduced efficacy in disease management (Lino et al. 2016). Furthermore, consumer demand for sustainably produced fruit with reduced pesticide residues has increased (Lopez Reyes et al. 2013). This trend has stimulated research into plant extracts and essential oils that induce resistance to diseases.

Studies on plant disease management using essential oils and crude plant extracts have demonstrated promising results in various plant–pathogen systems, due to the fungistatic activity, which inhibits mycelial growth and conidial germination (Souza et al. 2020). Accordingly, studies are required to evaluate their efficacy, whether through direct or indirect effects on the target pathogen (Bettiol and Morandi 2009).

Fontana et al. (2017) evaluated plant extracts of *Cinnamomum* sp., *Syzygium aromaticum* and *Plectranthus barbatus* for the control of *M. fructicola* in vitro and during postharvest storage of 'Chimarrita' peaches and reported reductions in mycelial growth, mycelial growth velocity index and high levels of fungal growth inhibition. Lian et al. (2022) evaluated thyme essential oil and observed reduced growth of *M. fructicola*, providing a basis for the development of antifungal controlled-release packaging and demonstrating that thyme essential oil contains antifungal compounds, including eugenol (2-methoxy-3-(2-propenyl)-phenol), D-limonene and thymol. Moreover, Cristofoli et al. (2025) reported fungistatic effects of aqueous plant extracts of *R. officinalis*, *A. sativum* and *Equisetum arvense* against *M. fructicola* and observed in vitro fungistatic and fungitoxic activity of the *A. sativum* extract at concentrations of 5%, 10%, 15% and 20%.

Given the diversity of bioactive compounds in plants, additional species may be evaluated for similar efficacy in the management of brown rot. This study evaluated the antifungal potential of essential oils and cold aqueous, hot aqueous and hydroalcoholic extracts of *Allium sativum*, *Syzygium aromaticum*, *Origanum vulgare*, *Rosmarinus officinalis*, *Artemisia absinthium* and *Eugenia uniflora* for the control of *M. fructicola* under in vitro and postharvest conditions using direct and indirect contact assays.

2 | Material and Methods

2.1 | Fungal Isolate and Conidial Production

The study was conducted at the Universidade Tecnológica Federal do Paraná, in Pato Branco, Paraná, Brazil. The fungus *Monilinia fructicola* was isolated from peach fruits exhibiting brown rot symptoms collected in an orchard at the Universidade Federal da Fronteira Sul (UFFS), Chapecó Campus, Santa Catarina, Brazil. Conidia were scraped from the fruit surface and transferred to Petri dishes containing potato dextrose agar (PDA). The plates were incubated at 24°C in the dark under controlled conditions. A pure culture was obtained, and molecular identification confirmed the isolate as *M. fructicola*, which was designated MF01 (Figures 1 and 2).

2.2 | Obtaining Essential Oils and Plant Extracts

Essential oils of *A. sativum*, *Origanum vulgare*, *Rosmarinus officinalis*, *Artemisia absinthium*, *Syzygium aromaticum* and *Eugenia uniflora* were obtained commercially in 300 mL amber bottles. Commercial crude plant extracts of *A. sativum* bulbs, *S. aromaticum* flower buds and aerial parts of *O. vulgare*, *R. officinalis* and *A. absinthium* were used. Cold aqueous extracts were prepared following Barbosa et al. (2018). Hydroalcoholic extracts (70% ethanol) were prepared according to Celoto et al. (2008).

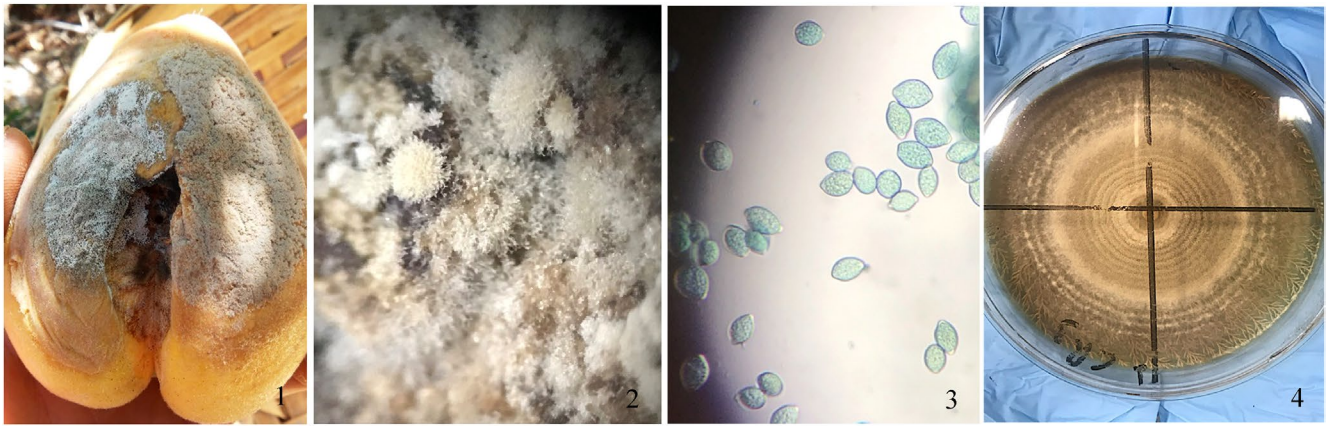

FIGURE 1 | Sources of inoculum of *Monilinia fructicola*. (1) Diseased fruits used as the initial inoculum. (2) Mycelium and conidia of *M. fructicola* on peach fruit. (3) Conidia of *M. fructicola*. (4) Pure colony of *M. fructicola* (isolate MF01).

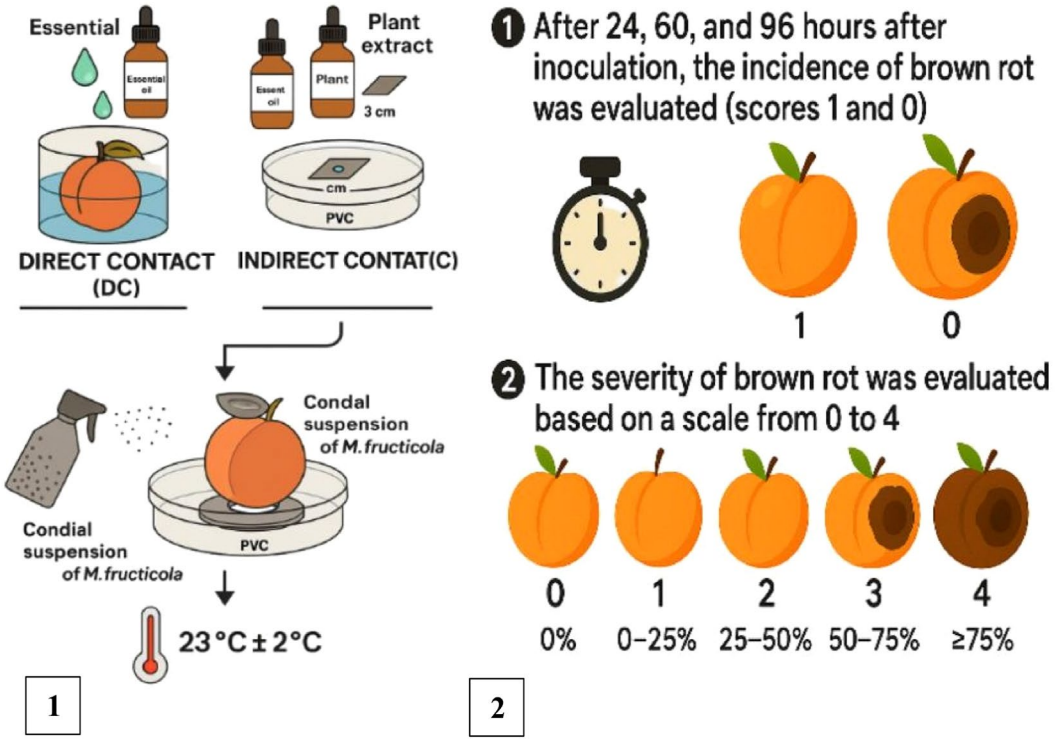

FIGURE 2 | Assessment of the incidence and severity of brown rot in peaches treated with essential oils and plant extracts. (1) Inoculation of peaches with *M. fructicola*, by direct contact (DC) and indirect contact (IC). (2) Assessment of disease incidence and severity using the diagrammatic scale (Scheme made with Artificial Intelligence).

2.3 | Effects of Essential Oils and Plant Extracts on Mycelial Growth of *Monilinia fructicola* In Vitro

The effects were evaluated using direct and indirect contact assays. In the direct contact assay, a solution containing essential oil (100 μL) and Tween 80 (100 μL) was prepared in 9.0-cm-diameter Petri dishes for each treatment, to a final concentration of 1% (v v^{-1}) in PDA medium (Vismara 2019). For plant extracts, a 10% concentration (v v^{-1}) was used, with 5 mL of each extract spread onto the surface of solidified PDA (Silva et al. 2018). A 5-mm-diameter mycelial disk of *M. fructicola* was then placed at the center of each plate. Mycelial growth was assessed 10 days after inoculation (Seixas et al. 2011).

In the indirect contact assay, a sterile filter paper disk affixed to the center of the Petri dish lid was impregnated with 10 μL of each essential oil or plant extract solution. A 5-mm-diameter mycelial disk of *M. fructicola* was placed in the center of the PDA medium (adapted from Júnior et al. 2009). Distilled water and the fungicide captan (Captan 500 WP) were used as negative and positive controls, respectively. Plates were incubated at 24°C in the dark for 7 days. Mycelial diameter was measured daily using a ruler. Mycelial growth and mycelial growth inhibition were calculated for both direct and indirect contact assays (Hillen et al. 2012).

The experiment was conducted in a completely randomised design with six replicates, using an 8 × 2 factorial arrangement (treatment × contact type), with each Petri dish constituting an experimental unit. The treatments consisted of essential oils or extracts of *R. officinalis*, *A. sativum*, *S. aromaticum*, *O. vulgare*, *A. absinthium*, *Eugenia uniflora*, distilled water (negative control) and captan (positive control). Data met the assumptions of normality (Shapiro–Wilk test) and required no transformation. The data were subjected to analysis of variance (ANOVA), and means were compared using the Scott–Knott test ($\alpha = 0.05$) in R software (R Core Team 2019).

2.4 | Minimum Inhibitory Concentration of Essential Oils and Plant Extracts Against *Monilinia fructicola*

The concentrations were determined using sterile stock solutions of each essential oil (1% v v^{-1}) and plant extract (10% v v^{-1}). A conidial suspension of *M. fructicola* was prepared at a concentration of 10^5 conidia mL^{-1}. Aliquots (100 μL) of the fungal suspension in potato dextrose broth were added to each well of a 96-well plate and pre-incubated for 48 h at 24°C. Serial twofold dilutions were then performed by adding 100 μL of each essential oil or plant extract solution to the first well and transferring 100 μL sequentially across the plate. Assays were conducted in triplicate and incubated for an additional 48 h. Following incubation, 10 μL of 1% (w v^{-1}) 2,3,5-triphenyltetrazolium chloride (TTC) was added to each well to assess fungal respiratory activity by colorimetric detection.

2.5 | Fungicidal Effects of Essential Oils and Plant Extracts Against *Monilinia fructicola*

This effect was evaluated by transferring aliquots of essential oil and plant extract solutions from the minimum inhibitory

concentration test to plates containing solid PDA (spot test). Growth from each spot was observed after incubation to determine whether inhibition was fungicidal (no growth) or fungistatic (growth resumed).

2.6 | Fungitoxic Effects of Essential Oils and Plant Extracts on *Monilinia fructicola* Hyphae

This effect on *M. fructicola* hyphae were evaluated using scanning electron microscopy. Mycelial samples were randomly collected from direct or indirect assays in which partial or complete inhibition of pathogen growth was observed. Hyphal morphology was examined for treatment-induced defects using a Hitachi TM3000 scanning electron microscope. Hyphal dimensions were measured in micrometres (μm).

2.7 | Incidence and Severity of Brown Rot in Peaches Treated With Essential Oils and Plant Extracts

For that assessment a conidial suspension of *M. fructicola* was prepared from 10-day-old cultures by adding 20 mL of sterile distilled water to the plates and gently dislodging the spores with a Drigalski spatula. The suspension was adjusted to a final concentration of 1.0×10^5 spores mL^{-1}. Only treatments that showed satisfactory inhibition in both direct and indirect contact in vitro assays were selected for postharvest application on dry, uninjured fruits. Fruits were divided into two groups corresponding to direct and indirect contact treatments.

For direct contact, fruits were surface-disinfested, air-dried and then immersed for 10 min in essential oil (1% v v^{-1}) or plant extract (10% v v^{-1}) solutions. Treated fruits were placed on PVC rings inside transparent polypropylene containers (34 cm in diameter) with lids.

For indirect contact, the same disinfestation and immersion procedure was followed, but 1 mL of the essential oil (1% v v^{-1}) or plant extract (10% v v^{-1}) solution was applied to a 3 cm^2 germination paper affixed to the inner surface of the container lid (Fabiane 2011). All containers were stored at room temperature (23°C ± 2°C). After 24 h, 1 mL of conidial suspension (1×10^5 spores mL^{-1}) was sprayed onto the fruit surface using a hand sprayer until runoff (Aquino et al. 2012). The conidial suspension was applied to fruits in both indirect and direct contact treatments. Negative controls were treated with distilled water, and positive controls were treated with the fungicide captan according to the manufacturer's recommendations. Disease incidence and severity were evaluated at 24, 60 and 96 h after inoculation. Incidence was recorded as the percentage of fruits showing symptoms (0 = no symptoms; 1 = with symptoms), and severity was assessed using a 0–4 scale, where 0 = no symptoms; 1 = 1%–25% surface affected; 2 = 26%–50%; 3 = 51%–75%; and 4 = > 75% surface affected (adapted from Wagner Júnior et al. 2005). Figure 2 shows the experimental setup for this assay.

The experimental design was completely randomised with four replicates, each consisting of 12 fruits, for both direct and indirect contact treatments. Incidence and severity data were tested for normality using the Shapiro–Wilk test and subjected to Box–Cox transformation when necessary. Transformed data were analysed by analysis of variance (ANOVA) and treatment means were compared using the Scott–Knott test ($\alpha = 0.05$) in R software (R Core Team 2019).

2.8 | Biochemical Analyses

Biochemical analyses were performed on treatments that exhibited disease severity below 25%. At 24, 60 and 96 h after inoculation with an *M. fructicola* conidial suspension, fruit samples (epidermis and mesocarp) were excised using a sterile scalpel to obtain a section of approximately 1 cm^2 in area and 0.5 cm in depth; the remaining fruit tissue was discarded. Crude enzyme extracts were prepared by macerating 0.5 g of fruit tissue from each treatment in a mortar with 0.2 g of glass beads, 0.1 g of Dowex 1-X8 resin and 0.2 g of polyvinylpolypyrrolidone (PVPP). Then, 5 mL of 0.1 M sodium borate buffer (pH 8.8) containing 1 mM ethylenediaminetetraacetic acid (EDTA), 1 mM dithiothreitol (DTT) and 50 mM ascorbic acid was added. Samples were then centrifuged at 20,000 g for 30 min at 4°C (Guzzo and Martins 1996). The supernatants were used as crude extracts to determine total soluble protein content and the activities of chitinase, β-1,3-glucanase, and phenylalanine ammonia-lyase (PAL).

Protein content was determined using the Bradford assay (Bradford 1976); 40 μL of supernatant was mixed with 460 μL of distilled water, and 1 mL of Bio-Rad reagent [diluted 1:4 (v v^{-1})], vortexed, and absorbance was measured by spectrophotometry at 595 nm. Chitinase and β-1,3-glucanase activities were measured according to Wirth and Wolf (1992), with modifications. Chitinase activity was determined by the release of soluble dyed oligomers from carboxymethylated chitin labelled with Remazol Brilliant Violet 5R (CM-Chitin-RBV; Sigma–Aldrich). A 500 μL aliquot of crude extract was mixed with 500 μL of 0.2 M sodium phosphate buffer and 100 mg of CM-chitin-RBV substrate (2.0 mg mL^{-1} suspension). The mixture was incubated at 50°C for 60 min in a water bath and then boiled for 5 min to stop the reaction. After centrifugation at 5000 *g* for 10 min, the absorbance of the supernatant was measured by spectrophotometry at 595 nm.

β-1,3-glucanase activity was determined using dyed insoluble curdlan (Curdlan-RBB; Sigma–Aldrich) at 4 mg mL^{-1} as the substrate. The reaction mixture consisted of 200 μL of crude extract, 400 μL of 50 mM sodium acetate buffer and 200 μL of substrate suspension (4.0 mg mL^{-1}). The mixture was incubated at 40°C for 120 min, and the reaction was stopped by adding 200 μL of 1.0 M HCl solution, followed by cooling on ice for 10 min and centrifugation at 10,000 *g* for 5 min. The absorbance of the supernatant was measured by spectrophotometry at 600 nm (Guzzo and Martins 1996). Phenylalanine ammonia-lyase (PAL) activity was measured based on the production of trans-cinnamic acid from L-phenylalanine. The reaction mixture contained 1.5 mL of crude extract, 1.0 mL of Tris–HCl buffer (pH 8.0) and 0.5 mL L-phenylalanine (49.6 mg mL^{-1}). The mixture was centrifuged at 6000 *g* for 10 min at 4°C. After incubation at 40°C for 1 h, the reaction

TABLE 1 | Mycelial growth (cm) of *Monilinia fructicola* according to treatment, extraction method, and direct or indirect contact application.

Treatments	Direct contact	Indirect contact
Essential oil		
Negative control (distilled water)	8.17 aA	8.45 aA
Rosmarinus officinalis	8.88 aA	8.58 aA
Allium sativum	0.50 cA	0.50 cA
Syzygium aromaticum	0.50 cA	0.50 cA
Artemisia absinthium	5.50 bB	8.17 aA
Origanum vulgare	0.50 cA	0.50 cA
Eugenia uniflora	8.47 aA	5.17bA
Positive control (captan)	0.50 cA	0.50 cA
Cold aqueous extract		
Negative control (distilled water)	8.74 aA	9.00 aA
Rosmarinus officinalis	8.29 aA	7.72 bA
Allium sativum	2.75 eA	5.37 cA
Syzygium aromaticum	3.81 dB	7.80 bA
Artemisia absinthium	6.79 bB	7.62 bA
Origanum vulgare	7.49 bA	7.26 bA
Eugenia uniflora	6.37 cB	9.00 aA
Positive control (captan)	0.65 fA	0.65 dA
Coefficient of variation (%)	9.38	
Hot extract		
Negative control (distilled water)	8.88 aA	9.00 aA
Rosmarinus officinalis	5.23 dB	9.00 aA
Allium sativum	3.87 eB	5.88 cA
Syzygium aromaticum	6.34 cB	8.11 bA
Artemisia absinthium	7.73 bA	9.00 aA
Origanum vulgare	7.58 bA	7.78 bB
Eugenia uniflora	7.41 bA	7.96 bA
Positive control (captan)	0.50 fA	0.50 dA
Coefficient of variation (%)	8.64	
Hydroalcoholic extract		
Negative control (distilled water)	8.73 aA	9.00 aA
Rosmarinus officinalis	5.49 dB	8.61 aA
Allium sativum	0.63 eB	6.35 bA
Syzygium aromaticum	0.50 eB	8.48 aA
Artemisia absinthium	8.00 bB	8.83 aA
Origanum vulgare	6.53 cB	8.57 aA
Eugenia uniflora	6.88 cB	8.92 aA
Positive control (captan)	0.50 eA	0.50 cA
Coefficient of variation (%)	8.23	

Note: Means followed by the same uppercase letter within a row, or lowercase letter within a column, belong to the same group according to the Scott–Knott cluster test ($\alpha = 0.05$).

was stopped by placing the tubes in an ice bath. Absorbance was measured by spectrophotometry at 290 nm (Rodrigues et al. 2006) (Figure 2).

Data were tested for normality using the Shapiro–Wilk test and subjected to Box–Cox transformation when necessary. Data were analysed by analysis of variance (ANOVA), followed by the Scott–Knott mean comparison test ($\alpha = 0.05$) using R software (R Core Team 2019).

3 | Results

3.1 | Effects of Essential Oils and Plant Extracts on Mycelial Growth of *Monilinia fructicola* In Vitro

A significant treatment × contact type interaction was observed for mycelial growth of *Monilinia fructicola*, depending on the extraction method (Table 1).

No mycelial growth was observed in either direct or indirect contact treatments with essential oils of *Allium sativum*, *Syzygium aromaticum* and *Origanum vulgare*, or with the positive control (captan); these treatments belonged to the same statistical group. This complete inhibition was not observed with plant extracts, except for the hydroalcoholic extracts of *A. sativum* and *S. aromaticum*, which grouped with captan and exhibited the lowest mycelial growth (Table 1). Overall, mycelial growth was lower under direct contact than under indirect contact, regardless of the extraction method.

TABLE 2 | Minimum inhibitory concentration (%) of essential oils and plant extracts (cold aqueous, hot aqueous and hydroalcoholic) against *Monilinia fructicola* in vitro.

Treatments	Essential oil	Cold aqueous	Hot aqueous	Hydroalcoholic
Negative control (distilled water)	—	—	—	—
Rosmarinus officinalis	—	—	—	—
Allium sativum	0.04	0.31	2.50	0.31
Syzygium aromaticum	0.16	—	—	0.31
Artemisia absinthium	—	—	—	—
Origanum vulgare	0.16	—	—	—
Eugenia uniflora	—	—	—	—
Positive control (captan)[a]		—		

[a]Recommended concentration for peach cultivation: 2.4 g L^{-1} of water.

3.2 | Minimum Inhibitory Concentration of Essential Oils and Plant Extracts Against *Monilinia fructicola*

Essential oils and plant extracts of *Artemisia absinthium*, *Rosmarinus officinalis* and *Eugenia uniflora* exhibited no inhibitory activity at the tested concentrations, regardless of the extraction method (Table 2).

The minimum inhibitory concentration of *A. sativum* essential oil against *M. fructicola* was 0.04% (Table 2), demonstrating strong antifungal activity. The essential oil of *S. aromaticum* and *O. vulgare* exhibited the same effect but at a minimum inhibitory concentration of 0.16%, which was four times higher than that of *A. sativum* essential oil (Table 2).

3.3 | Fungicidal Effects of Essential Oils and Plant Extracts Against *Monilinia fructicola*

The cold and hot aqueous extracts of *A. sativum* exhibited inhibitory effects that were fungistatic, as fungal growth resumed in the spot test, albeit at a slower rate than in the negative control (distilled water). The hydroalcoholic extracts of *A. sativum* and *S. aromaticum* had a minimum inhibitory concentration of 0.31% but showed no fungicidal effect.

3.4 | Fungitoxic Effects of Essential Oils and Plant Extracts on *Monilinia fructicola* Hyphae

Scanning electron microscopy was used to assess morphological alterations in *M. fructicola* hyphae and conidia by comparing the negative control (Figure 3A) with treated samples (Figure 3B–L). Hyphae and conidia in the negative control appeared normal, with intact structure and no visible alterations.

The cold aqueous extract of *R. officinalis* in direct contact caused no changes in *M. fructicola* conidia (Figure 3B). In contrast, the hydroalcoholic extract of *R. officinalis* in direct contact resulted in cellular disorganisation of the hyphae (Figure 3C). Direct and indirect contact with *R. officinalis* essential oil caused conidial wilting (Figure 3D,E, respectively).

No morphological alterations were observed in hyphae or conidia following direct contact with cold (Figure 3F) or hot (Figure 3G) aqueous extracts of *A. sativum*, hot aqueous extract of *A. absinthium* (Figure 3I) or the hydroalcoholic extract of *O. vulgare* (Figure 3K), compared with the negative control (Figure 3A).

Direct contact with the cold aqueous extract of *S. aromaticum* caused septal thickening (Figure 3H). Indirect contact with *A. absinthium* essential oil induced hyphal wilting and increased septation (Figure 3J). Indirect contact with the hot aqueous extract of *O. vulgare* caused hyphal wilting and twisting (Figure 3L).

3.5 | Incidence and Severity of Brown Rot in Peaches Treated With Essential Oils and Plant Extracts

Although several treatments exhibited promising in vitro effects, their efficacy was further evaluated in postharvest assays on 'Dourado' peaches. A significant treatment × evaluation time interaction was observed for brown rot incidence in direct contact assays (Table 3) and indirect contact assays (Table 4).

In direct contact assays, no brown rot incidence (Table 3) or severity (Table 4) was observed on the first day after inoculation. Thereafter, disease developed in most treatments, except in the positive control (captan) and *O. vulgare* essential oil, which completely suppressed incidence and severity throughout the 7-day evaluation period. The essential oil of *Allium sativum* prevented incidence (Table 3) and severity (Table 4) until the third day, a delay not observed for the other treatments.

In indirect contact assays, treatments with *A. sativum*, *S. aromaticum* and *O. vulgare* essential oils delayed incidence and severity until the second day after inoculation. Subsequent disease control was lost in these treatments, except for the positive control (captan) (Tables 5 and 6).

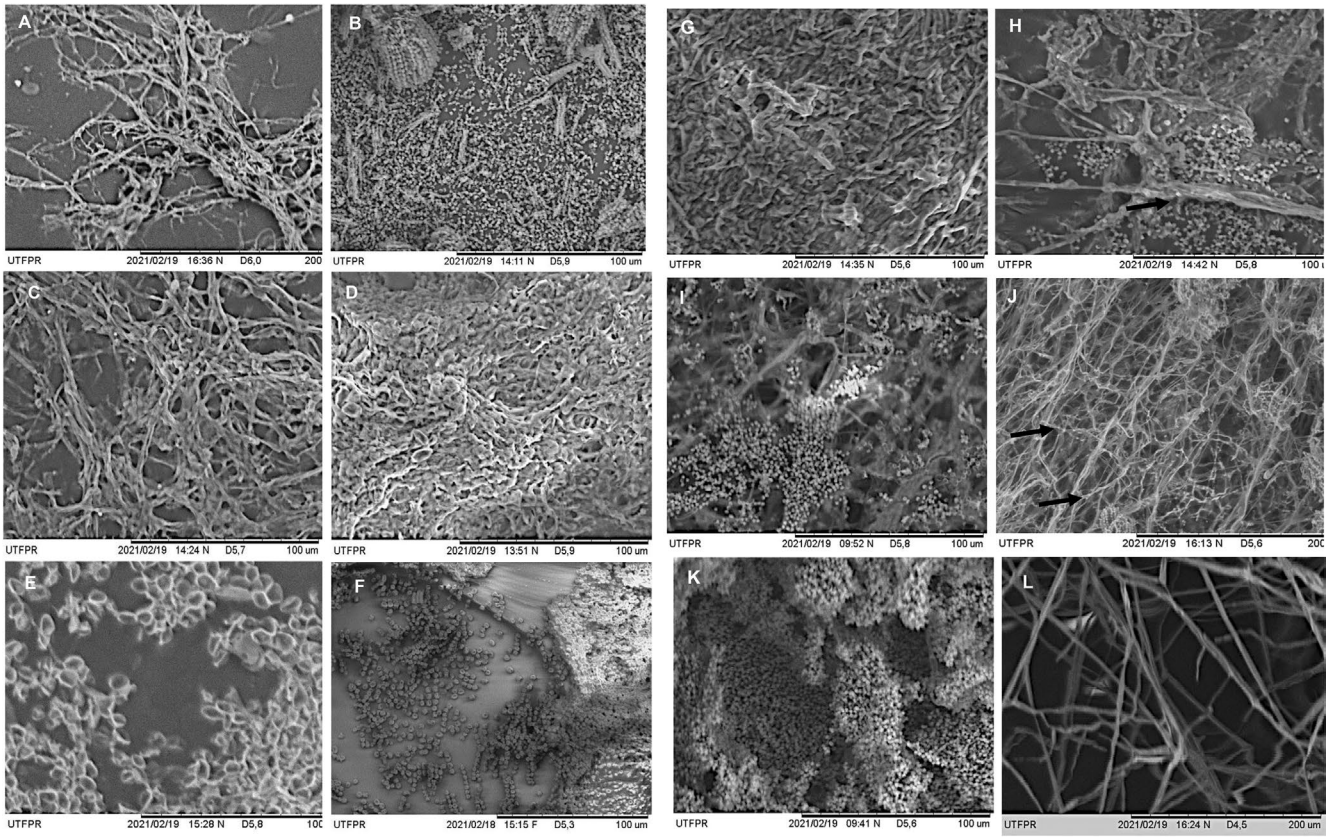

FIGURE 3 | Hyphae and conidia of *Monilinia fructicola*, observed under SEM at 800× magnification. (A) Control; (B) Cold extract of *Rosmarinus officinalis* CD; (C) Hydroalcoholic extract of *R. officinalis*; (D) Essential oil of *R. officinalis* CD; (E) Essential oil of *R. officinalis* CI; (F) Cold extract of *Allium sativum* CD; (G) Hot extract of *Allium sativum* CD; (H) Cold extract of *Sizygium aromaticum* CD; (I) Hot extract of *Artemisia* CD; (J) Essential oil of *A. absinthium* CI; (K) Hydroalcoholic extract de *Origanum vulgare* CD; (L) Cold extract de *O. vulgare* CI.

TABLE 3 | Incidence (%) of brown rot in 'Dourado' peach fruits treated with essential oils (EO), cold aqueous (CA), hot aqueous (HA) and hydroalcoholic (HY) plant extracts in direct contact assays after inoculation with *Monilinia fructicola*.

	Evaluation time (days)						
Treatment	**1**	**2**	**3**	**4**	**5**	**6**	**7**
Negative control (distilled water)	0.0 aB	0.31 aB	1.49 aA	1.55 aA	1.58 aA	1.58 aA	1.58 aA
CA *A. sativum*	0.0 aB	0.0 bB	1.46 aA	1.54 aA	1.58 aA	1.58 aA	1.58 aA
HA *R. officinalis*	0.0 aB	0.0 bB	1.41 aA	1.54 aA	1.58 aA	1.58 aA	1.58 aA
HA *A. sativum*	0.0 aB	0.0 bB	1.42 aA	1.54 aA	1.58 aA	1.58 aA	1.58 aA
HA *S. aromaticum*	0.0 aB	0.0 bB	1.51 aA	1.55 aA	1.58 aA	1.58 aA	1.58 aA
HY *A. sativum*	0.0 aB	0.0 bB	1.36 aA	1.54 aA	1.57 aA	1.58 aA	1.58 aA
HY *S. aromaticum*	0.0 aC	1.04 aB	1.49 aA	1.53 aA	1.58 aA	1.58 aA	1.58 aA
EO *A. sativum*	0.0 aC	0.0 bC	0.0 bC	0.62 bB	0.62 bB	0.62 bB	1.10 bA
EO *S. aromaticum*	0.0 aB	0.31 bB	0.31 bB	0.31 bB	0.62 bA	0.62 bA	0.62 cA
EO *O. vulgare*	0.0 aA	0.0 bA	0.0 bA	0.0 cA	0.0 cA	0.0 cA	0.0 dA
Positive control (captan)	0.0 aA	0.0 bA	0.0 bA	0.0 cA	0.0 cA	0.0 cA	0.0 dA
Coefficient of variation (%)				33.99			

Note: Means followed by the same uppercase letter within a row, or lowercase letter within a column, belong to the same group according to the Scott–Knott cluster test ($\alpha = 0.05$).

TABLE 4 | Severity of brown rot in 'Dourado' peach fruits treated with essential oils (EO), cold aqueous (CA), hot aqueous (HA) and hydroalcoholic (HY) plant extracts in direct contact assays after inoculation with *Monilinia fructicola*.

	Evaluation time (days)						
Treatment	**1**	**2**	**3**	**4**	**5**	**6**	**7**
Negative control (distilled water)	0.0 aB	0.25 bB	1.04 aA	1.08 aA	1.09 aA	1.09 aA	1.09 aA
CA *A. sativum*	0.0 aB	0.0 bB	1.00 aA	1.06 aA	1.09 aA	1.09 aA	1.09 aA
HA *R. officinalis*	0.0 aB	0.0 bB	1.01 aA	1.05 aA	1.09 aA	1.09 aA	1.09 aA
HA *A. sativum*	0.0 aB	0.0 bB	1.00 aA	1.03 aA	1.09 aA	1.09 aA	1.09 aA
HA *S. aromaticum*	0.0 aB	0.0 bB	1.04 aA	1.07 aA	1.09 aA	1.09 aA	1.09 aA
HY *A. sativum*	0.0 aB	0.0 bB	1.00 aA	1.02 aA	1.09 aA	1.09 aA	1.09 aA
HY *S. aromaticum*	0.0 aB	0.75 aA	1.02 aA	1.05 aA	1.08 aA	1.08 aA	1.09 aA
EO *A. sativum*	0.0 aB	0.0 bB	0.0 bB	0.50 bA	0.50 bA	0.50 bA	0.77 aA
EO *S. aromaticum*	0.0 aB	0.25 bB	0.25 bB	0.26 bB	0.51 bA	0.51 bA	0.51 bA
EO *O. vulgare*	0.0 aA	0.0 bA	0.0 bA	0.0 cA	0.0 cA	0.0 cA	0.0 cA
Positive control (captan)	0.0 aA	0.0 bA	0.0 bA	0.0 cA	0.0 cA	0.0 cA	0.0 cA
Coefficient of variation (%)				38.78			

Note: Means followed by the same uppercase letter within a row, or lowercase letter within a column, belong to the same group according to the Scott–Knott cluster test ($\alpha = 0.05$).

TABLE 5 | Incidence (%) of brown rot in 'Dourado' peach fruits treated with essential oils (EO) in indirect contact assays after inoculation with *Monilinia fructicola*.

	Evaluation time (days)						
Treatment	**1**	**2**	**3**	**4**	**5**	**6**	**7**
Negative control (distilled water)	0.0 aC	0.58 aC	4.92 aB	5.74 aA	6.31 aA	6.31 aA	6.31 cA
EO *A. sativum*	0.0 aA	0.0 aA	0.58 cA	0.58 bA	0.58 bA	0.58 bA	1.17 bA
EO *S. aromaticum*	0.0 aD	0.0 aD	2.98 bC	5.11 aB	5.97 aA	6.31 aA	6.31 cA
EO *O. vulgare*	0.0 aD	0.0 aD	2.84 bC	5.42 aB	6.31 aA	6.31 aA	6.31 cA
Positive control (captan)	0.0 aA	0.0 aA	0.0 cA	0.0 bA	0.0 bA	0.0 bA	0.0 aA
CV (%)				21.76			

Note: Means followed by the same uppercase letter within a row, or lowercase letter within a column, belong to the same group according to the Scott–Knott cluster test ($\alpha = 0.05$).

3.6 | Biochemical Analysis

Total soluble protein content was lowest in the negative control (distilled water) and the positive control (captan) at all three evaluation times. At 24 h after inoculation, treatments formed two statistical groups, with the highest protein content observed in fruits treated with essential oils of *A. sativum*, *S. aromaticum* and *O. vulgare* under both direct and indirect contact. At 60 h, three groups were formed; the highest protein content was observed in fruits treated with *A. sativum* essential oil under indirect contact. At 96 h, *A. sativum* essential oil under indirect contact formed the second-highest group, whereas the highest protein content was observed in fruits treated with *S. aromaticum* and *O. vulgare* essential oils (direct and indirect contact) and *A. sativum* essential oil (direct contact) (Table 7).

Phenylalanine ammonia-lyase (PAL) activity at 24 h after inoculation formed three statistical groups, with essential oil of *O. vulgare* in direct contact and the positive control (captan) forming the group with the highest activity. At 60 h, two groups were formed, with essential oils of *S. aromaticum* and *O. vulgare* in direct contact exhibiting the highest activity. At 96 h, four groups were formed, with essential oil of *O. vulgare* in direct contact exclusively forming the group with the highest activity (Table 8).

In addition to PAL induction, essential oils, particularly in direct contact—activated pathogenesis-related (PR) proteins, notably chitinase. At 24 h, chitinase activity formed three groups, with essential oils of *S. aromaticum* and *A. sativum* in both direct and indirect contact forming the group with the highest activity. At 60 h and 96 h, the highest chitinase activity

TABLE 6 | Severity of brown rot in 'Dourado' peach fruits treated with essential oils (EO) in indirect contact assays after inoculation with *Monilinia fructicola*.

	Evaluation time (days)						
Treatment	**1**	**2**	**3**	**4**	**5**	**6**	**7**
Negative control (distilled water)	0.0 aC	0.25 aC	1.80 aB	2.90 aA	3.25 aA	3.25 aA	3.25 aA
EO *A. sativum*	0.0 aA	0.0 aA	0.25 cA	0.25 cA	0.25 cA	0.25 bA	0.50 bA
EO *S. aromaticum*	0.0 aE	0.0 aE	1.0 bC	1.60 bC	2.36 bB	3.25 aA	3.25 aA
EO *O. vulgare*	0.0 aD	0.0 aD	1.0 bC	1.80 bB	3.07 bA	3.25 aA	3.25 aA
Positive control (captan)	0.0 aA	0.0 aA	0.0 cA	0.0 cA	0.0 cA	0.0 bA	0.0 cA
CV (%)				21.78			

Note: Means followed by the same uppercase letter within a row, or lowercase letter within a column, belong to the same group according to the Scott–Knott cluster test ($\alpha = 0.05$).

TABLE 7 | Total soluble protein content ($mg\,g^{-1}$ fresh tissue) over time in 'Dourado' peach fruits treated with essential oils (EO) of *Allium sativum*, *Syzygium aromaticum* and *Origanum vulgare* in direct and indirect contact assays after inoculation with *Monilinia fructicola*.

	Evaluation time (days)		
Treatment	**24**	**60**	**96**
Negative control (distilled water)	8.29 bA	6.77 cA	7.92 cA
EO *A. sativum*—direct contact	14.04 aB	11.20 bB	17.46 aA
EO *S. aromaticum*—direct contact	13.40 aA	11.50 bA	15.30 aA
EO *O. vulgare*—direct contact	13.11 aA	14.96 bA	14.33 aA
EO *A. sativum*—indirect contact	13.74 aB	22.78 aA	11.65 bB
EO *S. aromaticum*—indirect contact	12.42 aA	11.52 bA	15.38 aA
EO *O. vulgare*—indirect contact	13.75 aA	13.87 bA	15.26 aA
Positive control (captan)	5.0 bA	5.84 cA	7.75 cA
CV (%)		20.51	

Note: Means followed by the same uppercase letter within a row, or lowercase letter within a column, belong to the same group according to the Scott–Knott cluster test ($\alpha = 0.05$).

TABLE 8 | Phenylalanine ammonia-lyase (PAL) activity (ΔA_{290} $min^{-1}\,mg^{-1}$ protein $\times 10^{-2}$) over time in 'Dourado' peach fruits treated with essential oils (EO) of *Allium sativum*, *Syzygium aromaticum* and *Origanum vulgare* in direct and indirect contact assays after inoculation with *Monilinia fructicola*.

	Evaluation time (days)		
Treatment	**24**	**60**	**96**
Negative control (distilled water)	0.009 cA	0.007 bA	0.008 dA
EO *A. sativum*—direct contact	0.011 cA	0.008 bB	0.011 dA
EO *S. aromaticum*—direct contact	0.013 bB	0.016 aB	0.020 bA
EO *O. vulgare*—direct contact	0.018 aB	0.017 aB	0.024 aA
EO *A. sativum*—indirect contact	0.010 cB	0.010 bB	0.015 cA
EO *S. aromaticum*—indirect contact	0.009 cA	0.008 bA	0.011 dA
EO *O. vulgare*—indirect contact	0.005 dB	0.006 bB	0.010 dA
Positive control (captan)	0.018 aB	0.009 bB	0.015 cA
CV (%)		15.14	

Note: Means followed by the same uppercase letter within a row, or lowercase letter within a column, belong to the same group according to the Scott–Knott cluster test ($\alpha = 0.05$).

was observed exclusively in these treatments under direct contact (Table 9).

4 | Discussion

The reduced mycelial growth observed with essential oils and hydroalcoholic extracts (Table 1) is attributed to their higher extraction efficiency of bioactive compounds, better preservation of their chemical properties and consequently stronger antifungal activity compared with cold and hot aqueous extracts. Cold and hot aqueous extractions are more time-consuming and less efficient at recovering the full spectrum of metabolites, often requiring larger amounts of plant material.

The strong inhibitory effect of the essential oil and hydroalcoholic extract of *Allium sativum* (Table 1) can be attributed to organosulfur compounds such as allyl methyl disulfide, diallyl disulfide, diallyl trisulfide, and diallyl tetrasulfide. These bioactive compounds are involved in plant defence mechanisms

TABLE 9 | Chitinase activity (units mg^{-1} protein) over time in 'Dourado' peach fruits treated with essential oils (EO) of *Allium sativum*, *Syzygium aromaticum* and *Origanum vulgare* in direct and indirect contact assays after inoculation with *Monilinia fructicola*.

	Evaluation time (days)		
Treatment	**24**	**60**	**96**
Negative control (distilled water)	0.33 bA	0.31 bA	7.92 cA
EO *A. sativum*—direct contact	0.43 aA	0.43 aA	0.43 aA
EO *S. aromaticum*—direct contact	0.42 aA	0.43 aA	0.41 aA
EO *O. vulgare*—direct contact	0.29 cA	0.20 cB	0.27 cA
EO *A. sativum*—indirect contact	0.42 aA	0.34 bB	0.32 bB
EO *S. aromaticum*—indirect contact	0.38 aA	0.32 bB	0.32 bB
EO *O. vulgare*—indirect contact	0.36 bA	0.33 bA	0.33 bA
Positive control (captan)	0.29 cB	0.34 bA	0.27 cB
CV (%)		11.40	

Note: Means followed by the same uppercase letter within a row, or lowercase letter within a column, belong to the same group according to the Scott–Knott cluster test ($\alpha = 0.05$).

against pathogens and are known to cause cellular and tissue damage in microorganisms (Hile et al. 2004).

The inhibitory activity observed with the essential oil and hydroalcoholic extract of *Syzygium aromaticum* (Table 1) is primarily due to eugenol, which exhibits well-documented antifungal properties. Wang et al. (2010) reported that eugenol disrupts fungal membranes by altering permeability, leading to membrane destabilisation and rupture. The efficacy of *Origanum vulgare* essential oil is largely attributable to its major components, thymol and carvacrol, which have broad-spectrum antimicrobial activity against bacteria and fungi (Adam et al. 1998).

Greater inhibition of mycelial growth via direct contact (Table 1) may result from the higher volatility of low-molecular-weight monoterpenes and sesquiterpenes present in essential oils. Indirect contact was less effective, as also reported by Farkas and Mohácsi-Farkas (2014), likely because many bioactive compounds in plant extracts have molecular weights exceeding those of sesquiterpenes and therefore exhibit lower volatility (Mendes-Pinto 2009).

The varying efficacy of different *Allium sativum* preparations highlights the influence of extraction method and solvent on antifungal activity (Table 2). This result is consistent with those reported by Rodrigues et al. (2009), who observed the lowest minimum inhibitory concentrations for aqueous and alcoholic extracts of *A. sativum* bulbs against *Candida albicans* strains.

Differences in pathogen inhibition between in vitro (Tables 1 and 2) and postharvest (Tables 3–6) assays may arise from the preventive nature of in vitro treatments, in which bioactive compounds were present before fungal development began. Additionally, the absence of host fruit metabolism in vitro likely prevented degradation of, or interactions with, extract compounds that would otherwise reduce antifungal efficacy under postharvest conditions. Similarly, Fontana et al. (2017) applied *S. aromaticum* extract to 'Chimarrita' and 'Precocinho' peaches and observed no difference from the negative control (distilled water) for the former cultivar, and reduced—although still high—disease incidence for the latter.

Plant extracts failed to control brown rot incidence and severity (Tables 3–6), possibly because aqueous and 70% ethanolic solvents were inefficient at extracting or preserving key secondary metabolites, or because the applied concentrations were insufficient relative to the higher inoculum load on fruit compared with in vitro assays. Furthermore, the tested plant extracts may not have induced the synthesis of signalling molecules involved in fruit secondary metabolism, such as ethylene, salicylic acid or jasmonic acid. These molecules are essential for defence responses, including the induction of systemic acquired resistance (SAR) (Sá et al. 2008).

Abiotic and biotic stresses, including pathogen infection and physical damage, trigger physiological responses that upregulate genes involved in phenylpropanoid metabolism, leading to the induction of specific proteins (Coltro et al. 2014). These stresses can enhance the activity of oxidative enzymes, such as peroxidases, thereby reducing phenolic compound content, while simultaneously increasing phenylalanine ammonia-lyase (PAL) activity (Andersen and Markham 2005).

Fruits immersed in essential oils exhibited browning, particularly when treated with *Syzygium aromaticum* and *Origanum vulgare* essential oils, accompanied by epidermal degradation (crumbly texture). This discoloration progressed from the epidermis to the mesocarp over the evaluation period. Nevertheless, fruits treated with *O. vulgare* essential oil showed no brown rot symptoms or fungal growth until the seventh day post-inoculation (Tables 3 and 4). Apart from the browning effect, *O. vulgare* essential oil was as effective as the positive control (captan) in suppressing disease development (Tables 3 and 4).

The essential oil of *O. vulgare* has a high thymol content, similar to that of thyme. Santoro et al. (2018) demonstrated effective control of brown rot in peaches and nectarines using thyme essential oil, rich in p-cymene and thymol, applied in the vapour phase (indirect contact) within diffuser chambers, without inducing fruit discoloration. The authors also reported no fruit weight loss, potentially due to the formation of a surface coating that reduced gas exchange, respiratory rate and transpiration. Thus, essential oils rich in phenolic monoterpenes show promise for postharvest disease control applications.

Based on the incidence and severity results under both direct and indirect contact, the secondary compounds present in essential oils exhibited satisfactory antifungal activity. Further

studies are needed to optimise application methods and elucidate the causes of epidermal browning, potentially by identifying specific components responsible for both antifungal efficacy and fruit discoloration.

The absence of disease incidence may be associated with increased total soluble protein content available for the synthesis of secondary defence metabolites (Table 7), together with induction of the pathogenesis-related protein chitinase (Table 9) and phenylalanine ammonia-lyase (PAL) (Table 8). This increase in protein content is likely associated with the induction of systemic acquired resistance (SAR), which is directly linked to pathogenesis-related proteins involved in plant defence against pathogens (Van Loon et al. 2006).

The superior efficacy of *Origanum vulgare* essential oil under direct contact for suppressing brown rot incidence (Table 3) and severity (Table 4) can be explained by its induction of phenylalanine ammonia-lyase (PAL) activity (Table 8). At all three evaluation time points, *O. vulgare* essential oil in direct contact consistently belonged to the group with the highest PAL activity, supporting the hypothesis that this enzyme contributed to the synthesis of defence metabolites against brown rot.

Increased PAL activity has also been reported by Khumalo et al. (2017) following vapour-phase treatment with thyme essential oil against brown rot caused by *Monilinia laxa*. Peaches exposed to thyme oil vapour ($96\,\mu L\,L^{-1}$) for 24 h, inoculated with 10^5 conidia mL^{-1}, and stored for 14 days at 0°C followed by 6 days of shelf-life simulation at 15°C exhibited reduced disease incidence and elevated PAL activity, along with increased catechin, chlorogenic acid, and caffeic acid contents, thereby enhancing antioxidant capacity. Thus, similar to thymol-rich thyme oil, *O. vulgare* essential oil (containing approximately 3% thymol) likely activated comparable defence pathways.

Induction of chitinase activity elicited defence responses in peaches, thereby reducing or inhibiting the infection process. Activation of chitinase and/or β-1,3-glucanase can promote lignification, reactive oxygen species (ROS) production, phytoalexin biosynthesis, callose formation and expression of defence-related genes. Moreover, chitinase in peaches disrupts fungal hyphal integrity, releasing chitin fragments that function as elicitors for pattern recognition receptors (PRRs) (Pusztahelyi 2018).

No significant treatment × time interaction or main effects were detected for β-1,3-glucanase activity. This lack of response may reflect prioritisation of chitinase synthesis in this pathosystem, given that *M. fructicola* (Ascomycota) has a cell wall composed primarily of β-glucans and chitin (Massola and Krugner 2011).

Essential oils of *A. sativum* and *O. vulgare*, particularly under direct contact, showed promising results by controlling postharvest disease and inducing fruit defence responses. Further studies should evaluate deodorised formulations for direct contact applications, as indirect contact was less effective, or test higher concentrations under controlled atmospheres. For example, Servili et al. (2017) achieved a 65% reduction in grey mould (*Botrytis cinerea*) incidence on table grapes using vapour-phase rosemary (*Rosmarinus officinalis*) essential oil combined with hypobaric treatment (50 kPa), although transient organoleptic residues were detected, persisting for 24 h but dissipating after 48 h.

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Ethics Statement

The authors have nothing to report.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in RIUT at http://repositorio.utfpr.edu.br/jspui/handle/1/25349.

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