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REVIEW ARTICLE

Nature's protection: Harnessing essential oils for sustainable plant pathogen control

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Abstract

Essential oils (EOs) are volatile, aromatic compounds obtained from different plant parts. They contain bioactive compounds, including terpenes, phenolics and aldehydes. phenylpropanoids and other aromatic and aliphatic compounds. Due to the presence of thesebioactive compounds, EO possess strong antifungal, antibacterial and antiviral properties, making EOs effective at combating a wide range of plant pathogens. Typically, EO is composed of two to three primary components and a mixture of numerous minor components, each of which contributes to its biological activity, such as the disruption of microbial cell membranes, the induction of oxidative stress, the impairment of mitochondrial activity and the inhibition of spore germination and biofilm formation. These diverse modes of action contribute to the broad-spectrum antimicrobial efficacy of EOs against plant pathogens. For instance, essential oils extracted from *Cymbopogon* spp. (lemongrass), *Melaleuca alternifolia* (tea tree) and *Thymus vulgaris* (thyme) have shown significant antimicrobial activity against pathogens such as *Magnaporthe oryzae* (rice blast fungus), *Pseudomonas syringae* (a bacterial plant pathogen) and Tomato leaf curl virus (a viral disease affecting tomato crops). Due to their potent monoterpenes, EOs are considered promising candidates for integrated pest management (IPM) strategies. Their biodegradability and relative safety further enhance their potential as plant-protective agents, underscoring their role in promoting agricultural productivity and environmental sustainability.

Keywords: antibacterial; antifungal; antiviral; bioactivity; essential oil; plant pathogen

Introduction

Essential oils are volatile, aromatic compounds derived from various plant parts, such as leaves, roots, stems, fruits, seeds, fruit peels, wood, bark, resin and flowers, through hydrodistillation, steam distillation, or dry distillation methods. Individual essential oils usually contain 20-60 major compounds; the total number of different compounds identified across various essential oils exceeds 200. They contain various chemical compounds, depending upon the plant species from which they are derived and they belong to various chemical families, including terpenes, aldehydes, ketones, phenolics and other secondary metabolites and these compounds have various biological properties. Since ancient times, essential oils have been recognized for their anaesthetic, antioxidant and antiseptic qualities. Several of these oils have also been used in traditional medicine (1-3).

Currently, a significant portion of crop loss occurs at harvest due to pathogen infestation, which includes a broad range of diseases, from viruses and viroids to prokaryotic bacteria, eukaryotic fungi, oomycetes and nematodes. These plant diseases cause 40 billion dollars in losses globally and are extremely persistent (4). Controlling these plant diseases via chemical pesticides increases resistance. The use of essential oils is a viable option for controlling plant diseases because essential oils and their components have strong antifungal, antibacterial and antiviral qualities to control diseases. Since essential oils one of an alternative to synthetic fungicides because they are typically degraded into less harmful substances, some components may remain persistent and may be toxic to nontarget organisms (5-9). It is one of the reliable disease management techniques in organic disease management systems and is also a component of integrated disease management. Treatment is based on natural substances such as essential oils with safe qualities favourable to human health and the environment (10). To reduce the presence of potentially harmful inorganic compounds in agricultural products, developing natural products such as essential oils for disease management has become a priority. Therefore, the current study concentrates on combining information and findings from several studies on EO properties, with an emphasis on antifungal, antibacterial and antiviral activities.

Chemical composition of essential oils

The bioactive compounds present in essential oils have been shown to exhibit inhibitory effects on plant pathogens. Chemical analysis of numerous essential oils has revealed that they typically contain 2-3 major components present at relatively high concentrations (20-70 %), along with numerous minor constituents present at relatively low concentrations, which also contribute significantly to the overall activity and properties of the oil. These dominant compounds are largely responsible for the wide array of biological activities exhibited by EOs (11).

Essential oils generally consist of terpenes, terpenoids, phenylpropanoids and other aromatic and aliphatic compounds with low molecular weights. Terpenes and terpenoids are synthesized through the mevalonate pathway in the cytoplasm and the methylerythritol phosphate (MEP) pathway in plastids, whereas phenylpropanoids are produced via the shikimate pathway (12-14). Terpenes, constructed from isoprene units and represented by the general formula $(C_5H_8)_n$, exhibit a wide range of structural diversity, including acyclic, monocyclic, bicyclic and tricyclic forms. Based on their structural complexity, terpenes are categorized into various classes, such as monoterpenes ($C_{10}H_{16}$), sesquiterpenes ($C_{15}H_{24}$), diterpenes ($C_{20}H_{32}$) and triterpenes ($C_{30}H_{40}$).

Notably, monoterpenes constitute approximately 90 % of the bioactive compounds found in many essential oils derived from herbs and citrus plants. However, in woody or resinous essential oils such as sandalwood and patchouli, sesquiterpenes and their oxygenated derivatives can be the dominant components. Thus, the relative abundance of terpene classes varies significantly among different essential oils. Terpenes are pure hydrocarbons composed only of carbon and hydrogen, whereas terpenoids are chemically distinct compounds derived from terpenes by the addition of oxygen or other functional groups. The essential oils have different varieties of chemical compounds, although their composition is highly variable based on the plant source. The typical constituents are monoterpene hydrocarbons (e.g., p-cymene, limonene, α-pinene, α-terpinene), oxygenated monoterpenes (camphor, carvacrol, eugenol, thymol), diterpenes (cembrene C, kaurene, camphorene), sesquiterpene hydrocarbons (β-caryophyllene, germacrene D, humulene), oxygenated sesquiterpenes (spathulenol, caryophyllene oxide), monoterpene alcohols (geraniol, linalool, nerol) and sesquiterpene alcohols (patchoulol), as well as other aldehydes (citral, cuminal), acids (geranic acid, benzoic acid), ketones (acetophenone, benzophenone), lactones (bergapten), phenolic compounds (eugenol, thymol, carvacrol, catechol), esters (bornyl acetate, ethyl acetate) and coumarins (fumarins, benzofuran). However, not all essential oils contain all these compounds; their occurrence and quantity vary with the botanical origin and process of extraction (15-17). Some important compound structures are shown in in Fig. 1. The bioactivities of the essential oil compounds are shown in Table 1-3.

Antimicrobial activities of essential oils

Antifungal activities of EOs against plant diseases

Essential oils exhibit significant antifungal properties and are promising candidates for phytopathogen control under *in vitro* conditions. Essential oils derived from plants have various effects on different phytopathogens (Table 1). Oomycetes such as *Phytophthora colocasiae*, which cause leaf blight of taro, presented decreased mycelium development, sporangium formation and zoospore germination when exposed to ginger essential oil under *in vitro* conditions (18). Similarly, the mycelial and spore development of *Phytophthora capsici* was significantly suppressed by *Zanthoxylum armatum* fruit essential oil (ZEO). ZEO disrupts membrane integrity and ultrastructure, causing cell content leakage and cell death and increasing defense-related enzyme activities in pepper fruit. The main effective components of ZEO, D-limonene and linalool, play roles in controlling disease (19). In terms of the antifungal potential of Eos compounds, the essential oil of *Salvia rosmarinus* contains 1,8-cineole, which reliably reduces the conidiophore length, mycelial biomass and production of aflatoxin in *Aspergillus flavus* (20). The primary component of *Lepechinia mutica* essential oil was carnosol. It is especially effective against blast disease caused by *Pyricularia oryzae* (21).

The essential oil of celery seeds resulted in a 75 % reduction in cucumber powdery mildew (*Podosphaera fusca*) and induced defence mechanisms in plants in a greenhouse test (22). Savoury and thyme oils reduce the lesion length of *Colletotrichum gloeosporioides* Penz. in avocados (23). *Zataria multiflora* essential oil significantly inhibited *Rhizopus stolonifer* and *Botrytis cinerea* in a concentration-dependent manner, with the lowest minimum inhibitory concentration (MIC) and minimum fungicidal concentration (MFC) values observed

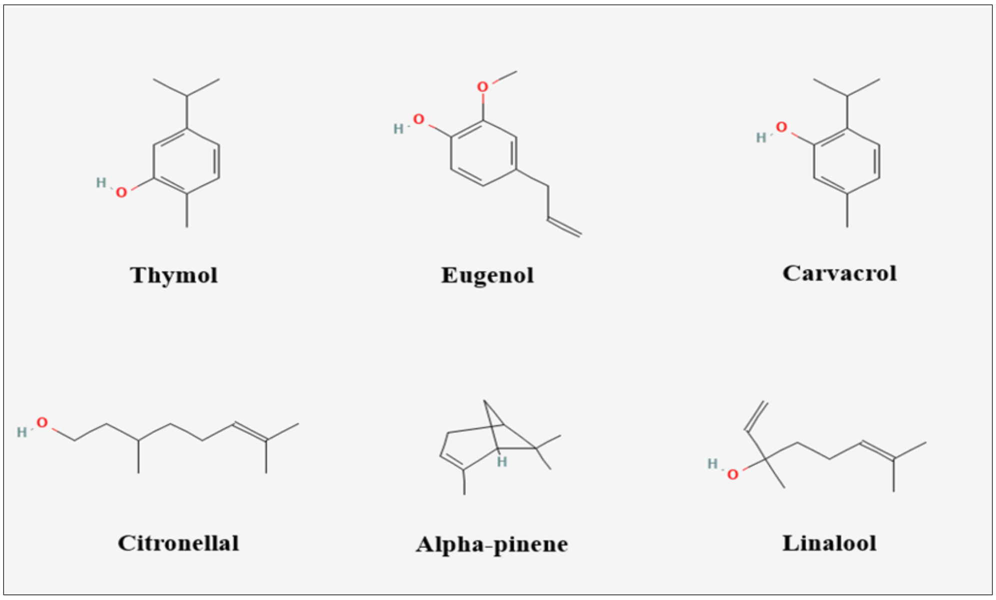

Fig. 1. Chemical structures of several major chemical components in essential oils. These are some of the structures of essential oil compounds.

Table 1. Antifungal activity of essential oils against fungi

Essential oil extracted from plant	Plant parts used for extraction	Major compounds present	Target fungi	Reference
Ocimum gratissimum	Leaves	Thymol, 3,7,7-trimethyl-1,2,3-Cycloheptatriene, γ-terpinene, eugenol and β-thujene	*Phytophtora infestans*	(29)
Calocedrus decurrens	Leaves	δ-3-Carene, myrcene and α-pinene	*Phytophthora plurivora*	(30)
Zingiber officinale	Rhizomes	Citral and 3,7-dimethyl 1-2,6 octadienal	*Phytophthora colocasiae*	(18)
Tetradium glabrifolium	Fruit	D-limonene, β-elemene and 2-tridecanone	*Phytophthora capsici*	(31)
Cinnamomum camphor	Peel	Methyl eugenol and safrole	*Pseudocercospora psidii*	(32)
Ferula gummosa	Stem resin	β-Pinene, γ-Terpinene and α-pinene	*Botrytis cinerea*	(33)
Thymus munbyanus subsp. *coloratus*	Aerial parts	Camphor, myrcene and borneol	*Aspergillus flavus*	(34)
Erigeron canadensis	Aerial parts	Limonene, germacrene D and cis-lachnophyllum ester	*Aspergillus flavus*	(35)
Oliveria decumbens Vent.	Leaves, stems and flowers.	Thymol, carvacrol, myristicin and elemicin	*Penicillium digitatum*	(36)
Anethum graveolens	Seeds	D-Carvone, anethole and 4-allylanisole	*Sclerotinia sclerotiorum*	(37)
Origanum dubium	Leaves and flowering tops	Carvacrol, linalool, p-cymene and γ-terpinene	*Sclerotinia sclerotiorum*	(38)
Rosmarinus officinalis	Aerial part	Camphor, α-pinene and 1,8-cineole	*Colletotrichum gloeosporioides*	(39)
Cinnamomum verum and *Thymus vulgaris* L. oil	Bark and leaves	Cinnamaldehyde, 2-Propenal, 3-phenyl-, trans-Cinnamic acid, 2-Propenoic acid, 3-phenyl-, α-Pinene	*Colletotrichum gloeosporioides*	(40)
Piper lanceaefolium	Leaves	Viridiforol, α-pinene and gurjunene	*Fusarium solani*	(41)
Cinnamomum zeylanicum and *Cymbopogon martinii*	Leaves	Geranial, eugenol and geraniol	*Fusarium verticillioides*	(42)

against *B. cinerea* (150 and 300 μL/L), whereas higher concentrations were needed for *R. stolonifer* (600 μL/L), indicating limited efficacy at lower doses (24).

Thymus vulgaris essential oil inhibited the mycelial growth of *Fusarium oxysporum* f.sp. *radicis-lycopersici* (FORL) at a concentration of 4 μL/petri via the agar dilution method (25). Turmeric EO inhibited the mycelial development and spore germination of *Aspergillus flavus*. While *in vivo* studies have suggested a potential inhibitory effect, the efficacy may vary due to environmental factors and interactions within plant tissue (26). *Melaleuca alternifolia* EO suppressed *Alternaria solani* and prevented early blight in tomato through direct antifungal activity and resistance mediated by peroxidase and phenylalanine ammonia-lyase defence mechanisms (27). The mycelial growth and conidial germination of *Alternaria alternata* were suppressed by Mentha EO at 40 μL/mL (28). These findings underscore the efficacy of essential oils as natural, sustainable antifungal agents capable of targeting multiple fungal pathogens while promoting plant defence responses.

Antibacterial activities of EOs against plant diseases

Bacteria cause plant diseases and major economic losses. Pathogenic prokaryotes can live in various environments, such as inside and outside the host plant. The development and growth of pathogenic bacteria can be controlled by essential oils and their compounds, which have antibacterial activity. The antibacterial properties of essential oils control a wide range of plant pathogens (43). The antibacterial activity of essential oils can be achieved in two ways: controlling bacterial growth (bacteriostatic) or destroying bacterial cells (bactericidal) (44). The antibacterial activity of essential oils is generally greater against gram-positive bacteria than against gram-negative bacteria, primarily due to the presence of an outer membrane in gram-negative bacteria that are rich in lipopolysaccharides (LPSs). This outer membrane, along with porins and efflux pumps, forms a complex barrier that limits the penetration of hydrophobic compounds such as essential oils (45). Different phytopathogens are affected by essential oils extracted from plants, as shown in Table 2.

In vitro studies indicated that *Dysphania ambrosioides* essential oil possesses antibacterial properties against several phytopathogenic bacteria, including *Erwinia amylovora*, *Pseudomonas syringae* pv. *tabaci*, *P. syringae* pv. *syringae* and *Agrobacterium tumefaciens.* This EO provided resistance to wildfire diseases caused by *P. syringae* pv. *tabaci* on tobacco. It also acts against *Agrobacterium tumefaciens*, which causes crown gall in tomatoes. The essential oil was effective against *P. syringae* pv. *tabaci*, *P. syringae* pv. *syringae* and *E. amylovora* at a concentration of 1000 μg/mL, demonstrating inhibitory effects (46). *Eryngium triquetrum* essential oil, containing 74.8 % falcarinol, effectively inhibited *Pectobacterium atrosepticum* (responsible for potato blackleg) and *Pseudomonas cichorii* (which affects lettuce, celery and chrysanthemum) under *in vitro* conditions (47). Thyme and suico essential oils control *Streptomyces scabiei*, causing potato common scab. Thyme EO (rich in thymol and o-cymene) and suico EO (containing dihydrotagetone and trans-tagetone) cause cell envelope damage in *S. scabiei* (48). *Pectobacterium betavasculorum* is a causal organism of sugar beet soft rot and vascular wilt disease. Bacterial activity was efficiently inhibited by the essential oils of *Pimpinella anisum* and *T. vulgaris* (49). These findings underline the potential of essential oils as eco-friendly alternatives to chemical bactericides, capable of targeting a range of important plant pathogens through diverse mechanisms.

Antiviral activities of EOs against plant diseases

Essential oils possess antiviral properties against plant viruses and show potential for managing plant virus infections, particularly under controlled conditions. They work through various mechanisms, including preventing viral replication, disrupting viral coat proteins and stimulating plant immune responses. As a result, essential oils offer a promising,

Table 2. Antibacterial activity of essential oils against bacteria

Essential oil extracted from plant	Plant parts used for extraction	Major compounds present	Target bacteria	Reference
Cymbopogon flexuosus	Leaves	Aromadendrene, linalyl anthranilate and caryophyllene	*Ralstonia solanacearum*, *Xanthomonas campestris*	(50)
Schinus molle	Aerial parts	Spathulenol, β-caryophyllene and caryophyllene oxide	*Xanthomonas citri*	(51)
Artemisia arborescens	Aerial parts	Trans-thujone and camphor	*Xanthomonas campestris* pv. *campestris* and *Pseudomonas syringae*	(52)
Carum carvi	Fruit	Carvone and limonene	*Xanthomonas campestris* pv. *vesicatoria*	(53)
Citrus bergamia	Peel	Linalyl acetate	*Xanthomonas campestris*	(54)
Croton grewioides Baill	Leaves	Eugenol, methyl eugenol and methyl chavicol.	*Xanthomonas campestris* pv. *campestris*	(55)
Melaleuca alternifolia	Aerial parts	Terpinen-4-ol	*Xanthomonas oryzae* pv. *oryzae*	(56)
Eryngium triquetrum	Aerial parts	Oxygenates falcarinol, byoctanal and nonanal	*Pectobacterium atrosepticum*, *Pseudomonas cichorii*	(47)
Mentha X *piperita*	Whole plant	Menthol and menthone	*Clavibacter michiganensis*, *Xanthomonas campestris*, *Pseudomonas savastanoi* and *P. syringae* pv. *phaseolicola*	(57)
Thymus vulgaris L. and *Tagetes minuta* L.	Aerial parts	o-Cymene, thymol, dihydrotagetone, verbenone and trans-tagetone	*Streptomyces scabiei*	(48)
Dysphania ambrosioides	Aerial parts	Ascaridole, α-terpinene, p cymene and thymol	*Agrobacterium tumefaciens*, *Pseudomonas syringae* pv. *tabaci*, *P. syringae* pv. *syringae* and *Erwinia amylovora*	(46)
Cinnamomum verum	Bark	Trans-cinnamaldehyde, salicylaldehyde and hydrocinnamaldehyde	*Agrobacterium tumefaciens*	(58)

sustainable and environmentally friendly approach for reducing viral transmission risk, primarily by deterring insect vectors; however, their effectiveness under field conditions is still under investigation, as they may require high concentrations, frequent applications and careful management to avoid phytotoxicity (10). The impacts of plant-derived essential oils on various plant viruses are presented in Table 3.

The essential oils derived from plants such as *T. vulgaris*, *Rosmarinus officinalis* and *Origanum vulgare* can effectively lower viral levels and strengthen plant defense mechanisms against viruses, including the tomato leaf curl New Delhi virus and Zucchini yellow mosaic virus. By activating the phenylalanine ammonia-lyase gene, which is essential for plant defense responses, these oils reduce the intensity of symptoms and the rate at which viruses replicate (59). Compounds such as carvacrol and thymol, which are found in *Satureja montana* essential oils, act against cucumber mosaic virus (CMV) and tobacco mosaic virus (TMV), often leading to a reduction in lesion numbers under certain conditions. This effect is typically dose dependent and influenced by the timing of application, with pretreatment frequently yielding stronger results. The broad-spectrum antiviral properties of essential oils are largely attributed to their diverse chemical compositions, particularly those of terpenes and phenolic compounds, which can disrupt viral integrity and inhibit replication (60).

The essential oil compounds can disrupt viral replication and reduce virus-induced damage in plants. For example, thyme (*T. vulgaris* L.) essential oil, which is rich in thymol, has demonstrated protective effects against CMV when it is applied before infection, although its effectiveness varies with the timing of application (61). The essential oil derived from *Micromeria croatica*, as well as its primary components β-caryophyllene and caryophyllene oxide, decreases viral infection in plants. When administered either before or at the time of infection with CMV, the oil and its key compounds reduced the effects of the virus on both localized and widespread areas of the plant. Additionally, essential oils influence the expression of the alternative oxidase gene (*aox*) in *Arabidopsis* plants infected with the virus (62). Tea tree and lime peel essential oils effectively suppressed TMV replication and enhanced the plant's innate defense responses through the upregulation of key enzymatic activities, including phenylalanine ammonia-lyase (PAL) and peroxidase (POD) (63). These findings highlight the potential of essential oils as antiviral agents capable of inhibiting plant viruses and enhancing plant innate immune responses.

Bioactivity of essential oils against plant pathogens

Cell membrane disruption

Peptidoglycans are essential structural components of bacterial cell walls, maintaining cell shape and integrity in both gram-

Table 3. Antiviral activity of essential oils against viruses

Essential oil extracted from plant	Plant parts used for extraction	Major compounds present	Target virus	Reference
Melaleuca alternifolia oil and *Citrus latifolia* oil	Leaves and peel	Terpinene-4-ol and Transisolimonene	Tobacco mosaic virus (TMV)	(63)
Origanum vulgare L. subsp. *hirtum* and *Thymus vulgaris* L.	Aerial parts	Carvacrol and thymol	Cucumber mosaic virus	(61)
Origanum vulgare, *Thymus vulgaris* and *Rosmarinus officinalis*	Aerial parts	Fenchone	Zucchini yellow mosaic virus or tomato leaf curl New Delhi virus	(59)
Hypericum perforatum ssp. *veronense*	Aerial parts	β-Caryophyllene and germacrene D	Tobacco mosaic virus	(64)

positive and gram-negative bacteria. However, the two groups differ significantly in their cell wall architecture. Gram-positive bacteria have a thick peptidoglycan layer, while gram-negative bacteria possess a thinner peptidoglycan layer and an outer membrane rich in lipids. This outer membrane contains lipopolysaccharides and porins, forming a selective barrier that regulates the entry and exit of compounds (65, 66). EOs exhibit activity against both gram-positive and gram-negative bacteria, although gram-negative bacteria are generally more resistant due to their outer membrane. The high phenolic content of essential oils (EOs), such as carvacrol, eugenol and thymol, is the primary cause of cytoplasmic membrane rupture, which results in the passive flux of protons and other ions (67). For example, *Origanum compactum* EO has been shown to impact the membrane integrity of both gram-positive and gram-negative bacteria. Compared with gram-negative bacteria, gram-positive bacteria are generally more susceptible to the bactericidal impact of finger citron (*Citrus medica* L. var. *sarcodactylis*) EO because gram-negative bacteria exhibit notable resistance to hydrophobic compounds. When bacteria are exposed to essential oils, their protective outer membrane becomes damaged. This damage causes bacteria to leak ions and proteins, causing severe damage. Furthermore, the essential oil increases the porosity of the bacterial membrane, making it weaker and more permeable. Ultimately, essential oils weaken bacterial membranes, leading to the leakage of cell components and increasing their vulnerability to external conditions effects are visually demonstrated in Fig. 2 (68, 69).

Essential oils from *Lippia gracilis*, which are rich in thymol and carvacrol, exhibit potent antibacterial activity against *Xanthomonas campestris* pv. *campestris* (Xcc), causing black rot in Brassicaceae. Both thymol and carvacrol demonstrated potent activity, with MIC and MBC values of 0.25 mg/mL (70). Similarly, the essential oils from *Macleaya cordata* R. Br. leaves disrupt the cell membrane of *Ralstonia solanacearum*, increasing its permeability. This causes leakage of electrolytes, proteins and sugars, ultimately leading to cell breakdown and death. As a result, the number of viable bacteria decreases (71).

Plant essential oils can inhibit pathogenic fungi through multiple mechanisms, including disrupting cell membranes and interfering with cell wall synthesis, these mechanisms differ from their antibacterial activity (58). Rosemary essential oil (REO) is composed of 1,8-cineole (52.2 %), camphor (15.2 %) and α-pinene (12.4 %), which suppresses the growth of *Fusarium verticillioides* by 150 µg/mL. At 300 µg/mL, REO highly inhibits the fungus by disrupting its cell wall and leading to leakage of its contents. Therefore, REO is a potent antifungal agent (72). Lemon citrus essential oil (EO) treatment disrupted the permeability of the *Penicillium italicum* cell membrane, leading to leakage of intracellular electrolyte ions from the mycelium. Additionally, EO-induced lipid peroxidation in *P. italicum* filament membranes may contribute to cell membrane damage (73). The essential oil of *Tetradium glabrifolium* fruit can damage a pathogen's cell membrane, which can lead to *Phytophthora capsici* intercellular contents leaking out of the cell (31).

Induction of oxidative stress

Reactive oxygen species (ROS) are highly reactive molecules containing oxygen that are generated primarily as byproducts of normal metabolic processes. However, their levels can significantly increase under conditions of cellular stress. ROS play a dual role in biological systems: at moderate levels, they are involved in cell signalling and homeostasis, but at elevated levels, they can cause oxidative stress, leading to damage to cellular components such as lipids, proteins and DNA. One of the proposed mechanisms by which essential oils exert antimicrobial effects is the induction of reactive oxygen species (ROS) accumulation in certain pathogens, although other mechanisms, such as membrane disruption, enzyme inhibition and metabolic interference, may also contribute. This accumulation disrupts the redox balance within the cells, leading to oxidative stress. Reactive oxygen species (ROS), including superoxide anions (O_2^-), hydrogen peroxide (H_2O_2) and hydroxyl radicals (•OH), are generated in cells and can lead to oxidative stress when present in excess. However, ROS are not uniformly harmful; for example, H_2O_2 at low concentrations plays a key role in cell signalling. The overproduction of these ROS in pathogens leads to oxidative stress, which can impair cellular functions, damage essential biomolecules and ultimately result in cell death (Fig. 3). This mechanism highlights the potential of essential oils as natural antimicrobial agents by leveraging the vulnerability of pathogens to oxidative stress (74, 75).

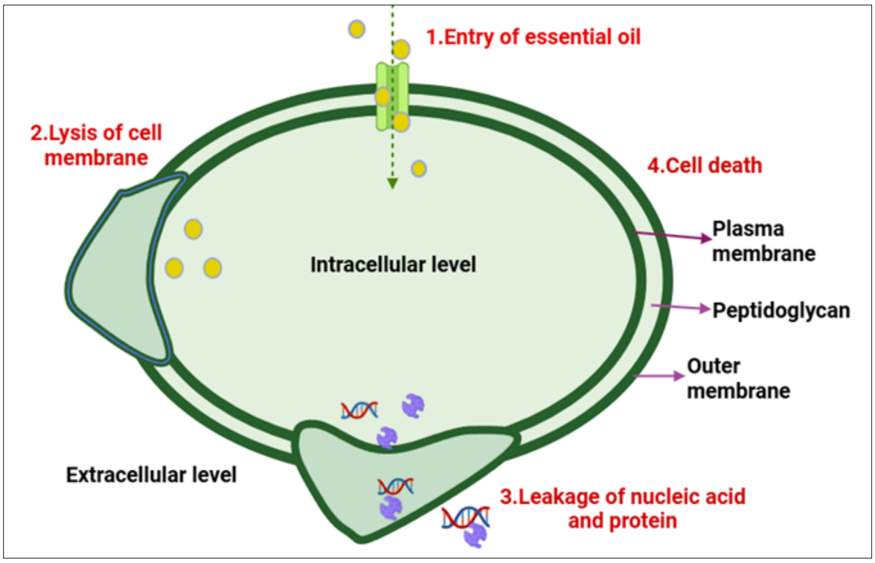

Fig. 2. Cell membrane disruption. Essential oil entry into bacterial cells. Membrane lysis causes structural damage. Leakage of nucleic acids and proteins from the cell. Cell death due to membrane disruption.

ROS generation contributes to the antibacterial activity of some essential oils. To illustrate, *Rosmarinus officinalis* and *Myrtus communis* essential oils affect bacteria by generating ROS and affecting antioxidation enzymes (76). Tea tree oil EO exhibits antibacterial activity against *Xanthomonas oryzae* pv. *oryzae* (Xoo), which is responsible for bacterial leaf blight (BLB) in rice. Its mode of action involves stimulating the production of reactive oxygen species (ROS), which induce oxidative stress. This stress, in turn, leads to bacterial damage, ultimately inhibiting the growth and survival of the pathogen (56).

The antifungal activity of certain essential oils is attributed to the generation of ROS. For example, *Cinnamomum verum* and *Cymbopogon citratus* essential oils inhibited *Rhizoctonia solani* 100 % at a concentration of 5 mg/paper disc. They have key constituents, including trans-cinnamaldehyde, geranial, neral and salicylaldehyde and exhibit strong antifungal activity by inducing ROS generation (58). The cell membranes of *Rhizoctonia solani* may have been damaged by the production of intracellular ROS by thymol and carvacrol, which may have resulted in cell death (77). *Portulaca oleracea* essential oil treatment induced oxidative stress and reactive oxygen species (ROS) accumulation in *Pestalotiopsis neglecta*, increasing lipid peroxidation in cell membranes. This led to severe membrane damage and leakage of the cell contents (78). *Ligusticum chuanxiong* essential oil (LCEO) demonstrated the strongest antifungal activity (EC50: 81.79 mg/L), with butylidenephthalide as its main active component. It suppressed mycelial growth, sclerotia formation and germination while lowering oxalic acid and polygalacturonase levels, weakening fungal infection (79). Seed coating with *Artemisia absinthium* essential oil (AEO) results in the generation of ROS in the outer layer of seeds without affecting seed or plant growth when *Fusarium oxysporum* sp. *oxysporum radicis lycopersici* affects the tomato crop (80). This oxidative stress-based mechanism demonstrates the promising potential of essential oils as natural antimicrobial agents by exploiting the inherent vulnerability of pathogens to redox imbalance (Fig. 3).

Mitochondrial function disruption

Mitochondria are the primary sites for energy production, where the tricarboxylic acid (TCA) cycle drives ATP generation through oxidative processes. This cycle is central to metabolism, providing energy, biosynthetic intermediates and redox regulation. Mitochondrial dehydrogenases catalyze key reactions, transferring electrons to the electron transport chain (ETC) for ATP synthesis via oxidative phosphorylation. Certain essential oils (EOs) have been shown to disrupt mitochondrial function by inhibiting mitochondrial dehydrogenases, thereby impairing the TCA cycle and ATP synthesis in specific pathogens. The resulting energy deficit impairs ATP-dependent cellular functions, contributing to the antimicrobial or cytotoxic activity of EOs (81, 82).

Turmeric EO may suppress mitochondrial dehydrogenases in *Aspergillus flavus*, disrupting the TCA cycle and ATP production. Inhibition of mitochondrial ATPase depletes intracellular ATP, which in turn impairs metabolic processes and may contribute to reduced plasma membrane ATPase activity and membrane dysfunction, alongside other cellular stress factors. This leads to structural and permeability damage to the cell membrane, ultimately interfering with the normal metabolism of the fungus (26). *Acorus calamus* EO contains a β-asarone compound that has strong antifungal effects on *Aspergillus niger* by affecting mitochondrial dehydrogenase activity and the plasma membrane ergosterol concentration, which causes cell death (83). Tea tree essential oil disrupts the mitochondria of *Botrytis cinerea*, altering their structure and increasing membrane permeability. At a concentration of 2 ml/L, TTO causes significant mitochondrial damage, resulting in ATP depletion and reduced activity of key TCA cycle enzymes, such as malic dehydrogenase, succinate dehydrogenase and ATPase (84). Dill seeds essential oil combats *Aspergillus flavus* by disrupting its mitochondria. It inhibits ergosterol synthesis, alters the cell structure and reduces ATPase and dehydrogenase enzyme activity (85). Citral, a compound found in essential oils, damages the mitochondria of *Penicillium digitatum*, leading to structural disruption and ATP leakage. However, fungi may activate compensatory mechanisms to mitigate mitochondrial stress, which could influence the overall efficacy of citral-induced cell death. It also interferes with the TCA cycle by lowering the activity of essential enzymes such as citrate synthetase, isocitrate dehydrogenase and succinate dehydrogenase. This disruption affects mitochondrial membrane permeability and energy metabolism, contributing to its antifungal action (86). This activity

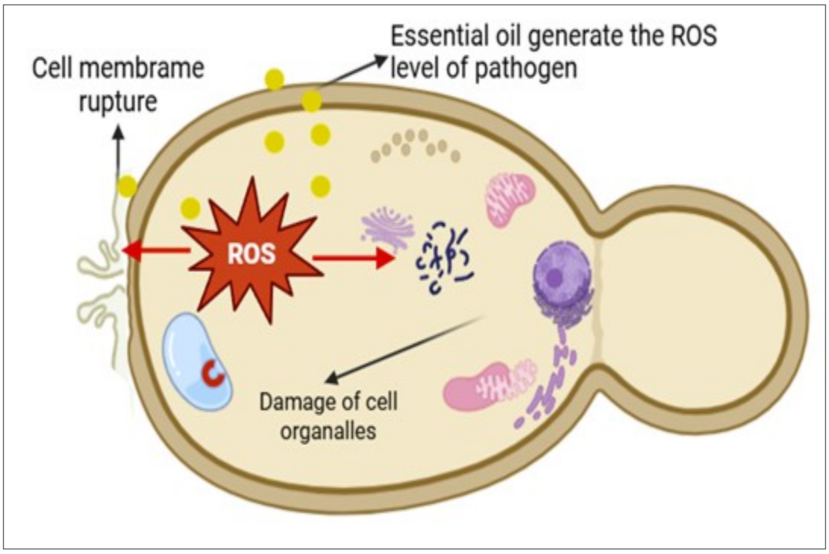

Fig. 3. Generation of ROS. Essential oils increase reactive oxygen species (ROS) levels in pathogens. ROS cause membrane rupture, leading to structural damage. Damage to cell organelles disrupts cellular functions. Cell death due to oxidative stress and organelle dysfunction.

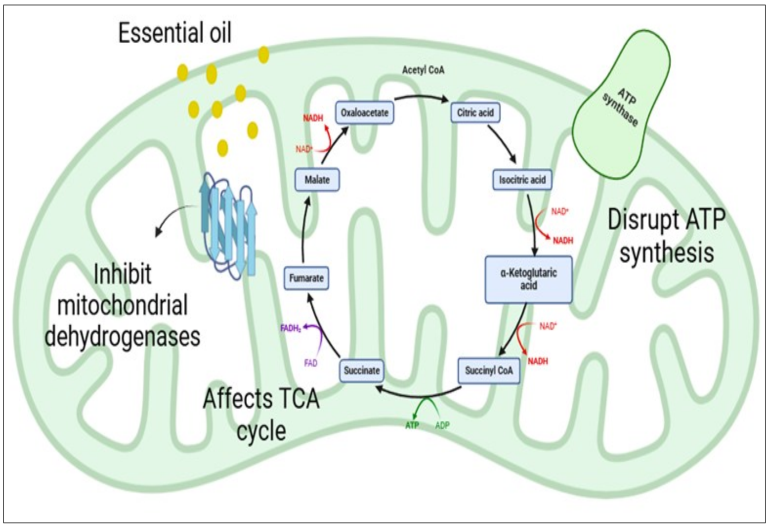

Fig. 4. Disruption of mitochondrial function. Essential oils inhibit mitochondrial dehydrogenases, affecting enzyme activity. Disrupts the TCA cycle, leading to impaired energy production. Reducing ATP synthesis affects cellular metabolism. Overall, mitochondrial dysfunction leads to cell damage and death.

is shown in Fig. 4.

Inhibition of spore germination

Essential oils (EOs) are plant-derived natural compounds with strong antimicrobial properties. One of the mechanisms of their action is inhibiting spore germination in bacteria and fungi. Spores are resilient structures that enable microorganisms to survive harsh conditions and their germination is crucial for pathogen proliferation. Some essential oils disrupt spore germination through multiple mechanisms, including damaging structural integrity, interfering with enzymatic activity, altering membrane permeability and modulating cellular signalling or metabolic processes. This prevents spores from transitioning into active, growing cells, effectively suppressing the growth and spread of spore-forming pathogens (87). *Syzygium aromaticum* oil inhibited the mycelial development and spore germination of *Fusarium oxysporum* f. sp. *lycopersici* at 125 ppm under *in vitro* conditions (88). *Tetradium glabrifolium* fruit essential oil effectively suppresses *Phytophthora capsici* spore production and germination. At concentrations of 2.5-10 mg/L, it reduced the number of spores by up to 94.34 %, with complete inhibition at 20 mg/L. Spore germination was delayed and did not reach 100 % at 20 mg/L, highlighting the potent antifungal activity of TFO (31). *Artemisia scoparia* essential oil showed the strongest inhibition, completely stopping the germination of *Colletotrichum gloeosporioides* conidia at a concentration of 10 μL/mL (89). An increase in *Zingiber officinale* essential oil (EO) content reduced sporangia and zoospore germination. The minimum inhibitory concentration for zoospores and sporangia was 625 ppm. Citral and 3,7-dimethyl-1,2,6-octadienal are major components of *Z. officinale* EO and are suspected to contribute to the observed spore deformities; their individual effects were not tested in this study (18). *Sanguinaria canadensis* EO exhibited the most potent antifungal activity, mainly due to its key components: D-limonene, β-myrcene and β-linalool. It effectively inhibited spore germination at concentrations ranging from 800-1000 μg/mL (90). *Litsea cubeba* essential oil (LCEO) successfully inhibited the growth of *Colletotrichum scovillei* spores, the fungus responsible for pepper anthracnose, at a minimum concentration of 0.60 mg/mL. Microscopic observation revealed that treated spores appeared deformed, shrivelled and collapsed, indicating

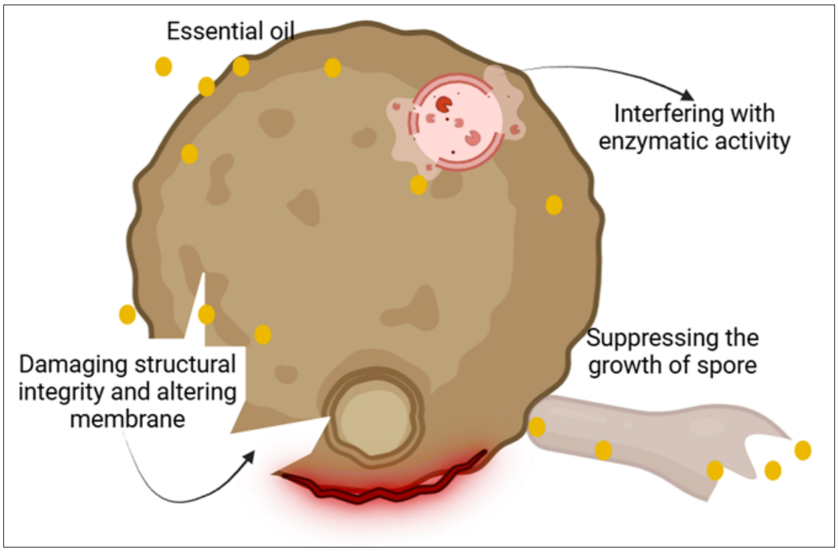

Fig. 5. Suppression of spore germination. Essential oils damage structural integrity and alter the fungal membrane. Interference with enzymatic activity disrupts metabolic functions. This fungus suppresses spore growth, preventing fungal reproduction. Leads to fungal inhibition and cell death.

that LCEO causes physical damage and disrupts their structure (91). These findings are summarized in Fig. 5.

Effects on quorum sensing and biofilm formation

The quorum-sensing (QS) system regulates bacterial communication, coordinating processes such as niche invasion, defense, mobility and biofilm formation. Biofilms are dense bacterial communities encased in a protective exopolymer matrix, enabling surface adhesion and resistance to harsh conditions. Essential oils (EOs) can interfere with quorum sensing (QS) by disrupting the production of acyl-homoserine lactones (AHLs), the key signalling molecules in this process. Through this mechanism, EOs are capable of inhibiting biofilm formation and may weaken established biofilms. However, fully eliminating mature biofilms is difficult and often requires a combination of treatment strategies due to their robust resistance (92-94). Several metabolites present in essential oils have quorum-sensing properties. The thymol-carvacrol-chemotypes (I and II) present in *Lippia origanoide* have antiquorum-sensing properties against phytopathogenic bacteria (95). The oils from cinnamon bark, bay, clove and pimento berries presented the strongest antibiofilm properties because they interfered with the quorum-sensing activity of bacteria (96). *Origanum vulgare* and *T. vulgaris* restrict biofilm formation in *P. syringae* (97). *Xanthomonas oryzae* pv. *oryzae* (Xoo) uses quorum sensing (QS) to regulate its virulence and biofilm formation. Treatment with 500 ppm thyme oil significantly reduces bacterial motility (swimming and swarming) and exopolysaccharide production, effects that may be partially due to QS disruption by thymol, its active component, but could also involve general antimicrobial mechanisms such as membrane damage (98). This activity is shown in Fig. 6.

Conclusion

This study revealed that essential oils show strong potential as alternatives to synthetic fungicides because of their antibacterial, antiviral, antifungal, insecticidal and repellent properties. However, their practical application is often limited by lower stability, higher volatility and variable efficacy, which must be addressed through improved formulation strategies to ensure consistent performance. A treatment based on a natural substance, such as an essential oil with safe qualities favourable to human health and the environment. While not all essential oils are inherently safe, those chosen for this application have been evaluated for their safety and efficacy. A treatment based on a natural substance, such as essential oil, with safe qualities favourable to human health and the environment. This review also calls for more research and development to maximize the use of EOs in plant disease management and improve their application in various agricultural practices. However, to ensure their constant effectiveness, issues such as chemical composition variations and a lack of standardization must be addressed. To determine their role among current businesses, future studies should focus on elucidating mechanisms of action, optimizing delivery methods and exploring practical applications while addressing economic, regulatory and technological challenges that hinder large-scale implementation. To fully utilize essential oils and encourage their safe and sustainable use, a multidisciplinary approach is needed. A multidisciplinary approach involving plant pathologists, chemists, agronomists and toxicologists is essential to promote the sustainable and safe use of essential oils in agriculture.

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Authors' contributions

LP formulated the manuscript, contributed by developing ideas, reviewing the manuscript, VS assisted in data collection, AK correction and grammar check, JS helped in summarizing and revising the manuscript and AG contributed to summarizing.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of

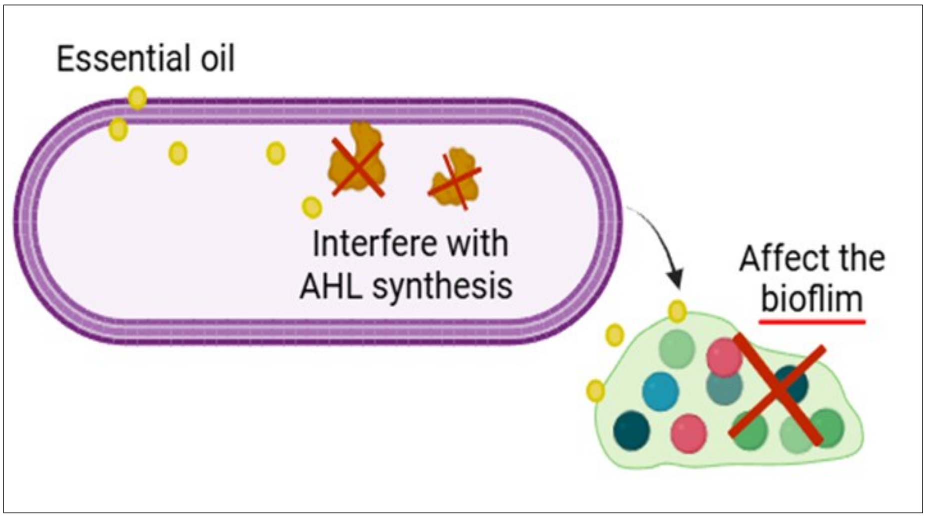

Fig. 6. Inhibition of quorum sensing and biofilm formation. Essential oils interfere with AHL synthesis, disrupting quorum sensing. Prevents biofilm formation, weakening bacterial protection. Reduced bacterial communication affects bacterial survival and virulence. This leads to increased bacterial susceptibility to treatments.

interests to declare.

Ethical issues: None

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