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Potential of essential oils in control of pathogenic plant viruses

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ABSTRACT

Essential oils are complex mixtures of aromatic compounds produced through secondary metabolism in plants. They contain various substances such as hydrocarbons, alcohols, ketones, aldehydes, organic acids, and phenols. These oils have been used in medicine since ancient civilisations, including Egypt and China, as recorded in historical documents. Apart from their biological and ecological functions, essential oils also display antimicrobial, antiviral, and insecticidal properties. This paper focuses on the antiviral effects of essential oils. Plant viruses pose a significant threat to agricultural crops, as no effective treatments are currently available, leading to considerable economic losses. Numerous *in vitro* studies have shown that essential oils and their compounds from various medicinal and aromatic plants can act as powerful antiviral and virucidal agents. They work by inhibiting viral replication at different stages of the infection cycle in DNA and RNA viruses across different host cells. Essential oils are gaining attention as potential novel drugs with antimicrobial and antiviral properties. In plant protection, essential oils are recognised for their antiviral, antimycotic, and antiparasitic effects, and are considered promising for developing safe antimicrobial agents.

Keywords:plants, essential oils, components, antiviral properties, biopesticides

ИЗВОД

Етерична уља су сложене мешавине ароматичних једињења произведених кроз секундарни метаболизам у биљкама. Садрже различите супстанце попут угљоводоника, алкохола, кетона, алдехида, органских киселина и фенола. Ова уља се користе у медицини још од древних цивилизација, укључујући Египат и Кину, што је забележено у историјским документима. Поред својих биолошких и еколошких функција, етерична уља такође показују антимикробна, антивирусна и инсектицидна својства. Овај рад се фокусира на антивирусне ефекте етеричних уља. Биљни вируси представљају значајну претњу пољопривредним усевима, јер тренутно не постоје ефикасни третмани, што доводи до значајних економских губитака. Бројна ин витро истраживања су показала да етерична уља и њихови састојци из различитих лековитих и ароматичних биљака могу деловати као снажни антивирусни агенси. Делују тако што инхибирају виралну репликацију у различитим фазама циклуса инфекције у ДНК и РНК вирусима кроз различите врсте домаћинских ћелија. Етерична уља привлаче пажњу као потенцијални нови лекови са антимикробним и антивирусним својствима. У заштити биљака, етерична уља су препозната по својим антивирусним, антигљивичним и антипаразитским ефектима, те се сматрају обећавајућима за развој сигурних антимикробних агенаса.

Кључне речи: биљке, етерична уља, састојци, антивирусна својства, биопестициди

1. Introduction

Organic agriculture aims to introduce an ecological dimension into agricultural production, i.e., managing agriculture while respecting the principles of environmental conservation. By eliminating the use of all synthetic plant protection products and adopting crop cultivation technologies based on organic production principles, it contributes to the preservation of soil fertility, its physical and chemical properties, stimulates soil microbiological activity, and results in higher-quality products (Golijan Pantović et al., 2023; Dimitrijević et al., 2024).

The plant world is characterised by a large number of species that show potential for use in food, medicinal purposesand agricultural applications (Popović et al., 2013; Božović et al., 2018; Bojović et al., 2019; Rakašćan et al., 2021; Jovović et al., 2021; Lakić et al., 2022). Depending on which groups of biomolecules they contain, medicinal plants can belong to: plants with alkaloids, plants with phenolic compounds, plants with sulphur compounds, plants characterised by the presence of essential oils, etc. Essential oils (EO) are mixtures of various compounds that capture the aromatic essence of plants. They are found in over 17,500 plant species, particularly in families such as *Zingiberaceae, Poaceae, Apiaceae, Umbelliferae, Asteraceae, Lamiaceae, Rutaceae, Compositae, Lauraceae, Cupressaceae, Acoraceae, Rosaceae, Oleaceae, Myristicaceae, Myrtaceae*, and others (Ebadollahi, 2013; Baser and Buchbauer, 2015; Nieto, 2017; Butnariu and Sarac, 2018). Despite their widespread presence, the bioactivities of many essential oils are still not fully understood. There are approximately 3,000 essential oils derived from around 2,000 plants used in various applications (Sköld et al., 2006; Raut and Karuppayil, 2014).

Several factors influence the quality and quantity of essential oils in plants, including the plant organ, chemotypes, methods of extraction, the plant growth stage, age, soil type and texture, and climate. The ecological roles of essential oils have been well studied and include interactions with animals for repelling predators, inhibiting plant germination through allelopathy, and attracting pollinating insects (Harrawijn et al., 2001). Essential oils are known for their strong antimicrobial properties, making them valuable in cosmetics as natural preservatives. They also play a significant role in agriculture as insecticides, in food technology as flavours and preservatives, in perfumery, and in medicine as healing agents and in aromatherapy (Fernández-López and Viuda-Martos, 2018). Over the past few decades, essential oils have been extensively researched for their potential benefits across various biological systems (Shaaban et al., 2012). Essential oils exhibit a remarkable range of bioactivities, highlighting their potential in diverse fields.

In recent decades, there has been a growing interest in the biological activity of essential oils, which demonstrate antiviral, antifungal, and antiparasitic properties (Golijan Pantović et al., 2024a). These characteristics make essential oils promising candidates for the development of safe antimicrobial agents (Taglienti et al., 2022; Šovljanski et al., 2024). Plant-derived essential oils (plant-EOs) are gaining attention due to the global trend toward sustainable agricultural practices, especially in organic farming (Frabboni et al., 2019; Sumalan et al., 2019; Rawat, 2021; Popović et al., 2021; Chang et al., 2022; Golijan, 2022; Golijan and Sečanski, 2022; Golijan Pantović et al., 2022; Golijan Pantović and Sečanski, 2023; Golijan Pantović and Gordanić, 2023; Golijan Pantović et al., 2023a; Šarčević-Todosijević et al., 2019 a,b; Šarčević-Todosijević et al., 2023a, 2023b; Gordanić et al., 2023; Šarčević-Todosijević et al., 2024a, 2024b, 2024c, 2024d; Arslan and Bulut, 2024a, b; Golijan Pantović, 2025).

Plant viruses are a major concern for agricultural crops because there is no available treatment for virus control, leading to significant economic losses worldwide (Lecoq and Katis, 2014). Unlike bacterial and fungal infections, which can be treated with compounds of natural or synthetic origin, no curative treatments exist for plant viruses (Golijan Pantović et al., 2023b). Therefore, most defence strategies focus on prevention, such as using certified, pathogen-free propagation materials and controlling insect vectors (Golino et al., 2017; Kolašinac et al., 2017; Golijan and Marković, 2018; Golijan Pantović et al., 2024b). Other control measures include the use of virus-resistant plant varieties developed through breeding (Martín-Hernández and Picó, 2020; Sečanski et al., 2022). Additionally, approaches like engineered mild virus strains for cross-protection or transgenic plants show promise, although these methods are currently limited to a few plant/virus species (Hamim et al., 2018).

The use of plant essential oils (EOs) and their active components for direct or indirect antiviral or virucidal effects, along with insect pest control and management, is an intriguing approach. Many studies have focused on medicinal human and animal viruses. This knowledge can be further documented, developed, and applied to plant pathogenic viruses and insect vectors, facilitating data-driven agriculture and management (Sarowska et al., 2021). Currently, biopesticides derived from plant essential oils are evaluated and accepted in many countries through public or specific regulations, which assess the active compounds and substances. Appropriate extraction methods are crucial for producing natural products, as they play a key role in determining the biological activities of plant EOs (Phatthalung and Tangkananond, 2022).

The goal of this work was to describe the potential of using essential oils in the control of plant viruses.

2. Localisation of essential oils

Essential oils are present in nearly all plant organs, particularly in flowering parts, but they can also be found in roots, rhizomes, bark, leaves, fruits, and seeds. The composition of essential oils varies over organs of the same plant species, depending on environmental conditions. For example, in warmer climates, the essential oil content tends to be higher (Gorunović and Lukić, 2001). Essential oils can be located in undifferentiated cells or in specialised, larger cells called idioblasts (e.g., in Lauraceae and Zingiberaceae). They are predominantly found in secretory organs (Gorunović and Lukić, 2001), which include:

1. **Glands** – where essential oils accumulate beneath the cuticle, found in plants from the Lamiaceae and Asteraceae families.
2. **Secretory schizogenous channels** – formed by the repeated division of a single cell and the separation of cells, common in the Myrtaceae family.
3. **Secretory channels** – where the secretory products also form resins, typical of the Apiaceae family.

Essential oil synthesis occurs in the secretory cells of the epithelium, and the oils are secreted into specific intercellular spaces (lumen or lacuna). The lumen of channels and cavities can be formed in three ways:

1. **Schizogenous** – by splitting the cell walls of adjacent cells, with a merocrine secretion process.
2. **Lysigenous** – by the autolytic rupture of certain cells, with a holocrine secretion process.

Schizo-lysigenous – a combination of the previous two processes (Jančić et al., 1995).

3. Composition of essentials oils

Essential oils (EOs) are highly complex mixtures, typically consisting of 60 to 300 nonpolar and semipolar lipophilic components of low molecular weight, with two or three major compounds dominating. These compounds include terpenoids, straight-chain compounds without side chains, aromatic and phenolic components, and sulphured derivatives (Masango, 2005; Arshad et al., 2014). The primary volatile constituents in essential oils are classified into terpenoids and polypropanoids (Andrade et al., 2011; Sangwan et al., 2001).

The taste and aromas of essential oils are significantly influenced by factors such as the place of plant origin, climatic conditions, plant species (Martinez et al., 2006), season of harvest, geographical location, methods of drying, and the techniques used in extraction (Hussain et al., 2008; Dima and Dima, 2015).

As previously mentioned, terpenes are secondary metabolites formed through the combination of isoprene units (C5), which is 2-methyl-1,3-butadiene, following a head-to-tail model. Different combinations of isoprene units lead to the formation of various terpene groups, both functionally and structurally (Rubio et al., 2013). These compounds are classified based on the number of isoprene units in their structural formula $(C5H8)n$, where "n" represents the number of linked isoprene units. For example, two isoprene units form monoterpenes (C10H16), while other combinations produce diterpenes (C20), triterpenes (C30), tetraterpenes (C40), and other variations such as hemiterpenes (C5) and sesquiterpenes (C15).

Monoterpenes, diterpenes, and sesquiterpenes are the primary groups of terpenes found in spices and herbs (Table 1), and they possess notable biological activities (Eslahi et al., 2017).

Monoterpenes are characterised by a wide range of structures, including monocyclic, bicyclic, and acyclic components, and they contain various organic functional groups. These include hydrocarbons such as camphene, p-cymene, and myrcene; alcohols such as borneol, menthol, and linalool; aldehydes such as citronellal and geranial; ketones like camphor, carvone, and pulegone; esters such as citronellyl acetate, linalyl acetate, and menthyl; ethers like 1,8-cineole and menthofurane; peroxides like ascaridole; and phenols such as thymol and carvacrol (Pavela, 2015).

Sesquiterpenes, formed by combining three isoprene units (C15), undergo chain extension and increased cyclisation, which leads to a wide variety of structures. Compared to monoterpenes, sesquiterpenes have similar structures but are more complex and diverse. They include:

1. **Hydrocarbons**: β-bisabolene, β-caryophyllene, azulene, cadinenes, logifolene, elemenes, curcumenes, zingiberene, and farnesenes.
2. **Alcohols**: Cedrol, bisabolol, β-nerolidol, β-santalol, farnesol, patchoulol, carotol, and viridiflorol.
3. **Ketones**: Nootkatone, germacrone, cis-β-vetinone, longipinan-2,7-dione, and turmerones.
4. **Epoxides**: Caryophyllene oxide and humulene epoxides (Eslahi et al., 2017).

Aromatic compounds are less commonly found than terpenes, but they also contribute to the characteristic aromas and properties of various plants (Kulić and Đukić, 2003). These compounds include alcohols (such as cinnamic alcohol), aldehydes (like cinnamaldehyde), phenols (such as chavicol and eugenol), methoxy compounds (including methyleugenol, elemicine, estragole, and anethole), and methylene dioxy derivatives (like safrole, myristine, and apiole) (Grayson, 2000).

Table 1.
Monoterpenes, sesquiterpenes and aromatic compounds in different plants

Monoterpenes
Cannabis, orange, rosemary, angelica, bay leaves, thyme, celery, parsley, ylang–ylang, laurel, hops, mugwort, mint, tea tree, wormwood, bergamot and sweet basil
Sesquiterpenes
Lemon, bergamot, mint, angelica, coriander, celery, eucalyptus, caraway, citronella, juniper, geranium, lavender, lavandin, mandarin, lemongrass, peppermint, orange, pine, petitgrain, sage, rosemary and thyme
Aromatic compounds
Anise, nutmeg, clove, tobacco, parsley, fennel, star anise, sassafras, tarragon and some other botanical groups (*Lamiaceae, Apiaceae, Rutaceae, Myrtaceae*)

Source: Grayson (2000), Bakkali et al. (2008), Kulić et al. (2008), Pavela (2015)

4. Biosynthesis of essential oils

The biosynthesis of mono-, sesqui-, and diterpenes occurs through the linkage of isoprene units in a (1→4)pattern, known as the "head-tail" linkage, which is asymmetric. For tri- and tetraterpenes, biosynthesis involves dimerisationwith a (4→4) linkage, known as the "tail-tail" linkage, which is symmetric. Figure 1 illustrates the biosynthesis pathways of major volatile organic compounds.

The biosynthesis process of terpenes begins with two molecules of acetyl-CoA, which, in the presence of ketoacylthiolase**,** form acetoacetyl-CoA. When another acetyl-CoA molecule is added, under the influence of HMG-CoA synthase (hydroxy-methyl-glutaryl-CoA synthase), (3S)-3-hydroxy-3-methylglutaryl-CoA (HMG-CoA) is formed. The CoA residue is then removed and, with the aid of NADPH (nicotinamide adenine dinucleotide phosphate coenzyme) and HMG-CoA reductase, mevalonic acid (MVK) is formed. Mevalonic acid is converted into monophosphate with the help of ATP (adenosine triphosphate) and MVK kinase, followed by the conversion into pyrophosphateusing another ATP molecule and MVK-phosphokinase. The tertiary hydroxyl group is phosphorylated with the help of an additional ATP molecule. Finally, MVKPP decarboxylase facilitates the elimination of phosphoric acid and carbon dioxide, resulting in the formation of isopentenyl pyrophosphate (IPP). IPP, in the presence of IPP isomerase, reaches an equilibrium with 3-dimethylallyl pyrophosphate (DMAPP). Isopentenyl pyrophosphate (IPP) and 3,3-dimethylallyl pyrophosphate (DMAPP) are the fundamental biogenetic isoprene units of all terpenes. When IPP and DMAPP condense, they form geranyl pyrophosphate (GPP), which contains 10 carbon atoms. GPP is the direct precursor to all monoterpenes and plays a crucial role in the biosynthesis of all higher terpenes. The biosynthesis of monoterpenes begins when GPP is converted into the cis-isomer nerol, which readily undergoes cyclisation to form carbocation. Through subsequent rearrangement and oxidation reactions, a variety of other monoterpenes are produced (Matejić, 2013).

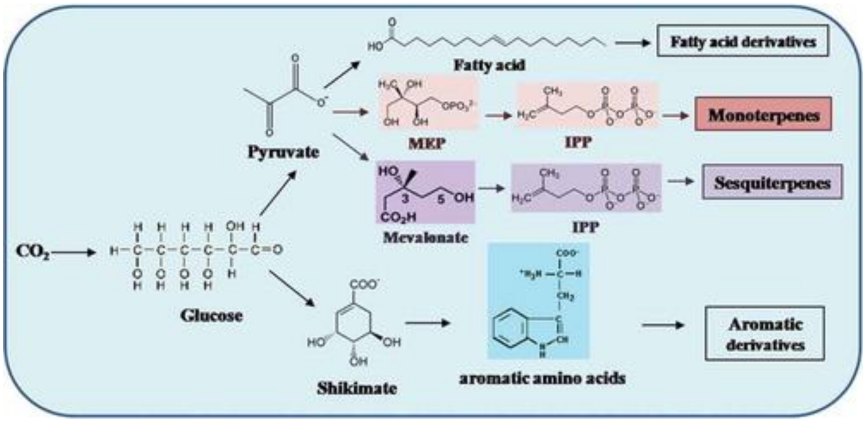

Figure 1. Biosynthesis pathways of major volatile organic compounds (MEP, 2-methyl-erythritol-4- phosphate; IPP, isopentyl pyrophosphate).
Source: Rehman et al. (2015)

When geranyl pyrophosphate (GPP) condenses with another molecule of isopentenyl pyrophosphate (IPP) in the presence of prenyltransferase, it forms farnesyl pyrophosphate (FPP, C15), the precursor for all sesquiterpenes**.** For diterpenes, the precursor is geranylgeranyl pyrophosphate (GGPP, C20), which is formed by adding an IPP molecule to FPP or by condensing two molecules of GPP. Further dimerisation of FPP leads to the formation of squalene (C30)**,** the immediate precursor for the biosynthesis of all terpenes (Matejić, 2013).

5. Antiviral activity of EO and the mode of action

5.1. Multifunctional roles of essential oils (EOs): Allelopathy, adaptation to abiotic stresses and systemic acquired resistance (SAR)

Hudson (1990) highlighted that many components extracted from higher plants exhibit antiviral activity. These components include tannins**,** flavones**,** and alkaloids, which have demonstrated in vitro effectiveness against a variety of viruses. Phytochemicals responsible for these antiviral effects encompass a wide array of compounds, such as saponins**,** flavonoids**,** alkaloids**,** terpenoids**,** furyl compounds**,** polyphenolics**,** sulphides**,** thiophenes**,** lignans**,** coumarins, as well as peptides and proteins. Many of these phytochemicals act through overlapping and complementary mechanisms, contributing to antiviral activity. Their modes of action include preventing the formation of viral DNA or RNA, or inhibiting the replication of viruses at different stages of their life cycle (Iftikhar et al., 2013).

Additionally, Sharifi-Rad et al. (2017) emphasised the multifunctional roles of active essential oils (EOs)**.** These roles include allelopathy, adaptation to abiotic stresses, signalling among plants (intra- and inter-plant communication), and direct defence against herbivores and pathogens, as well as indirect defence mechanisms. Plant EOs also exhibit important hydrophobic properties**,** such as surface tension, contact angle value, droplet volumes, and lubricating abilities, which can affect the external surface properties of viral hosts, potentially impacting the viral infection process (Siejak et al., 2021). These findings support the potential of plant EOs and phytochemicals as natural alternatives in antiviral treatments, especially in the context of sustainable agriculture and natural product-based therapeutics.

Systemic acquired resistance (SAR) presents a promising alternative to traditional plant protection methods, particularly when combating plant viral diseases. SAR can be induced by various biological and chemical agents, and recent approaches have shown that induced resistance can be highly specific to certain strains or groups of viruses (Gholizadeh et al., 2004). This specificity is crucial for developing targeted and effective strategies for managing plant diseases. In addition, toxic compounds can be utilised to activate host defence mechanisms, offering a potential management approach for viral infections (Durrant and Dong, 2004).

While biodegradable and highly selective pesticides are being sought to address the problem of extended toxicity, they must also be environmentally friendly. In this context, plant essential oils (EOs) and their bioactive components have demonstrated effectiveness in enhancing the physical, chemical, and biological stability of plants, as well as improving their antiviral effectiveness. A noteworthy example is the management of viral diseases affecting potatoes (Jovović et al., 2021). Potatoes are susceptible to 27 viral diseases, with potato leaf roll virus (PLRV) and potato virus Y (PVY)being the most globally distributed and destructive. To reduce the dependency on chemical pesticides, research by Iftikhar et al. (2013) focused on identifying non-toxic and environmentally safe compounds for managing PLRV. The study involved testing the antiviral activity of essential oils and latex extracts from various plants, including *Eucalyptus citriodora* (leaves), clove (buds), and fennel(seeds), as well as latex from *Aloe vera*, *Calotropis procera*, and *Ficus elastica*. The results showed that *Aloe vera* latex and clove essential oil exhibited the most significant inhibition of viral mRNA at a concentration of 10%, indicating their potential as effective biocontrol agents. The phytochemical analysis of the essential oils and latices revealed the presence of bioactive compounds such as tannins, phlobatannins, saponins, flavonoids, sterols, and terpenes, with essential oils generally containing higher levels of these compounds than the plant latices. Latices from *Ficus elastica*, *F. nitida*, and *Euphorbia pulcherrimia* were tested for antiviral activity against zucchini yellow mosaic virus (ZYMV), bean yellow mosaic virus (BYMV), and tobacco necrosis virus (TNV). The strongest effect was observed with *F. nitida* latex, which completely inhibited TNV, significantly reduced BYMV and ZYMV infections, and decreased BYMV transmission by aphids. Transmission electron microscopy revealed that the latex caused aggregation, deformation, and lysis of virus particles (Mahmoud et al., 2010). Latex from plants is known to contain a wide variety of enzymes in relatively high concentrations. These include glycosidases, which break down complex sugars; proteases, which degrade proteins; acid phosphatases, involved in phosphate metabolism; amylases, which hydrolyze starch; and chitinases, which can degrade fungal cell walls. Additionally, latex contains trypsin inhibitors that can interfere with protein digestion in herbivores and 1,3-glucanases that target β-glucans in microbial cell walls (Freitas et al., 2007). The presence of these diverse enzymes suggests that plant latex plays a multifunctional role in defense against pathogens, herbivores, and potentially in regulating internal metabolic processes.The free radical scavenging activity of plant latex is considered an important mechanism contributing to its antiviral properties. By neutralising reactive oxygen species (ROS) and other free radicals, latex can reduce oxidative stress in plant tissues, which may otherwise facilitate viral replication and spread. Many of the bioactive compounds in latex, particularly tannins and flavonoids, are phenolic in nature and are known for their strong antioxidant activity, which not only protects plant cells from oxidative damage but may also directly interfere with virus particles or inhibit virus-host interactions. Beyond phenolics, latex is a complex mixture containing a wide range of proteins, including defence-related enzymes such as chitinases, glucanases, and protease inhibitors, which contribute to its broad-spectrum protective effects. Detailed studies on the biochemistry, structural composition, and functional roles of latex components, particularly in plant defence, have been extensively reviewed and highlight the multifunctional nature of latex in protecting plants from pathogens, herbivores, and environmental stresses (Wititsuwannakul and Wititsuwannakul, 2001).

Latex is a fluid produced by specialised plant cells called laticifers, which are found in approximately 6% of all vascular plant species. This milky substance has garnered increasing interest due to its complex metabolic processes and potential biological functions, though much about its full role remains poorly understood (Hagel et al., 2008; Pickard, 2008). Despite the growing interest in laticifers, only a small number of latex-producing plants have been studied in detail. Many of these plants, particularly those involved in toxic events or displaying pharmacological properties, still require more basic biological investigations to fully comprehend their mechanisms. One widely held hypothesis regarding the biological significance of latex in plants is its defensive role. It is believed that latex serves as a defence mechanism against herbivores, insects, and phytopathogens, possibly by deterring feeding or protecting against pathogen invasion. In particular, the latex from some plants may contain compounds that interact with viral proteins. These components are thought to conjugate with viral proteins, disrupting their structure and preventing the virus from functioning properly. This provides an antiviral property to certain plant latices, a feature that has been observed in several plants known to produce toxic or antiviral compounds. Furthermore, many antiviral proteins found in plant latices contain ribosome-inactivating proteins (RIPs), which are known to inhibit protein synthesis by cleaving ribosomal RNA. These proteins play a crucial role in the antiviral activity of plant latex by interfering with the replication of viruses, offering a form of natural resistance against viral infections (Iftikhar et al., 2013). Thus, latex-producing plants may hold considerable promise for the development of biological control agents or antiviral therapies, and further research into their composition and mechanisms could lead to more effective and environmentally friendly alternatives to synthetic pesticides and antiviral drugs.

Plant latex plays a complex role in virus biology, exhibiting both antiviral and pro-viral effects depending on the plant and virus species. While latex can create a hostile environment that limits viral colonisation, certain viruses, such as the papaya meleira virus (PMeV), are able to successfully inhabit the latex of *Carica papaya*. These dual effects highlight the intricate interactions between plant latex and viruses. Furthermore, the bioactive compounds present in latex represent a promising source for the development of novel molecules with antiviral or pro-viral properties, offering potential applications in both agriculture and medicine (Merchán-Gaitán et al., 2024).

5.2. Antimicrobial and antiviral activity of tea tree oil (TTO)

Melaleuca alternifolia, commonly known as tea tree oil (TTO), is a natural oil derived from the leaves of the *Melaleuca alternifolia* plant. It is primarily composed of terpene hydrocarbons, mainly monoterpenes, sesquiterpenes, and their associated alcohols. Contemporary research has demonstrated that TTO exhibits broad-spectrum antimicrobial activity, including antibacterial, antifungal, antiviral, and antiprotozoal properties (Carson et al., 2006). This wide range of biological activities makes it a promising candidate for both therapeutic and agricultural applications.

The antiviral potential of TTO was initially investigated in the context of plant viruses, specifically tobacco mosaic virus (TMV), using tobacco plants. In a field trial with *Nicotiana glutinosa*, plants were treated with various concentrations of TTO (100, 250, and 500 ppm), followed by experimental infection with TMV. After 10 days, the results showed that plants treated with TTO had significantly fewer lesions per square centimetre of leaf compared to control plants, indicating that TTO was effective in reducing the spread and severity of the viral infection (Bishop, 1995).

In addition to its activity against plant viruses, TTO has also demonstrated activity against bacteriophages. A study by Chao et al. (2000) showed that exposure to 50% TTO at 4°C for 24 hours reduced the number of plaques formed by *Staphylococcus aureus* (SA) and *Escherichia coli* (E. coli) bacteriophages (T7), further highlighting its antiviral potential. TTO has shown activity against enveloped viruses (which are viruses surrounded by a lipid membrane) and non-enveloped viruses, although the range of viruses tested so far is still limited. This suggests that TTO could offer broad antiviral protection, making it a candidate for controlling both plant and animal viral diseases. However, further studies are needed to understand its full spectrum of antiviral activity. One of the significant agricultural pests affected by TTO is the tomato spotted wilt virus (TSWV), which is transmitted by *Thrips*. TSWV is a destructive virus affecting tomatoes and other crops, and its management is crucial for minimising losses. The potential use of TTO as a plant protection agent against such viruses is an area of growing interest. While research on its effectiveness against specific insect-vectored viruses like TSWV is still limited, the general antiviral properties of TTO make it a promising option for use in integrated pest and disease management strategies.

Tea tree oil with its broad-spectrum antimicrobial activity is a promising natural alternative for managing viral infections in both plants and animals. Its ability to act against various plant viruses, including TMV, and its potential applications in agricultural pest control, make it a valuable tool for sustainable crop protection and disease management.

Field experiments have been conducted to assess the properties of volatile essential oils when extracted from kaolin-based element films and their effects on the occurrence of *Frankliniella thrips* population dynamics and tomato spotted wilt virus (Reitz et al., 2008). In these studies, TTO, lemongrass oil, and geraniol were evaluated against untreated controls and standard insecticide treatments. The combination of the three essential oils with kaolin-based films resulted in a reduction in the occurrence of TSWV. Specifically, the reduction in virus occurrence was between 32 and 51% in 2005 and 6 and 25% in 2006. These reductions were comparable to the standard insecticide treatment. This indicates that essential oils, when used in combination with kaolin, have the potential to manage TSWV effectively, similarly to chemical insecticides (Dimetry et al., 2003; Arshad et al., 2014).

5.3. EOs antimicrobial and antiviral activity to tomato spotted wilt virus (TSWV)

In another study by Dikova et al. (2017), lavender oil (*Lavandula angustifolia Mill.*) demonstrated effectiveness in controlling TSWV in pepper plants. Lavender essential oil exhibited inhibitory effects on TSWV at concentrations of 3000 ppm, 5000 ppm, and 10000 ppm. These results suggest that lavender oil could be a useful biocontrol agent for managing TSWV in certain crops. On the other hand, fennel essential oildid not show any significant inhibiting effect on TSWV across five different concentrations (ranging from 1000 ppm to 10000 ppm). This highlights the varying efficacy of different essential oils and suggests that not all plant-based oils have the same level of antiviral activity against TSWV. The combination of essential oils with kaolin-based films appears to be a promising alternative pestmanagement strategy, reducing reliance on chemical insecticides while managing both thrip populations and TSWV. This strategy is particularly valuable for sustainable agricultural practices and minimising the environmental impact of synthetic pesticides. Lavender oil has shown significant potential for TSWV control in vitro and may be considered for inclusion in pest management programmes, especially for crops vulnerable to this virus. The results also underscore the importance of selecting the appropriate essential oil for specific pest or disease control. While TTO, lemongrass oil, and geraniol showed positive effects, oils like fennel oil may not be as effective for certain viral diseases like TSWV. These findings suggest that essential oils, especially when combined with kaolin, can play a critical role in managing viral infections and pest populations in agricultural settings, contributing to the development of integrated pest management systems that are both effective and environmentally sustainable.

Lu et al. (2013) investigated the in vitro antiviral activities of 29 essential oils extracted from Chinese indigenous aromatic plants against the tobacco mosaic virus (TMV). The study showed that several essential oils exhibited significant antiviral effects, with some oils showing more than 50% inhibition of TMV at 100 μg/ml. The essential oils extracted from ginger, lemon, tea tree, tangerine peel, artemisia, and lemongrass demonstrated more than 50% inhibition of TMV at the tested concentration. Among these, artemisia and lemongrass oils exhibited potent inactivation and curative effects both *in vitro* and *in vivo*. The essential oils extracted from artemisia and lemongrass were found to directly passivate TMV infection in a dose-dependent manner, suggesting that these oils can potentially interfere with the coat proteins of the virus or inhibit the formation of capsid proteins. These proteins are essential for the virus ability to adsorb to or enter the host cell. The major components of the effective essential oils were identified as:

- α-zingiberene (35.21%) – extracted from ginger and lemongrass,
- Limonene (76.25% and 80.95%) – found in lemon and tangerine peel oils,
- Terpinen-4-ol (41.20%) – detected primarily in tea tree oil,
- 1,8-cineole (27.45%) – found in tea tree oil,
- Terpinolene (10.67%) – found in lemongrass oil.

These compounds, such as citronellal, limonene, 1,8-cineole, and α-zingiberene, were responsible for more than 40% inhibition of TMV infection. In vivo tests further confirmed that the essential oils, particularly those extracted from artemisia and lemongrass, exhibited curative effects on TMV. These essential oils were found to interfere with the viral replication process, possibly through interactions with viral coat proteins or by disrupting the virus ability to infect host cells. The study performed by Lu et al. (2013) suggests that essential oils extracted from artemisia and lemongrass possess significant antiviral properties and can potentially be used as natural antiviral agents against TMV.

Helal (2019) investigated the antiviral activities of biocides formulated with essential oils extracted from fennel, oregano, peppermint, thyme, and ginger against two distinct viral infections: the tobacco necrosis virus (TNV) on common bean and the cucumber mosaic virus (CMV) on cucumber. The study assessed both protective and curative effects of these essential oil-based biocides, revealing promising results. Peppermint-derived biocide was the most effective against TNV, achieving 100% growth inhibition at a concentration of 4000 ppm. Thyme-derived biocide was most effective against CMV, showing complete growth inhibition at 3000 ppm. The biocides demonstrated strong protective and curative effects against both TNV and CMV. This suggests that they could not only prevent viral infections but also help recover plants after infection. The biocides enhanced plant defence mechanisms, as indicated by increased levels of total chlorophyll, protein, and phenols. This suggests that the essential oils may help activate the plant immune response against viral attacks. The treatment with biocides also resulted in elevated levels of oxidative stress markers such as peroxidase (POD), polyphenol oxidase (PPO), and phenylalanine ammonia lyase (PAL) compared to the control plants. These enzymes are part of the plant defence system and are involved in mitigating oxidative damage, highlighting the role of biocides in boosting plant resilience. The study suggests that essential oil-based biocides present a favourable alternative to chemical pesticides. These biocides are environmentally friendly, biodegradable, and have shown effective antiviral activity, providing a sustainable option for crop protection. The study supports the potential of plant-derived biocides in integrated pest management strategies, offering a more sustainable approach to combating viral diseases in agriculture (Helal, 2019).

Dunkić et al. (2010) studied the essential oil of *Saturejamontana* L. ssp. variegata (Lamiaceae), which was found to contain a high concentration of oxygenated monoterpenes (71.3%), with carvacrol (19.4%) and thymol (16.6%) as the major active compounds. This essential oil demonstrated significant antiviral activity when applied to local hosts *Chenopodium amaranticolor*and *Chenopodium quinoa* infected with tobacco mosaic virus (TMV) and cucumber mosaic virus (CMV). The oil reduced the number of local lesions caused by these viruses by 29.2% (TMV) and 24.1% (CMV).

- Thymol was more effective in reducing CMV infection, showing a 33.2% reduction in lesions.
- Carvacrol was more effective in reducing TMV infection, showing a 34.3% reduction in lesions.

Additionally, star anise (*Illicium verum*) and fennel (*Foeniculum vulgare*) essential oils have been reported to potentially inhibit viruses such as potato virus X, tobacco ringspot virus, and tobacco mosaic virus (Phatthalung and Tangkananond, 2022), further supporting the antiviral potential of essential oils.

Oraby and El-Borollosy (2013) discussed the efficacy of plant essential oils (EOs) in managing insect vectors, which played a significant role in transmitting plant viruses. By reducing the insect vector ability to transmit viruses, these EOs help increase both the quality and quantity of crop yields. This highlights the potential of plant EOs as a tool for the integrated pest and disease management.

Phatthalung and Tangkananond (2021) explored the anti-viral and insecticidal properties of 10 plant-derived EOs from Thai herbal plants (e.g., lemongrass, star anise, kaffir lime, lime, holy basil, sweet basil, kaempfer, galanga, black pepper, and betelvine) against the rice ragged stunt virus (RRSV) and the brown planthopper (BPH, Nilaparvatalugens Stål), an insect vector for this virus.

Lemongrass and star anise EOs exhibited 100% mortality in BPH at concentrations of 3% and 5%. The insect mortality occurred across all growth stages of BPH:

- ➢ Egg and nymph stages: abnormal shapes and structures, leading to destruction within 3 days post-treatment.
- ➢ Adult stage: malformed morphology, resulting in death within 5 days after treatment.

Both EOs were highly effective in inhibiting RRSV transmission, making them potential candidates for the development of new commercial antiviral agents.

The study highlights the promising potential of plant EOs, particularly lemongrass and star anise, as natural alternatives for managing both insect vectors and plant viruses. These EOs not only increase crop health by preventing viral transmission but also serve as eco-friendly alternatives to chemical pesticides, contributing to sustainable agricultural practices. Phatthalung and Tangkananond (2021) proposed that the mechanism by which plant essential oils (EOs) inhibited viral transmission involved altering the physiology of the insect vectors or the plants they infected (Figure 2). In conclusion, the plant EOs function at the level of the virus-vector interaction by interfering with the vector ability to transmit the virus or by physically disrupting the infection process on the plant tissue. This disruption, whether through the mechanical barrier formation or biochemical interference, results in a reduced viral transmission, offering a potential strategy for controlling plant viral diseases.

In the study performed by Singh et al. (2014), it was suggested that plant essential oils (EOs) could significantly modify the physiology of both insect vectors and host plants, disrupting the metabolism of infected cells. This disruption occurs because the external surfaces of viral particles and plant hosts are coated by the essential oils, which impairs the infectivity and transmissibility of the virus. Key points highlighted in the study include:

1. Inhibition of viral transmission: the plant EOs coat the viral particles and host plant surfaces, which limits the ability of the virus to infect or spread. By physically altering the viral particles, the oils reduce their ability to adhere to or penetrate the plant tissues, which prevents successful viral transmission.
2. Insect vector development and viral transmission: the developmental stages of insect vectors, especially the nymph stage, are critical for viral

transmission. Since the nymphs are often the ones that feed on infected plants and transfer viruses, interfering with their development can reduce viral spread. Adult insects, although important for migration and the population growth, are less involved in the direct transmission of the virus compared to nymphs.

3. Soft-bodied vs. hard-bodied insects: the study also demonstrated that soft-bodied insects, such as aphids or whiteflies, are generally more susceptible to plant EOs than hard-bodied insects (e.g. beetles). The soft bodies of such insects make them more vulnerable to the insecticidal properties of the EOs, which can disrupt their feeding or reproduction, thereby reducing their ability to transmit viruses.

4. Induced systemic resistance (ISR): plant EOs can also trigger induced systemic resistance in the host plants, enhancing their overall defence mechanisms against both insect pests and viral infections. This results in increased plant resistance, making it harder for insects to successfully infect or feed on the plant.

5. Integrated pest management: the ability of plant EOs to manage the damaging effects of insect vectors on crops, while also reducing their viral transmission ability, positions them as promising agents in integrated pest management strategies. By reducing both pest damage and viral spread, plant EOs offer a dual benefit for crop protection.

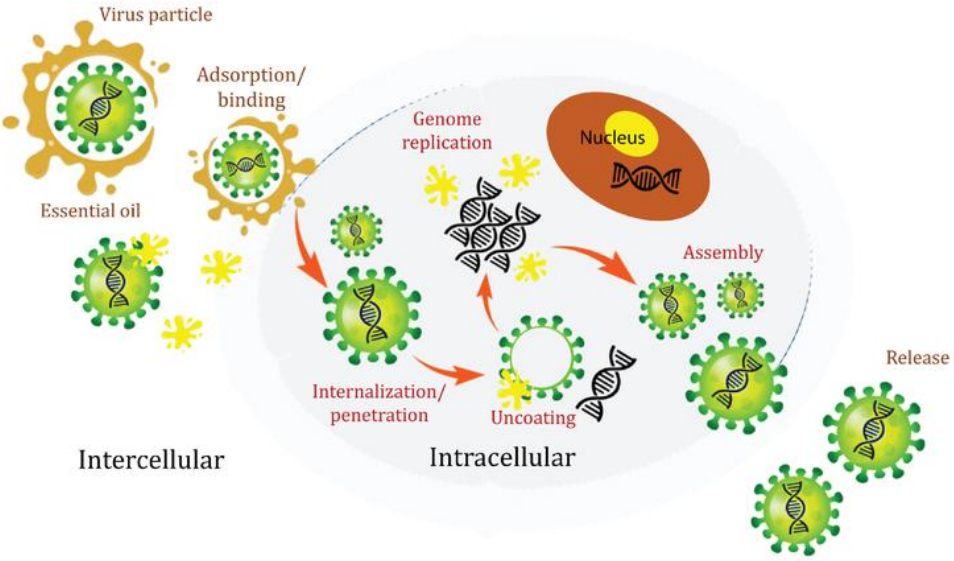

Figure 2. The mechanism of antiviral actions as possible targets for plant EO.
Source: Phatthalung and Tangkananond (2022)

The application of plant EOs can significantly influence the relationship among insect vectors, viral diseases, and host plants, reducing viral transmission while enhancing plant defences through systemic resistance. This makes them a valuable tool in sustainable agriculture for controlling plant viruses and pests.

The mechanism of action of essential oils (EOs) against viruses involves several stages in the viral infection cycle. EOs and their components can inhibit viral infectivity by targeting specific stages of the infection process. The viral life cycle consists of attachment, penetration, replication, and release of new virions. Inhibition at any of these stages can reduce or prevent viral replication. The effectiveness of EOs in inhibiting viruses is commonly determined through time-of-addition assays, which help identify which phase of the infection cycle the EO affects (Reichling, 2022).

Pre-viral infection (pre-treatment with EOs): In this approach, host cells are treated with the EO for an hour before the virus is introduced. If the result is negative, it suggests that the EO does not interfere with viral attachment or host cell receptor binding, meaning it does not block the virus from binding to the host cell before entry (Civitelli et a., 2014).

Simultaneous viral infection (virus and host treated together): Here, the virus is pre-treated with EOs for an hour and then added to the host cells. A positive result in this case indicates that the EO affects the free virions by modifying their envelope structure or masking viral proteins. This would prevent the virus from adsorbing to and entering the host cells effectively (Reichling, 2022).

Post-viral infection (treatment after infection): EOs are also tested by adding them to infected cells at various time intervals throughout the viral infection lifecycle. This includes adding the EO at different stages, such as during penetration, genetic material replication, or virion production. The results help determine which stage of the infection cycle the EO inhibits. If the EO interferes with viral replication, this suggests its action occurs during the post-entry or replication stages of infection. Given below are the modes of action (Reichling, 2022):

- Intercellular mode of action: EOs can directly affect free viruses, preventing them from binding to and entering host cells. This involves modifying the virus structure or interfering with the viral envelope, which is crucial for viral adsorption.
- Multiple mechanisms: the action of EOs can vary depending on the specific EO or its components. Some EOs may affect only the early stages of the infection (attachment or entry), while others might act later in the infection cycle, such as inhibiting viral replication or progeny production.

The time-of-addition assay remains the most commonly used technique to evaluate the antiviral properties of essential oils. By determining which phase of the viral lifecycle is impacted, researchers can better understand the mechanism of action of specific EOs and their components. EOs may inhibit viral infectivity through a variety of actions, from preventing attachment to directly interfering with virus particles. This highlights the potential for EOs to serve as effective antiviral agents (Ma and Yao, 2020).

The antiviral mechanisms of essential oils (EOs), as proposed by various authors, are based on a variety of actions that occur throughout the viral infection cycle. The diagram (Figure 3) referenced in the literature summarises the potential mechanisms of action of plant EOs, which can be categorised into direct and indirect effects. These actions affect the virus at various stages of its lifecycle, including viral adsorption, entry, replication, and virion release.

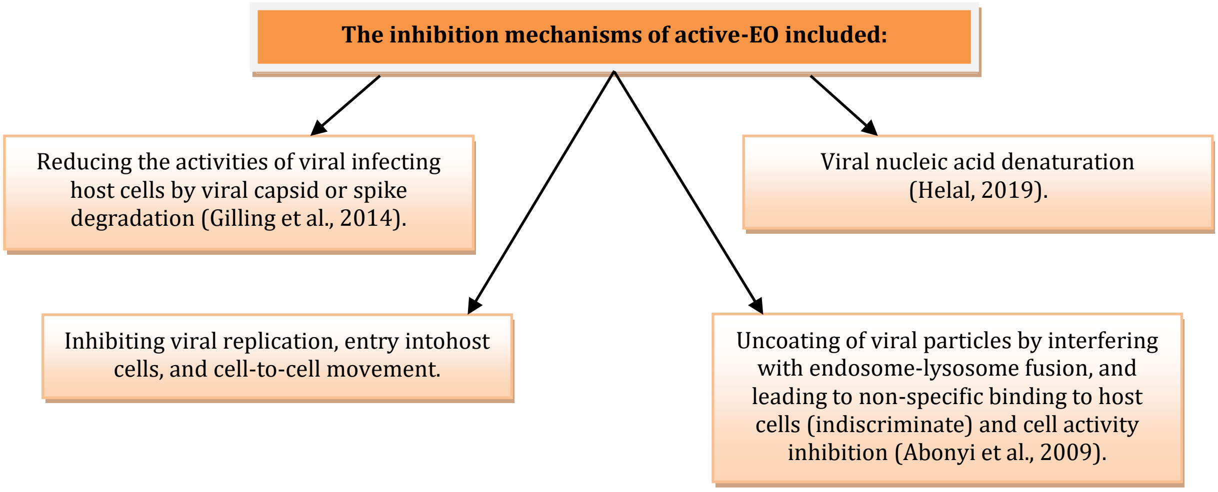

Figure 3. The inhibition mechanisms of active-EO.

Direct antiviral mechanisms

Direct antiviral action refers to the EOs directly interacting with the virus or its components to inhibit or inactivate its ability to infect host cells. These mechanisms include (Cliver, 2009):

1. Blocking viral adsorption: certain components of EOs, like carvacrol, can interfere with virus adsorption to the host cell. This occurs through binding to or masking viral capsid proteins, preventing the virus from attaching to the host cell. However, structural damage to the virus is not always part of this mechanism, and the virus may still retain its integrity without the ability to infect the host.
2. Inactivation of viral particles: EOs can also inactivate enveloped viruses more effectively than non-enveloped (naked) viruses. This is due to the lipid bilayer membrane of enveloped viruses, which is more susceptible to disruption by lipophilic EO compounds.
3. Blocking viral replication: some EOs can interfere with viral RNA or DNA synthesis, preventing the replication of the viral genome inside the host cell. This can be achieved by inhibiting enzymes like RNA polymerases or reverse transcriptases (depending on the virus).
4. Inhibition of virion release: EOs can also prevent the release of new virions from infected cells, thereby reducing viral spread.

Indirect antiviral mechanisms

Indirect antiviral actions generally involve modulating the host's immune system or enhancing the plant's defence responses:

1. Induced systemic resistance (ISR): EOs may enhance plant resistance to viral infections through systemic acquired resistance (SAR) or ISR. By boosting the plant's natural defence mechanisms, such as the production of reactive oxygen species (ROS), phytoalexins, or pathogenesis-related proteins, plant EOs make it harder for the virus to establish an infection (Reichling, 2022).
2. Modification of host physiology: plant EOs may alter the physiology of the host cells or the insect vectors that transmit the virus. By affecting the metabolism or surface properties of infected cells, EOs can reduce viral transmission rates and make it more difficult for the virus to spread (Dias et al., 2024).
3. Interference with viral replication machinery: indirectly, EOs may disrupt viral replication by inhibiting the host cell machinery that viruses rely on to replicate their genomes or synthesise new viral proteins (Feng et al., 2025).

Enzyme blocking and stability

The antiviral activities of EOs and their active components may involve the blocking of viral enzymes that are critical to viral replication or infectivity. For example, proteases or lipases involved in viral maturation and release can be inhibited by certain EO compounds. Additionally, EOs can affect the virus stability. Some essential oils destabilise viral membranes, especially in enveloped viruses, making them more vulnerable to environmental factors and reducing their infectivity (Ma and Yao, 2020).

Enveloped vs. non-enveloped (naked) viruses

EOs tends to have stronger antiviral effects against enveloped viruses because the lipid membranes of these viruses are more susceptible to disruption by the hydrophobic components of essential oils. Non-enveloped (naked) viruses, on the other hand, are generally more resistant to EO-induced inactivation because they lack a lipid membrane, which provides protection against many EO compounds. The antiviral properties of essential oils stem from their ability to affect various stages of the viral infection cycle through direct and indirect mechanisms. Their effectiveness may vary depending on the virus type, the host plant involved, and the EO composition. Therefore, plant essential oils represent a promising natural alternative for controlling viral infections, especially when considering their ability to act through multiple antiviral mechanisms (Ma and Yao, 2020).

6. Advantages of essential oils over synthetic agents

The increasing interest in EOs, particularly in agriculture and medicine, is largely due to the numerous advantages they offer over synthetic agents (Rawat, 2021; Basavegowda and Baek, 2021; Tanasă et al., 2024). Essential oils (EOs) are biodegradable, generally non-toxic, and pharmacologically complex, affecting multiple biological targets simultaneously with often fewer side effects. Their mixtures of volatile compounds can act synergistically, enhancing efficacy in diverse applications such as plant protection and modulation of viral or pest interactions. The biological and ecological functions of EOs extend far beyond their antimicrobial, antiviral, and insecticidal properties. These oils play a crucial role in survival and reproduction of plants by protecting them against excessive heat during intense sunlight, attracting pollinators with their fragrance, repelling herbivores, and reducing competition with other plant species through allelopathic effects. These multifaceted roles highlight the complexity and adaptability of plants in their natural environments.

7. Conclusions

Essential oils of plants perform a variety of biological and ecological functions, including protection from excessive heat, attraction of pollinators, repulsion of herbivores, and reduction of competition through allelopathic effects. Of particular interest in agriculture is their antiviral activity, which can modulate plant–virus interactions and reduce the incidence or severity of viral infections in crops. The complex chemical composition of EOs allows them to act on multiple viral targets simultaneously, potentially interfering with viral replication, transmission, or symptom development. This multi-targeted activity, combined with their natural origin and low environmental impact, makes essential oils a promising tool for sustainable management of plant viral diseases and highlights the need for further research into their mechanisms and applications.

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Declaration of competing interests

The authors declare that they have no conflict of interest.

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