International Journal of Pest Management

ISSN: 0967-0874 (Print) 1366-5863 (Online) Journal homepage: https://www.tandfonline.com/loi/ttpm20

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To cite this article: Khadija Basaid, Bouchra Chebli, El Hassan Mayad, James N. Furze, Rachid Bouharroud, François Krier, Mustapha Barakate & Timothy Paulitz (2020): Biological activities of essential oils and lipopeptides applied to control plant pests and diseases: a review, International Journal of Pest Management, DOI: 10.1080/09670874.2019.1707327

To link to this article: https://doi.org/10.1080/09670874.2019.1707327

INTERNATIONAL JOURNAL OF PEST MANAGEMENT
https://doi.org/10.1080/09670874.2019.1707327

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REVIEW

Biological activities of essential oils and lipopeptides applied to control plant pests and diseases: a review

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ABSTRACT

Plants are often subject to attack by fungi, nematodes and insects, which generate immense yield losses. Hence, the quest for crop protection solutions is ongoing, concurrent with greater awareness towards the use of synthetic chemicals in agricultural practice. Scientific research has shifted towards the use of natural products, which possess good efficacy and are environment friendly. This review details two classes of natural products. The first one is the plant essential oils with their volatile constituents, which have been proven to possess antifungal, nematicidal and insecticidal activities. The second class is the lipopeptides produced by antagonistic microorganisms. Their biological activities are discussed, as they have been shown effective against plant fungi and pests. Essential oils and lipopeptides have huge potential to be used as biopesticides. The combinatorial approach between essential oils, antagonistic microorganisms and lipopeptides for crop protection is discussed, potentially both can produce a synergistic effect, resulting from their combination against plant fungi, nematodes and pests.

Nomenclature: EC_{50}: The concentration required to kill 50% of the second stage juveniles or reduce the egg hatch by 50%; LC_{50}: The lethal concentration that causes the death of 50% insect larvae; RD_{50}: The essential oil dose capable of repelling 50% of the insect population; DC_{50}: The concentration required to cause 50% inhibition of insect feeding in foods treated with essential oils in comparison with controls (untreated foods)

ARTICLE HISTORY
Received 30 March 2019
Accepted 16 December 2019

KEYWORDS
Essential oils; antifungal; nematicidal; insecticidal; synergistic activity; lipopeptides

1. Introduction

Plants have a larger metabolic network than most other organisms. Apart from producing primary metabolites (PMs) like sugars, amino acids, nucleotides, lipids and energy sources (Aharoni and Galili 2011), plants produce a vast range of secondary metabolites (SMs). These play a key role in maintaining plant fitness, as they protect plants against external biotic and abiotic aggressions, such as microbial infections, herbivores (e.g., slugs and snails, arthropods and vertebrates) and UV radiation. They also play a role in attraction of pollinators, allelopathy and signaling (Dixon 1999).

Secondary metabolism guarantees flexible adaptation of plants to the demands of their continuously changing environment (Hartmann 2007). They are classified into three important groups. The first group is the preformed compounds, which includes compounds present in plants in their biologically active form, such as plant extracts, essential oils, phenolic compounds, flavonoids, plant growth substances and regulators. These preformed compounds stimulate the resistance of plants, as they have antimicrobial properties, by inhibiting the growth and development of bacteria and fungi (Barkai-Golan 2001; Martinez 2012). The second group is the inducible preformed compounds. It includes substances normally present in healthy tissues, which may be further induced in response to pathogen attack, to activate the resistance in plants. The third group concerns the phytoalexins and other induced inhibitory compounds, such as pathogenesis-related proteins, active oxygen species and lectins. They act as inhibitory substances following recognition of an invader (Martinez 2012).

Preformed and induced defense mechanisms provide plants with resistance to several microorganisms.

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Supplemental data for this article can be accessed at https://doi.org/10.1080/09670874.2019.1707327.

However, some microorganisms became virulent by the production of effector molecules, which suppress plant defense (Jones and Dangl 2006); allowing the propagation of virulent pathogens in the susceptible plant tissues (Berger et al. 2007). Plant pathogens including fungi and bacteria have developed different strategies to invade a plant. They can be necrotrophic, which need living tissue for growth and reproduction or biotrophic, which kill the host tissue at the beginning of the infection and feed on the dead tissue (Berger et al. 2007). Other plant pathogens like nematodes can adopt more sophisticated modes of biotrophic parasitism, causing morphological changes of the plant cells and leading to the appearance of many symptoms such as galls, root knots or cysts (Dangl and Jones 2001). All these attacks affect the quality of plants and generate yield losses.

Crop diseases are usually treated with synthetic pesticides. However, the overuse of these chemicals has raised the concern of both scientists and the public on many levels (Koul et al. 2008). The residues of pesticides may affect public health, as they remain in soil, water resources and crops and can be transferred to the food chain. On the other hand, the emergence of resistance in pathogens towards pesticides raises the question of their efficacy (Cabras et al. 1999; Koul et al. 2008; Martinez 2012).

An answer to these concerns lies in the use of plant derived compounds like essential oils. Essential oils (EOs) are promising biocontrol agents as they are biodegradable, cause minimal effects on non-target organisms and delay the occurrence of resistance in pests (Isman 2000). Further, they have shown a broad spectrum of antifungal, nematicidal and insecticidal properties (Soliman and Badeaa 2002; Chebli et al. 2003a; De Andrade Dutra et al. 2016; Avato et al. 2017; Reddy and Dolma 2018).

Another important alternative to pesticides among biological control agents are antagonistic microorganisms. Many yeast, fungal and bacterial strains have been shown to be effective against various plant pathogens (Wisniewski and Wilson 1992; Pusey et al. 2018). Thus many strains of *Agrobacterium, Pseudomonas, Bacillus, Alcaligenes, Streptomyces* and others have been reported as promising bacterial control agents. To fight against plant pathogens, they utilise different mechanisms such as parasitism, cross protection, antibiosis and competition (Shoda 2000).

The use of microorganisms as biological control agents showed promising effects for crop protection. Nevertheless, in many cases it can be difficult to achieve high levels of inhibition of pathogens using one biological control agent. The current trend is to combine several approaches in the context of an integrated pest management strategy (Zhang et al. 2008), which could lead to increased efficacy as biopesticide (Stević et al. 2014).

This study summarizes information on biological activities of EOs, mainly against plant attacking fungi, insects and nematodes. Moreover, it describes a detailed overview of lipopeptides produced by bacteria and their biological activities. There view ends with the study of the effect resulting from the combination of EOs with antagonistic microorganisms and lipopeptides for control of plant pathogens.

2. Essential oils

2.1. Essential oils, composition and ecological functions

Essential oils (EOs) are a mixture of volatile compounds, characterized by a strong odor, derived from secondary metabolism of plants. They can be synthesized by all plant organs, i.e., leaves, stems, flowers, fruits, buds, seeds, roots or bark and are stored in cavities, canals, secretory cells, epidermal cells or glandular trichomes (Bakkali et al. 2008). EOs are produced mainly by: Annonaceae, Apiaceae, Araceae, Asteraceae, Ericaceae, Burseraceae, Cistaceae, Cupressaceae, Geraniaceae, Gramineae, Lamiaceae, Lauraceae, Malvaceae, Myristicaceae, Myrtaceae, Oleaceae, Pinaceae, Piperaceae, Rosaceae, Rutaceae and Valerianaceae (Stewart 2005). The production of EOs is due to systemic and environmental reasons. For plant functions, EOs provide volatile compounds which reinforce photosynthesis under thermal and oxidative stress conditions (Vickers et al. 2009). Concerning the plant ecological functions, essential oil compounds participate in plants interactions within the environment, as allelopathic agents by inhibiting germination. In plant-animal interactions, EOs act by repelling predators (Al-Mousawi and Al-Naib 1975) and attracting insects pollinators (Pichersky and Gershenzon 2002).

Several methods are used to extract EOs from plants. The conventional ones include hydrodistillation, extraction by organic solvents, fats and cold expression. Innovative methods comprise extraction by microwaves and supercritical CO_2 extraction (Basile et al. 1998; Kim and Lee 2002; Aghel et al. 2004; Ferhat et al. 2007; Lucchesi et al. 2007). Many industries and fields utilize EOs properties such as food, cosmetic and pharmaceutical industries (Prakash and Gupta 2005; Sacchetti et al. 2005; Bakkali et al. 2008). Their importance in agriculture is mainly attributed to their use in biological control against plant pathogens.

Essential oils contain two classes of compounds. The first class concerns terpenes or terpenoids. Terpenes are hydrocarbons, which result from

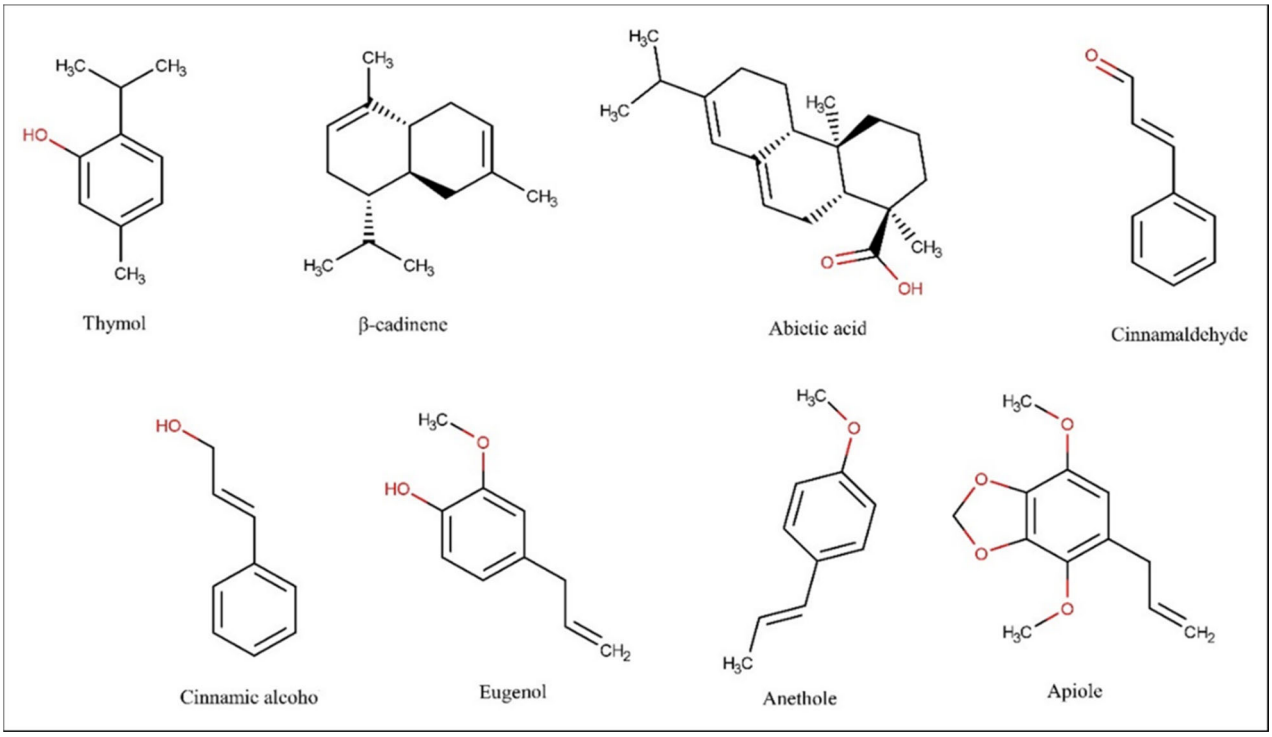

Figure 1. 2 D chemical structures of selected compounds of essential oils: terpenes [monoterpene (thymol $C_{10}H_{14}O$), sesquiterpene (β-cadinene $C_{15}H_{24}$), diterpene (abietic acid $C_{20}H_{30}O_2$)], and aromatic compounds [aldehyde (cinnamaldehyde C_9H_8O), alcohol (cinnamic alcohol $C_9H_{10}O$), phenol (eugenol $C_{10}H_{12}O_2$), methoxy derivative (anethole $C_{10}H_{12}O$) and methylene dioxy compound (apiole $C_{12}H_{14}O_4$)].

coupling many isoprene units (C_5H_8), and terpenoids are terpenes modified by enzymes, which add or remove methyl groups, or add oxygen molecules (Sikkema et al. 1995; Burt 2004). Among terpenes, monoterpenes consisting of two isoprene units ($C_{10}H_{16}$) were the most volatile (with low molecular weight). They have several functional groups such as carbides, alcohols, aldehydes, ketones and ethers, and can be acyclic, monocyclic or bicyclic. The sesquiterpenes resulting from three isoprene units ($C_{15}H_{24}$) have also several structures such as carbides, alcohols, ketones and epoxides (Bakkali et al. 2008; Kaloustian et al. 2008). In some cases, diterpenes are made of four isoprene units ($C_{20}H_{32}$) (Vila et al. 2002). The second class of essential oil compounds consist of volatile aromatic compounds, derived from phenylpropane (Kurkin 2003). They contain aldehydes, alcohols, phenols, methoxy derivatives and methylenedioxy compounds (Bakkali et al. 2008). Figure 1 shows some examples of essential oil compounds belonging to the two classes.

It is known that the composition and the amount of major and minor compounds of EOs influence their biological activities (Dorman and Deans 2000; Lahlou 2004). The qualitative and quantitative chemical profile of EOs and their yield depend on several intrinsic and extrinsic factors. Internal factors include genetic background of the plant (species, ecotype and chemotype) (Thompson et al. 2003), plant origin and population (Moghaddam and Mehdizadeh 2017), plant organ (Angioni et al. 2006), seasonal sampling period or developmental stage, as the formation of active metabolites notably occurs during intensive metabolism, such as periods of flowering and fruiting (Badi et al. 2004). Other bioactive compounds are produced during the harvest period (Lahlou 2004). External factors include environmental conditions (climate, geographical origin), cultivation conditions (soil properties, fertilization and mineral nutrition, irrigation frequency, sowing date and harvest time and methods), and postharvest techniques (drying methods, extraction method and time, quantification methods and conditions of analysis) (Moghaddam and Mehdizadeh 2017). All these factors are susceptible to the changing of chemical profile of plant species, resulting in alterations in biological activities of their oils.

2.2. Biological activities of essential oils

2.2.1. Antifungal activity of essential oils against post-harvest fungi

Several EOs extracted from different botanical families were tested for their in *vitro* and *in vivo* antifungal activities against plant fungi, including those causing diseases in postharvest such as : *Penicillium digitatum* (Pers.), *Penicillium italicum* Wehmer, *Penicillium expansum* Link., *Alternaria citri* Ellis & N. Pierce, *Botrytis cinerea* Pers: Fr., *Phytophthora citrophthora* (R.E. Sm. & E.H. Sm.), *Geotrichum*

citri-aurantii (Ferraris) E.E. Butler, *Alternaria alternate* (Fr. : Fr.) Keissl., *Aspergillus flavus* Link : Fr., *Aspergillus parasiticus* Speare, *Aspergillus ochraceus* G. Wilh. and *Fusarium moniliforme* J. Sheld. (Soliman and Badeaa 2002; Chebli et al. 2003a; 2004; Alilou et al. 2008; Vitoratos et al. 2013; Yazdanpanah and Mohamadi 2014; Soylu and Kose 2015).

Plant families that have been widely studied are Lamiaceae, Asteraceae, Myrtaceae, Apiaceae, Rutaceae, Lauraceae and Poaceae. Among these families, Lamiaceae is the most studied, with species of the genera *Thymus, Origanum, Lavendula, Rosmarinus, Asteriscus* and *Mentha*. Several species of this family have been tested for their wide chemical diversity, making them good candidates for the study of antifungal activity. Table 1 illustrates examples of EOs belonging to different botanical families, which have demonstrated an antifungal potential against postharvest fungi. As for examples species *Mentha piperita*, which gave 100% inhibition of *Geotrichum candidum* Link. at a small dose of 5 ppm (Verma et al. 2011). Likewise, *Zataria multiflora* species gave 100% inhibition of *P. expansum* at 50 ppm (Mohammadifar et al. 2012), and *Origanum compactum* and *Thymus glandulosus* completely inhibited *B. cinerea* at 100 ppm (Chebli et al. 2003b). *In vivo*, tested species include *Zataria multiflora*, that provided more than 95% inhibition of fruit decay by *A. citri* at 300 ppm (Ramezanian et al. 2016), and *Origanum vulgare* which gave 90% inhibition of fruit decay by *G. citri-aurantii* at 1000 ppm (Regnier et al. 2014).

Table 2 presents some examples of essential oil compounds, with *in vitro* antifungal activity against post-harvest phytopathogenic fungi. Phenols are the most active like thymol and carvacrol (Chebli et al. 2003b; Kim et al. 2016a). Alcohols and sesquiterpene lactones also possess an antifungal activity, as do aliphatic aldehydes (Thompson 1989; Wedge et al. 2000; Lee et al. 2008; López-Meneses et al. 2017).

The mechanism of action of EOs constituents on fungi was studied by several authors. Conner and Beuchat (1984) were among the first to relate antifungal action against yeast to interference with enzymes, which are involved in the production of energy and the synthesis of structural constituents. Sharma and Tripathi (2008) suggested another mechanism of action, which stated that EOs constituents attack cell walls, leading to the loss of cytoplasmic contents of mycelial cells. Related to their hydrophobic nature, they interfere with lipid membranes of fungal cells, causing an increase of cation permeability in membranes. Consequently, changes occur in the proton flux and the pH gradient inside fungal cells, which eventually affects their metabolism, leading to their death (Beckman 2000). This dysfunction of the membrane affects energy production in fungal cells, by inhibiting enzymes and key substrates in the production of ATP (El-Mogy and Alsanius 2012). Furthermore, spore germination and elongation of the germ tube may be affected, leading to inhibition of fungal growth (Da Cruz Cabral et al. 2013).

Lucini et al. (2006) reported that monoterpenes act on retarding the sclerotic differentiation and increasing the concentration of lipid peroxides, leading to the destruction of fungal cells. In addition to monoterpenes, phenols have an antifungal capacity, as they possess an aromatic ring with a hydroxyl group, which forms hydrogen bonds with the active sites of cellular enzymes (Figure 2) (Daferera et al. 2000).

2.2.2. Nematicidal activity of essential oils against plant-parasitic nematodes

Several EOs extracted from different botanical families have been studied for their *in vitro* and *in vivo* nematicidal activity, mainly against nematodes of the genera *Meloidogyne* and *Bursaphelenchus* (Oka et al. 2000; Kim et al. 2008). Plant families that have been widely studied include Lamiaceae, Asteraceae, Myrtaceae, Apiaceae, Rutaceae and Poaceae. Among these, Lamiaceae is the most studied, with species of the genera *Thymus, Rosmarinus, Artemisia*, *Mentha,* and *Origanum* (Table 3), given their traditional use in medicine, in addition to their local availability in large amounts. Examples of inhibitory species from this family tested *in vitro* comprise *Rosmarinus officinalis* and *Ocimum basilicum,* which gave 98.3% and 100% inhibition of *Meloidogyne incognita* (Kofoid and White) Chitwood at 15 ppm and 250 ppm respectively (Pandey et al. 2000; Avato et al. 2017). *In vivo, Plectranthus cylindraceus* and *Haplophyllum tuberculatum* reduced the number of *Meloidogyne javanica* (Treub) Chitwood eggs on the roots of tomato plants by 90.4% and 89.8% respectively, at a small dose of 5 µg/ml of soil (Onifade et al. 2008). Likewise, *Mentha rotundifolia* and *Origanum syriacum* controlled *M. javanica* on tomato plants at a dose of 200 mg/kg, by providing a gall index of 0 (Oka et al. 2000).

Examples of EOs and their constituents, active on plant parasitic nematodes are presented in (Table 3) and (Table 4).

Parasitism of nematodes is related to the effectors produced by the nematode glands (secretions), which manipulate the cellular machinery and alter the functions of the host plant cells (Haegeman et al. 2012; Hewezi and Baum 2013). Discovered effectors include the enzymes pectate lyases,

Table 1. Recent examples of essential oils *in vitro* antifungal activities against some post-harvest phytopathogenic fungi.

Fungi	Plant species	Family	Study	Inhibitory dose (% of inhibition)	References
***Botrytis cinerea* Pers: Fr.**	*Poliomintha longiflora*	Lamiaceae	*In vitro*	800 ppm (100%)	Cid-Pérez et al. (2016)
	Angelica archangelica	Apiaceae	*In vitro*	600 ppm (100%)	Fraternale et al. (2016)
	Melissa officinalis	Lamiaceae	*In vitro*	2000 ppm (76.81%)	El Ouadi et al. (2017)
***Penicillium expansum* Link.**	*Poliomintha longiflora*	Lamiaceae	*In vitro*	1200 ppm (100%)	Cid-Pérez et al. (2016)
	Melissa officinalis	Lamiaceae	*In vitro*	1000 ppm (100%)	El Ouadi et al. (2017)
***Alternaria citri* Ellis & N. Pierce**	*Zataria multiflora*	Lamiaceae	*In vitro*	300 ppm (100%)	Ramezanian et al. (2016)
	Thymus vulgaris	Lamiaceae	*In vitro*	400 ppm (100%)	Ramezanian et al. (2016)
	Zataria multiflora	Lamiaceae	*In vivo*	300 ppm (95.4%)	Ramezanian et al. (2016)
	Thymus vulgaris	Lamiaceae	*In vivo*	400 ppm (94.8%)	Ramezanian et al. (2016)
***Rhizopus stolonifer*(Ehrenb. : Fr.) Vuill.**	*Melissa officinalis*	Lamiaceae	*In vitro*	2000 ppm (100%)	El Ouadi et al. (2017)
***Aspergillus niger* Tiegh.**	*Thymus vulgaris*	Lamiaceae	*In vitro*	1250 ppm (100%)	Hossain et al. (2016)
	Origanum vulgare	Lamiaceae	*In vitro*	625 ppm (100%)	Hossain et al. (2016)
	Cinnamomum zeylandicum	Lauraceae	*In vitro*	2500 ppm (100%)	Hossain et al. (2016)
	Trachyspermum ammi	Apiaceae	*In vitro*	56.10^{-3} mg/ml air (100%)	Kim et al. (2016a)
	Pimenta dioica	Myrtaceae	*In vitro*	56.10^{-3} mg/ml air (100%)	Kim et al. (2016a)
	Allium sativum	Amaryllidaceae	*In vitro*	7.5 ppm (100%)	Arasu et al. (2019)
	Menthapulegium	Lamiaceae	*In vitro*	200 ppm (100%)	Mejdoub et al. (2019)
***Colletotrichum gloeosporioides*(Penz.) Penz. & Sacc.**	*Poliomintha longiflora*	Lamiaceae	*In vitro*	1000 ppm (100%)	Cid-Pérez et al. (2016)
***Alternaria solani* Sorauer**	*Eucalyptus staigeriana*	Myrtceae	*In vitro*	1000 ppm (100%)	Tomazoni et al. (2017)
	Eucalyptus globulus	Myrtaceae	*In vitro*	10,000 ppm (100%)	Tomazoni et al. (2017)
	Cinnamomum camphora	Lauraceae	*In vitro*	1500 ppm (100%)	Tomazoni et al. (2017)
	Angelica archangelica	Apiaceae	*In vitro*	750 ppm (100%)	Fraternale et al. (2016)
***Sclerotinia sclerotiorum* (Lib.) de Bary**	*Ziziphora clinopodioides*	Lamiaceae	*In vitro*	150 ppm (100%)	Ma et al. (2016a)
	Ziziphora clinopodioides	Lamiaceae	*In vivo*	10,000 ppm (97.1%)	Ma et al. (2016a)
	Piper aduncum	Piperaceae	*In vitro*	30 µl (100%)	Valadares et al. (2018)
***Aspergillus flavus* Link : Fr.**	*Thymus vulgaris*	Lamiaceae	*In vitro*	1250 ppm (100%)	Hossain et al. (2016)
	Origanum vulgare	Lamiaceae	*In vitro*	2500 ppm (100%)	Hossain et al. (2016)
	Cinnamomum zeylandicum	Lauraceae	*In vitro*	5000 ppm (100%)	Hossain et al. (2016)
	Poliomintha longiflora	Lamiaceae	*In vitro*	1400 ppm (100%)	Cid-Pérez et al. (2016)
	Allium sativum	Amaryllidaceae	*In vitro*	6.5 ppm (100%)	Arasu et al. (2019)
	Mentha pulegium	Lamiaceae	*In vitro*	100 ppm (100%)	Mejdoub et al. (2019)
***Aspergillus parasiticus* Speare**	*Thymus vulgaris*	Lamiaceae	*In vitro*	1250 ppm (100%)	Hossain et al. (2016)
	Origanum vulgare	Lamiaceae	*In vitro*	2500 ppm (100%)	Hossain et al. (2016)
	Cinnamomum zeylandicum	Lauraceae	*In vitro*	2500 ppm (100%)	Hossain et al. (2016)
	Trachyspermum ammi	Apiaceae	*In vitro*	56.10^{-3} mg/ml air (100%)	Kim et al. (2016a)
	Pimenta dioica	Myrtaceae	*In vitro*	56.10^{-3} mg/ml air (83.5%)	Kim et al. (2016a)
***Aspergillus ochraceus* Wilh.**	*Trachyspermum ammi*	Apiaceae	*In vitro*	56.10^{-3} mg/ml air (100%)	Kim et al. (2016a)
	Pimenta dioica	Myrtaceae	*In vitro*	56.10^{-3} mg/ml air (84.4%)	Kim et al. (2016a)
***Fusarium culmorum*(Wm.G. Sm.) Sacc.**	*Angelica archangelica*	Apiaceae	*In vitro*	300 ppm (100%)	Fraternale et al. (2016)
***Fusarium oxysporum* Schl.**	*Angelica archangelica*	Apiaceae	*In vitro*	300 ppm (100%)	Fraternale et al. (2016)
	Syzygium aromatica	Myrtaceae	*In vitro*	149.9 ppm (50%)	Xie et al. (2017)
***Rhizoctonia solani* (Kuhn.)**	*Syzygium aromatica*	Myrtaceae	*In vitro*	106.5 ppm (50%)	Xie et al. (2017)
***Fusarium solani* (Mart.) Sacc.**	*Angelica archangelica*	Apiaceae	*In vitro*	350 ppm (100%)	Fraternale et al. (2016)
***Alternaria tenuissima* var. alliicola T.Y Zhang**	*Cymbopogon citratus*	Poaceae	*In vitro*	1000 ppm (100%)	López-Meneses et al. (2017)
	Cinnamomum zeylandicum	Lauraceae	*In vitro*	5000 ppm (100%)	López-Meneses et al. (2017)
***Fusarium coeruleum* Lib. ex Sacc.**	*Angelica archangelica*	Apiaceae	*In vitro*	350 ppm (100%)	Fraternale et al. (2016)
***Fusarium sporotrichioides* Sherb.**	*Angelica archangelica*	Apiaceae	*In vitro*	350 ppm (100%)	Fraternale et al. (2016)
***Fusarium tabacinum* (J.F.H. Beyma) W. Gams**	*Angelica archangelica*	Apiaceae	*In vitro*	350 ppm (100%)	Fraternale et al. (2016)
***Fusarium verticillioides* (Sacc.) Nirenberg**	*Angelica archangelica*	Apiaceae	*In vitro*	300 ppm (100%)	Fraternale et al. (2016)
	Cymbopogon citratus	Poaceae	*In vitro*	1000 ppm (100%)	López-Meneses et al. (2017)
	Cinnamomum zeylandicum	Lauraceae	*In vitro*	5000 ppm (100%)	López-Meneses et al. (2017)
***Penicillium notatum* Westling**	*Allium sativum*	Amaryllidaceae	*In vitro*	1.1 ppm (100%)	Arasu et al. (2019)
***Rhizopus microsporus* Tiegh.**	*Allium sativum*	Amaryllidaceae	*In vitro*	3.1 ppm (100%)	Arasu et al. (2019)

polygalacturonases, β-1,4-endoglucanases and expansins, which degrade the cell wall and modify its structure (Davis et al. 2011). Furthermore, it was demonstrated that proteins analogous to CLAVATA3/ESR (CLE) present in the plant play a key role in meristem differentiation and interact with receptors at the level of the membrane, resulting in the formation and maintenance of the giant cells (Guo et al. 2011).

Table 2. Recent *in vitro* essential oils compounds inhibitory activity against post-harvest phytopathogenic fungi.

Fungi	Inhibitory compounds	Inhibitory dose (% of inhibition)	References
***Alternaria tenuissima* var. alliicola T.Y Zhang**	Citral	1000 ppm (100%)	López-Meneses et al. (2017)
	Geraniol	5000 ppm (100%)	López-Meneses et al. (2017)
	Trans-2-hexen-1-ol	5000 ppm (100%)	López-Meneses et al. (2017)
***Fusarium verticillioides* (Sacc.) Nirenberg**	Citral	1000 ppm (100%)	López-Meneses et al. (2017)
	Geraniol	1000 ppm (100%)	López-Meneses et al. (2017)
	Trans-2-hexen-1-ol	5000 ppm (100%)	López-Meneses et al. (2017)
***Fusarium solani* (Mart.) Sacc.**	Trans-cinnamaldehyde	1.31 ppm (50%)	Marei and Abdelgaleil (2018)
	Eugenol	35.43 ppm (50%)	Marei and Abdelgaleil (2018)
***Aspergillus parasiticus* Speare**	Thymol	56.10^{-3} mg/ml air (100%)	Kim et al. (2016a)
	Carvacrol	56.10^{-3} mg/ml air (100%)	Kim et al. (2016a)
	Eugenol	56.10^{-3} mg/ml air (100%)	Kim et al. (2016a)
	Methyl eugenol	56.10^{-3} mg/ml air (59.7%)	Kim et al. (2016a)
***Rhizoctonia solani* (Kuhn.)**	Cinnamaldehyde	75.4 ppm (50%)	Xie et al. (2017)
	Eugenol	58.9 ppm (50%)	Xie et al. (2017)
	Trans-cinnamaldehyde	2.57 ppm (50%)	Marei and Abdelgaleil (2018)
	(–)-menthone	24.69 ppm (50%)	Marei and Abdelgaleil (2018)
	Thymol	50 ppm (88.21%)	Wang et al. (2019)
	Carvacrol	50 ppm (78.76%)	Wang et al. (2019)
***Fusarium oxysporum* (Schltdl.)**	Cinnamaldehyde	156.9 ppm (50%)	Xie et al. (2017)
	Eugenol	52.9 ppm (50%)	Xie et al. (2017)
	Trans-cinnamaldehyde	1.56 ppm (50%)	Marei and Abdelgaleil (2018)
***Aspergillus ochraceus* Wilh.**	Thymol	28.10^{-3} mg/ml air (100%)	Kim et al. (2016a)
	Carvacrol	28.10^{-3} mg/ml air (100%)	Kim et al. (2016a)
	Eugenol	56.10^{-3} mg/ml air (100%)	Kim et al. (2016a)
	Methyl eugenol	56.10^{-3} mg/ml air (58%)	Kim et al. (2016a)
	Citral	400 ppm (100%)	Tang et al. (2018)
	Geraniol	300 ppm (98.38%)	Tang et al. (2018)
***Aspergillus flavus* Link : Fr.**	Citral	500 ppm (100%)	Tang et al. (2018)
	Geraniol	500 ppm (98.44%)	Tang et al. (2018)
***Aspergillus niger* Tiegh.**	Thymol	28.10^{-3} mg/ml air (100%)	Kim et al. (2016a)
	Carvacrol	28.10^{-3} mg/ml air (100%)	Kim et al. (2016a)
	Eugenol	56.10^{-3} mg/ml air (100%)	Kim et al. (2016a)
	Methyl eugenol	56.10^{-3} mg/ml air (66.2%)	Kim et al. (2016a)
	Trans-cinnamaldehyde	3.19 ppm (50%)	Marei and Abdelgaleil (2018)
***Alternaria solani* Sorauer**	Trans-cinnamaldehyde	2.44 ppm (50%)	Marei and Abdelgaleil (2018)
	(–)-menthone	9.31 ppm (50%)	Marei and Abdelgaleil (2018)
	Eugenol	36.37 ppm (50%)	Marei and Abdelgaleil (2018)
	Thymol	50 ppm (50.73%)	Wang et al. (2019)
	Carvacrol	50 ppm (60.42%)	Wang et al. (2019)
***Penicillium digitatum* (Pers.)**	Trans-cinnamaldehyde	0.75 ppm (50%)	Marei and Abdelgaleil (2018)
	(–)-menthone	43.54 ppm (50%)	Marei and Abdelgaleil (2018)
	Eugenol	16.14 ppm (50%)	Marei and Abdelgaleil (2018)
***Penicillium cyclopium* Westling**	α-phellandrene	1800 ppm (100%)	Zhang et al. (2017)
	Nonanal	400 ppm (100%)	Zhang et al. (2017)
***Botrytis cinerea* Pers: Fr.**	Trans-cinnamaldehyde	1.42 ppm (50%)	Marei and Abdelgaleil (2018)
	Thymol	50 ppm (90.50%)	Wang et al. (2019)
	Carvacrol	50 ppm (87.93%)	Wang et al. (2019)
***Phytophthora infestans* (Mot.)**	Trans-cinnamaldehyde	1.80 ppm (50%)	Marei and Abdelgaleil (2018)

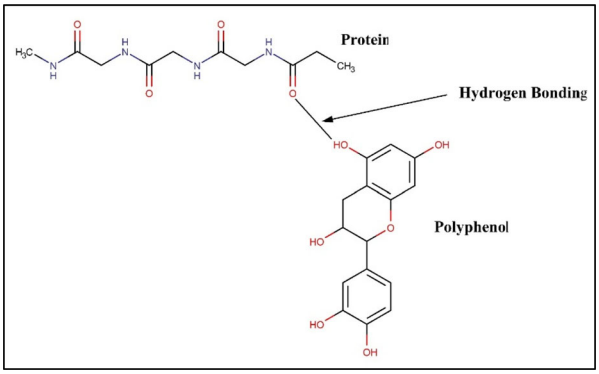

Figure 2. Mechanism of interaction between proteins and polyphenols (Adapted from Asano et al. 1982).

Additionally, the effector Hs19C07 plays a role in hormonal balance, in favor of the formation of the feeding tube (Lee et al. 2011).

Several hypotheses have been proposed to explain the mode of action of EOs against nematodes. Oka (2001) suggested that essential oil components affect nematodes nervous system by acting on acetylcholinesterase, an enzyme necessary for the degradation of acetylcholine (Ach), which is a main neurotransmitter in the central nervous system. The inhibition of the degradation of Ach leads to its accumulation and consequently the convulsion, paralysis and death of the nematode. Oka et al. (2000) related the action of EOs constituents on nematodes to their interference with the cell membranes, and the changes in their permeability. In addition, some aldehydes such as formaldehyde can make irreversible changes to protein structures located on the surface of nematodes (Oka 2001).

2.2.3. Insecticidal activity of essential oils against agricultural pests

A large number of EOs extracted from different families have shown insecticidal activity against several plant and stored grain infesting insects, and mainly against species of the genera *Schistocerca, Spodoptera, Tribolium, Acanthoscelides, Tetranychus*

Table 3. Recent effectiveness of essential oils produced by some plant species against plant parasitic nematodes.

Nematodes	Plant species	Family	Part used	Study	Inhibitory dose (% of inhibition or gall index)	References
***Meloidogyne incognita* (Kofoid and White)**	*Mentha canadensis*	Lamiaceae	Aerial parts	*In vitro*	139 ppm (50%)	Ji et al. (2016)
	Artemisia herba-alba	Asteraceae	Whole plant	*In vitro*	5 ppm (97.4%)	Avato et al. (2017)
	Rosmarinus officinalis	Lamiaceae	Whole plant	*In vitro*	15 ppm (98.3%)	Avato et al. (2017)
	Thymus satureioides	Lamiaceae	Whole plant	*In vitro*	15 ppm (85.7%)	Avato et al. (2017)
	Artemisia herba-alba	Asteraceae	Whole plant	*In vivo*	200 µg/kg soil (gal index = 2.4)	Avato et al. (2017)
	Citrus sinensis	Rutaceae	Whole plant	*In vivo*	200 µg/kg soil (gal index = 3)	Avato et al. (2017)
	Rosmarinus officinalis	Lamiaceae	Whole plant	*In vivo*	200 µg/kg soil (gal index = 3)	Avato et al. (2017)
	Thymus satureioides	Lamiaceae	Whole plant	*In vivo*	200 µg/kg soil (gal index = 3)	Avato et al. (2017)
	Conyza dioscoridis	Asteraceae	Leaves	*In vitro*	186 ppm (50%)	Abbassy et al. (2017)
	Melia azedarach	Meliaceae	Leaves	*In vitro*	315.3 ppm (50%)	Avato et al. (2017)
	Moringa oleifera	Moringaceae	Leaves	*In vitro*	347.3 ppm (50%)	Avato et al. (2017)
	Ocimum sanctum	Lamiaceae	Aerial parts	*In vitro*	282 ppm (50%)	Eloh et al. (2019)
	Cymbopogon schoenanthus	Poaceae	Leaves	*In vitro*	288 ppm (50%)	Eloh et al. (2019)
	Cinnamomum zeylanicum	Lauraceae	Stem and bark	*In vitro*	355 ppm (50%)	Eloh et al. (2019)
	Monarda didyma	Lamiaceae	Aerial parts	*In vitro*	1000 ppm (50%)	Laquale et al. (2018)
	Monarda fistulosa	Lamiaceae	Aerial parts	*In vitro*	1000 ppm (50%)	Laquale et al. (2018)
***Meloidogyne javanica* (Treub) Chitwood**	*Mentha pulegium*	Lamiaceae	Aerial parts	*In vitro*	1010 ppm (95%)	Kimbaris et al. (2017)
	Mentha spicata	Lamiaceae	Aerial parts	*In vitro*	950 ppm (95%)	Kimbaris et al. (2017)
	Piper hispidinervum	Piperaceae	Aerial parts	*In vitro*	1000 ppm (100%)	Andrés et al. (2017)
	Piper hispidinervum	Piperaceae	Aerial parts	*In vivo*	700 ppm (78%)	Andrés et al. (2017)
***Meloidogyne hapla*. Kor.**	*Alpinia galanga*	Zingiberaceae		*In vitro*	125 ppm (100%)	Jeon et al. (2016)
***Pratylenchus vulnus* Allen and Jensen**	*Artemisia herba-alba*	Asteraceae	Whole plant	*In vitro*	15 ppm (67%)	Avato et al. (2017)
	Citrus sinensis	Rutaceae	Whole plant	*In vitro*	15 ppm (73.2%)	Avato et al. (2017)
	Rosmarinus officinalis	Lamiaceae	Whole plant	*In vitro*	15 ppm (75.2%)	Avato et al. (2017)
***Xiphinema index* Thorne and Allen**	*Artemisia herba-alba*	Asteraceae	Whole plant	*In vitro*	2 ppm (100%)	Avato et al. (2017)
	Rosmarinus officinalis	Lamiaceae	Whole plant	*In vitro*	2 ppm (100%)	Avato et al. (2017)
	Thymus satureioides	Lamiaceae	Whole plant	*In vitro*	2 ppm (100%)	Avato et al. (2017)
***Heterodera avenae* Wollenweber**	*Mentha canadensis*	Lamiaceae	Aerial parts	*In vitro*	385.7 ppm (50%)	Ji et al. (2016)
	Kaempferia galanga	Zingiberaceae	Rhizomes	*In vitro*	91.78 ppm (50%)	Li et al. (2017)

Table 4. Recent *in vitro* active essential oil constituents against plant parasitic nematodes.

Nematodes	Inhibitory compounds	Inhibitory dose (% of inhibition)	References
***Meloidogyne incognita* (Kofoid and White)**	Menthol	147.4 ppm (50%)	Ji et al. (2016)
	α-terpinol	115.2 ppm (50%)	Ji et al. (2016)
	Thymol	15 ppm (90%)	Avato et al. (2017)
	1,8-cineole	15 ppm (63.5%)	Avato et al. (2017)
	Trans-2-hexenal	162 ppm (90%)	Lu et al. (2017)
	Cinnamyl acetate	81 ppm (50%)	Eloh et al. (2019)
	Methyl eugenol	117 ppm (50%)	Eloh et al. (2019)
	Cinnamyl alcohol	128 ppm (50%)	Eloh et al. (2019)
	Acetyl eugenol	141 ppm (50%)	Eloh et al. (2019)
	Isoeugenol	168 ppm (50%)	Eloh et al. (2019)
	Eugenol	216 ppm (50%)	Eloh et al. (2019)
	Benzyl benzoate	235 ppm (50%)	Eloh et al. (2019)
	Carvacrol	14.2 ppm (50%)	Laquale et al. (2018)
	γ-terpinene	118.3 ppm (50%)	Laquale et al. (2018)
***Meloidogyne javanica* (Treub) Chitwood**	Safrole	500 ppm (48.6%)	Andrés et al. (2017)
	Safrole/terpinolene (1/9)	500 ppm (50.43%)	Andrés et al. (2017)
	Safrole/terpinolene (1/1)	500 ppm (93.3%)	Andrés et al. (2017)
	Safrole/terpinolene (9/1)	500 ppm (100%)	Andrés et al. (2017)
	Safrole/terpinolene (16/1)	500 ppm (100%)	Andrés et al. (2017)
	Carvacrol	1000 ppm (98%)	Nasiou and Giannakou (2017)
	Piperitenone epoxide	50 ppm (95%)	Kimbaris et al. (2017)
	Piperitone epoxide	210 ppm (95%)	Kimbaris et al. (2017)
	Piperitenone	240 ppm (95%)	Kimbaris et al. (2017)
	R-(-)-carvone	350 ppm (95%)	Kimbaris et al. (2017)
	Geraniol	500 ppm (95%)	Nasiou and Giannakou (2018)
***Heterodera avenae* Wollenweber**	Menthol	242.5 ppm (50%)	Ji et al. (2016)
	α-terpinol	190.3 ppm (50%)	Ji et al. (2016)
	Ethyl cinnamate	100.60 ppm (50%)	Li et al. (2017)
	Ethyl p-methoxy cinnamate	83.04 ppm (50%)	Li et al. (2017)
	Trans-cinnamaldehyde	94.75 ppm (50%)	Li et al. (2017)
	Borneol	734.89 ppm (50%)	Li et al. (2017)
	1,8-cineole	921.21 ppm (50%)	Li et al. (2017)
***Pratylenchus vulnus* Allen and Jensen**	Carvacrol	29.5 ppm (50%)	Laquale et al. (2018)
	O-cymene	82.9 ppm (50%)	Laquale et al. (2018)

Table 5. Essential oils activity against plants insect and mite pests.

Insects	Plant species	Family	Part used	Inhibitory dose (% of inhibition)	References
***Tetranychus urticae* Koch**	*Achillea mellifolium*	Asteraceae	Aerial parts	3.586 µl/l air (50%)	Ebadollahi et al. (2016)
	Mentha longifolia	Lamiaceae	Leaves	11.08 mg/l air (50%)	Reddy and Dolma (2018)
	Mentha piperita	Lamiaceae	Leaves	15.86 mg/l air (50%)	Reddy and Dolma (2018)
	Cymbopogon flexuosus	Poaceae	Leaves	17.23 mg/l air (50%)	Reddy and Dolma (2018)
	Chrysopogon zizanioides	Poaceae	Leaves	18.82 mg/l air (50%)	Reddy and Dolma (2018)
***Tribolium castaneum* Herbst**	*Citrus limon*	Rutaceae		25.52 mg/l air (50%)	Abou-Taleb et al. (2016)
	Myrtus communis	Myrtaceae		26.51 mg/l air (50%)	Abou-Taleb et al. (2016)
	Schinus terebinthifolius	Anacardiaceae		28.19 mg/l air (50%)	Abou-Taleb et al. (2016)
	Origanum vulgare	Lamiaceae		9.97 mg/l air (50%)	Abou-Taleb et al. (2016)
	Callistemon viminalis	Myrtaceae		18.86 mg/l air (50%)	Abou-Taleb et al. (2016)
	Citrus sinensis	Rutaceae		24.57 mg/l air (50%)	Abou-Taleb et al. (2016)
	Tanacetum tomentosum	Asteraceae	Aerial parts	20 µl/0.25 l air (90%)	Haider et al. (2017)
	Ta. Dolichophyllum	Asteraceae	Aerial parts	20 µl/0.25 l air (77.50%)	Haider et al. (2017)
	Artemisia frigida	Asteraceae	Aerial parts	6.79 mg/l air (50%)	Zhang et al. (2019)
***Bruchus rufimanus* (Bohman)**	*Mentha suaveolens*	Lamiaceae	Leaves and flowers	100 µl/l air (100%)	Amzouar et al. (2016)
***Callosobruchus maculatus* (Fabr.)**	*Citrus latifolia*	Rutaceae	Fruit peels	10.02 µl/l air (50%)	De Andrade Dutra et al. (2016)
	Citrus reticulata	Rutaceae	Fruit peels	12.68 µl/l air (50%)	De Andrade Dutra et al. (2016)
	Citrus sinensis	Rutaceae	Fruit peels	12.98 µl/l air (50%)	De Andrade Dutra et al. (2016)
	Citrus paradisi Macf.	Rutaceae	Fruit peels	12.63 µl/l air (50%)	De Andrade Dutra et al. (2016)
***Sitophilus oryzae* (L.)**	*Artemisia judaica*	Asteraceae	Aerial parts	29.97 ppm (50%)	Abdelgaleil et al. (2016)
	Cupressus sempervirens	Cupressaceae	Leaves	17.16 ppm (50%)	Abdelgaleil et al. (2016)
	Myrtus communis	Myrtaceae	Leaves	27.40 ppm (50%)	Abdelgaleil et al. (2016)
	Origanum vulgare	Lamiaceae	Aerial parts	1.64 ppm (50%)	Abdelgaleil et al. (2016)
	Artemisia monosperma	Asteraceae	Leaves	0.15 mg/cm^2 (50%)	Abdelgaleil et al. (2016)
	Astoma seselifolium	Apiaceae	Leaves	0.16 mg/cm^2 (50%)	Abdelgaleil et al. (2016)
	Pelargonium graveolens	Geraniaceae	Leaves	0.17 mg/cm^2 (50%)	Abdelgaleil et al. (2016)
	Pituranthos tortuosus	Apiaceae	Aerial parts	0.19 mg/cm^2 (50%)	Abdelgaleil et al. (2016)
	Thymbra capitata	Lamiaceae	Aerial parts	3.4 µl/l air (50%)	Koutsaviti et al. (2018)
	Salvia pomifera	Lamiaceae	Aerial parts	4.4 µl/l air (50%)	Koutsaviti et al. (2018)
	Salvia fruticosa	Lamiaceae	Aerial parts	15.5 µl/l air (50%)	Koutsaviti et al. (2018)
	Laurus nobilis	Lauraceae	Leaves	8.0 µl/l air (50%)	Koutsaviti et al. (2018)
	Salvia officinalis	Lamiaceae	Aerial parts	9.9 µl/l air (50%)	Koutsaviti et al. (2018)
	Callistemon viminals	Myrtaceae	Leaves	16.17 ppm (50%)	Abdelgaleil et al. (2016)
	Citrus aurantifolia	Rutaceae	Fruit peels	29.37 ppm (50%)	Abdelgaleil et al. (2016)
	Citrus limon	Rutaceae	Fruit peels	9.89 ppm (50%)	Abdelgaleil et al. (2016)
	Citrus paradisi	Rutaceae	Fruit peels	24.13 ppm (50%)	Abdelgaleil et al. (2016)
	Citrus sinensis	Rutaceae	fruit peels	19.67 ppm (50%)	(Abdelgaleil et al. 2016)
	Hyssopus offcinalis	Lamiaceae		25 mg/l air (100%)	Kim et al. (2016b)
	Origanum majorana	Lamiaceae		25 mg/l air (100%)	Kim et al. (2016b)
	Thymus zygis	Lamiaceae		25 mg/l air (100%)	Kim et al. (2016b)
***Rhyzopertha dominica* (F.)**	*Mentha pulegium*	Lamiaceae	Leaves	6900 ppm (50%)	Brahmi et al. (2016)
	Mentha rotundifolia	Lamiaceae	Leaves	3300 ppm (50%)	Brahmi et al. (2016)
***Trichoplusia ni* (Hübner)**	*Bunium persicum*	Apiaceae	Fruits	277.9 ppm (50%)	Khanavi et al. (2017)
	Pistacia atlantica	Anacardiaceae	Aerial parts	653.5 ppm (50%)	Khanavi et al. (2017)
	Thymus kotschyanus	Lamiaceae	Aerial parts	449 ppm (50%)	Khanavi et al. 2017)
	Thymus vulgaris	Lamiaceae		54 µg/insect (50%)	Tak et al. (2016b)
	Cymbopogon citratus	Poaceae		123.8 µg/insect (50%)	Tak et al. (2016b)
	Rosmarinus officinalis	Lamiaceae		215.8 µg/larva (50%)	Tak et al. (2016a)
***Liposcelis bostrychophila* Badonnel**	*Artemisia frigida*	Asteraceae	Aerial parts	0.52 mg/l air (50%)	Zhang et al. (2019)
***Lasioderma serricorne* (F.)**	*Artemisia frigida*	Asteraceae	Aerial parts	4.53 mg/l air (50%)	Zhang et al. (2019)

and Sitophilus. Plant families that were mostly studied include Lamiaceae, Rutaceae, Asteraceae, Myrtaceae, Apiaceae, and Zingiberaceae (Table 5). Lamiaceae is the most studied family, with species of the genera *Thymus, Origanum, Salvia, Majorana, Rosmarinus, Mentha*, and *Lavendula*. Examples of inhibitory species include *Ocimum basilicum* and *Origanum vulgare*, which gave 90% inhibition to *Schistocerca gregaria* (Forskål) at small doses of 1.84 and 1.88 ppm respectively (Mansour et al. 2015). Elsewhere, *Satureia hortensis* inhibited completely *Spodoptera litura* Fab.at 100 µg/larva (Isman et al. 2001), and *Origanum onites* and *Satureja thymbra* both showed 100% inhibition activity of *Ephestia kuehniella* Zeller at 9 µl/l air (Ayvaz et al. 2010). Table 5 and Table 6 refer to some examples of EOs and their constituents that proved their effectiveness in inhibition of insect pests of plants.

The study of involved mechanisms showed that essential oils act on insects in several ways. They can be toxic by direct contact, like EOs of *Artemisia monosperma*, *Astoma seselifolium, Pelargonium graveolens* and *Pituranthos Tortuosus*, which are active against *S. oryzae*, with LC_{50} values of 0.15, 0.16, 0.17 and 0.19 mg/cm^2, respectively. Others act by fumigation, such as EOs of *Artemisia judaica, Callistemon viminals, Citrus aurantifolia, Citrus limon, Citrus paradisi, Citrus sinensis, Cupressus*

Table 6. Activity of essential oil compounds against plant insect and mite pests.

Insects	Inhibitory compounds	Inhibitory dose (% of inhibition)	References
***Sitophilus oryzae* (L.)**	Carvacrol	2.4 µl/l air (50%)	Koutsaviti et al. (2018)
	Cis-thujone	5.1 µl/l air (50%)	Koutsaviti et al. (2018)
	Cis- and trans-thujone	4.5 µl/l air (50%)	Koutsaviti et al. (2018)
	Sabinene hydrate	3.9 mg/l air (100%)	Kim et al. (2016b)
	Linalool	3.9 mg/l air (100%)	Kim et al. (2016b)
	α-terpineol	3.9 mg/l air (100%)	Kim et al. (2016b)
	Terpinen-4-ol	3.9 mg/l air (100%)	Kim et al. (2016b)
***Trichoplusia ni* (Hübner)**	Cuminaldehyde	128.7 ppm (50%)	Khanavi et al. (2017)
	P-cymene	39.8 ppm (50%)	Khanavi et al. (2017)
	γ-terpinene	65.4 ppm (50%)	Khanavi et al. (2017)
	Limonene	87.1 ppm (50%)	Khanavi et al. (2017)
	P-cymene / γ-terpinene (25/75)	38.1 ppm (50%)	Khanavi et al. (2017)
	Thymol	32.6 µg/insect (50%)	Tak et al. (2016b)
	P-cymene	125.8 µg/ml air (50%)	Tak et al. (2016b)
	α-pinene	181.8 µg/ml air (50%)	Tak et al. (2016b)
	α-terpineol	61.9 µg/insect (50%)	Tak et al. (2016a)
	1,8-cineole	229.6 µg/larva (50%)	Tak et al. (2016a)
	(±)-camphor	471.3 µg/larva (50%)	Tak et al. (2016a)
	α-terpineol	61.9 µg/larva (50%)	Tak et al. (2016a)
	1,8-cineole / (±)-camphor (50/50)	214.9 µg/insect (50%)	Tak et al. (2016a)
***Tetranychus urticae* koch**	Isofuranodiene	15.8 µg cm^{-2} (50%)	Benelli et al. (2017)
	Germacrone	42.7 µg cm^{-3} (50%)	Benelli et al. (2017)
	1,8-cineole	17.59 ppm (50%)	Abdelgaleil et al. (2019)
	(-)citronellal	44.54 ppm (50%)	Abdelgaleil et al. (2019)
	Limonene	11.55 ppm (50%)	Abdelgaleil et al. (2019)
	α-pinene	18.24 ppm (50%)	Abdelgaleil et al. (2019)
	Pulegone	7.48 ppm (50%)	Abdelgaleil et al. (2019)
	4-terpineol	31.74 ppm (50%)	Abdelgaleil et al. (2019)
***Drosophila melanogaster* Meig.**	Terpinolene	0.09 ppm (50%)	Zhang et al. (2016)
	3-carene	0.28 ppm (50%)	Zhang et al. (2016)
	Eugenol	0.03 ppm (50%)	Zhang et al. (2016)
	Thymol	0.07 ppm (50%)	Zhang et al. (2016)
	Carvacrol	0.04 ppm (50%)	Zhang et al. (2016)
	Isoeugenol	0.05 ppm (50%)	Zhang et al. (2016)
	Citral	0.06 ppm (50%)	Zhang et al. (2016)
	(±)-citronellal	0.015 ppm (50%)	Zhang et al. (2016)
	Cuminaldehyde	0.07 ppm (50%)	Zhang et al. (2016)
	(−)-verbenone	0.03 ppm (50%)	Zhang et al. (2016)
	(+)-pulegone	0.02 ppm (50%)	Zhang et al. (2016)
***Liposcelis bostrychophila* Badonnel**	Terpinen-4-ol	0.08 mg/l air (50%)	Zhang et al. (2019)
	Verbenone	0.14 mg/l air (50%)	Zhang et al. (2019)
	α-terpineol	0.58 mg/l air (50%)	Zhang et al. (2019)
	α-terpinyl acetate	0.39 mg/l air (50%)	Zhang et al. (2019)
***Lasioderma serricorne* (F.)**	Terpinen-4-ol	6.90 mg/l air (50%)	Zhang et al. (2019)
	Camphene	8.78 mg/l air (50%)	Zhang et al. (2019)
	α-terpineol	3.27 mg/l air (50%)	Zhang et al. (2019)
***Tribolium castaneum* Herbst**	Terpinen-4-ol	3.74 mg/l air (50%)	Zhang et al. (2019)
	Verbenone	7.09 mg/l air (50%)	Zhang et al. (2019)
	Camphene	4.10 mg/l air (50%)	Zhang et al. (2019)

sempervirens, Myrtus communis, Origanum vulgare, Rosmarinus officinalis, Schinus molle and *Schinus terebinthifolius.* They were toxic to *S. oryzae,* with LC_{50} values ranging from 1.64 mg/l to 29.97 mg/l (Abdelgaleil et al. 2016).

It was also shown that EOs of *Cinnamomum cassia, Litsea cubeba, Mentha piperita, Satureia hortensis, Perilla frutescens* and *Thymus vulgaris* and their major compounds (−)-perillaldehyde, carvacrol, cinnamaldehyde, thymol, (−)-menthol and citral, repelled the insect *L. serricorne* at a dose of 0.1 µl for Eos and at a dose of 1 µl or 1 mg for compounds (Hori 2003). Alternatively, they can hinder insects from feeding (Hummelbrunner and Isman 2001). Essential oils also inhibit insects by affecting their reproduction. Thus, it was described that EOs of *Mentha viridis, Mentha microphylla, Lavandula hybrida, Rosmarinus officinalis* and *Eucalyptus globulus* reduce fertility in the insect *Acanthoscelides obtectus* (Say), and those of *Eucalyptus globules* and *Origanum vulgare* reduce egg hatching (Papachristos and Stamopoulos 2002). Similarly, oxygenated compounds such as linalool, eugenol, carvacrol and terpineol inhibit reproduction of the insect *A. obtectus,* by inhibition of oviposition and emergence of the imagos (Regnault-Roger and Hamraoui 1995).

Many involved mechanisms of action of EOs on insects were described. Rattan (2010) attributed their action to the influence on biochemical processes, which interrupt the endocrinological balance of insects. Moreover, he suggested interference with the γ-aminobutyric acid (GABA) receptor in insects. Other authors referred the effect of essential oil compounds on insects to their action on octopamine, which plays key roles as a neurotransmitter, neuromodulator and neurohormone in invertebrate system. Monoterpenes cinnamyl alcohol, eugenol

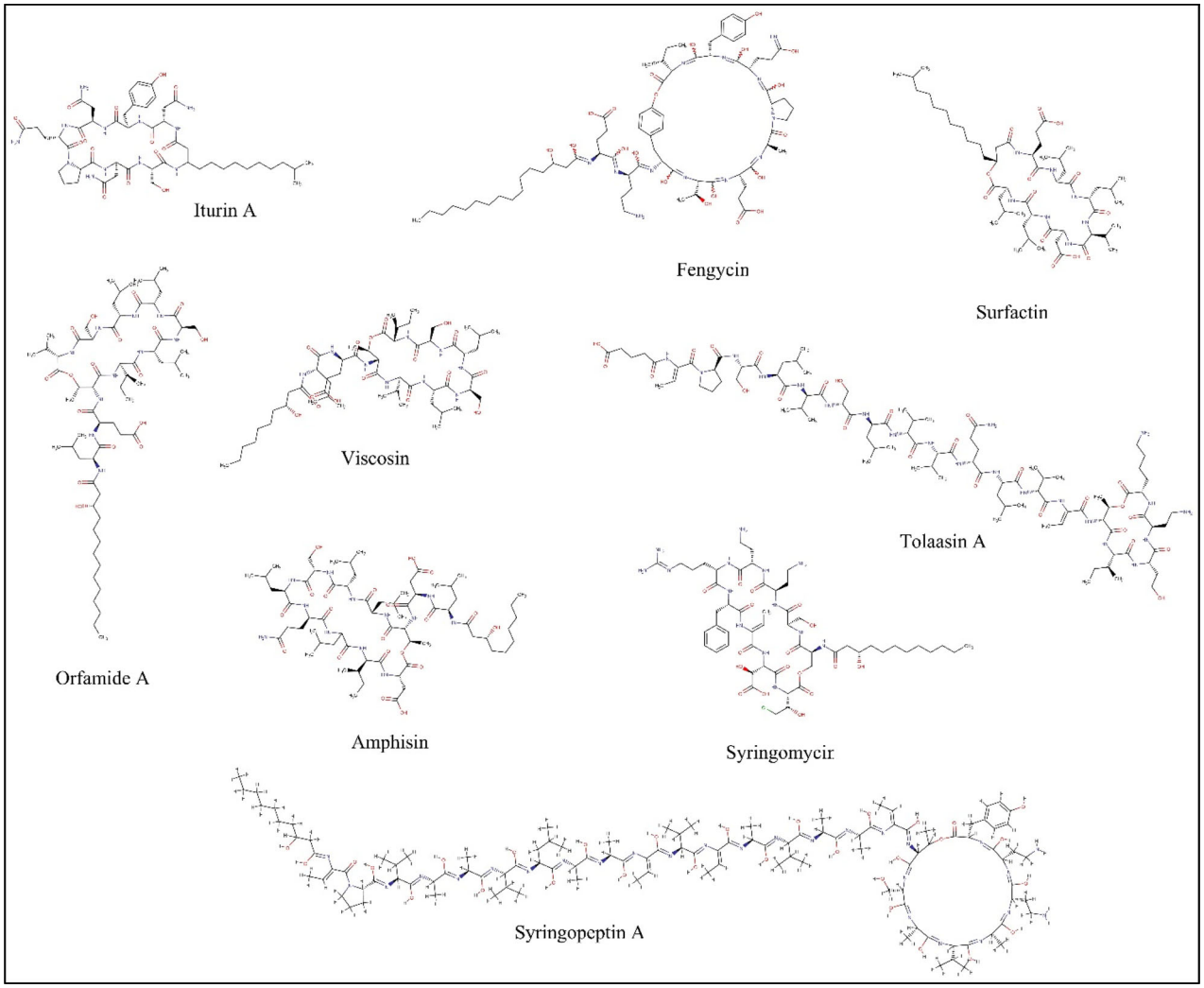

Figure 3. 2 D chemical structures of selected lipopeptides produced by *Bacillus* and *Pseudomonas*. *Bacillus* lipopeptides [iturins (iturin A $C_{48}H_{74}N_{12}O_{14}$), fengycins (fengycin $C_{72}H_{110}N_{12}O_{20}$) and surfactins (surfactin $C_{53}H_{93}N_7O_{13}$)]. *Pseudomonas* lipopeptides [viscosin (viscosin $C_{54}H_{95}N_9O_{16}$), orfamide (orfamide A $C_{64}H_{114}N_{10}O_{17}$), syringomycin (syringomycin $C_{53}H_{85}ClN_{14}O_{17}$), amphisin (amphisin $C_{66}H_{114}N_{12}O_{20}$), syringopeptin (syringopeptin $C_{113}H_{183}N_{27}O_{30}$) and tolaasin (tolaasin A $C_{91}H_{155}N_{21}O_{26}$)].

and trans-anethole act on octopamine by blocking octopamine receptors (Enan 2005; Rattan 2010). In the same context, Abdelgaleil et al. (2019) reported the efficacy of monoterpenes 1,8-cineole, (−)-citronellal, limonene, α-pinene, pulegone and 4-terpineol against the mite *T. urticae* to their inhibition of acetylcholinesterase, as they compete with acetylcholine, for its active center on acetylcholinesterase. Symptoms of a neurotoxic mode of action include hyperactivity, tremor, forced diuresis and convulsion, resulting in immobilization and death of the insect (Hummelbrunner and Isman 2001). Authors also reported inhibition of EOs to ATPase activity in targeted insects. Abdelgaleil et al. (2016) reported that EOs of *Callistemon viminalis* and *Origanum vulgare* inhibit ATPase activity in the insect *S. oryzae*. The same finding was found using essential oil of *Callistemon viminalis* against the insect *T. castaneum* (Abou-Taleb et al. 2016). Complex mixtures of molecules contained in EOs with differing mechanisms of action, may be efficient in preventing the development of resistant pathogens and pests. This is an additional benefit of developing biopesticides from EOs (Pavela and Benelli 2016).

Through analysis of recent studies that investigate the activities of EOs against plant pathogens, it can be noted that the majority of studies have been limited to laboratory experiments. Only few studies have explored the field effectiveness of EOs. This step is crucial for large scale application of EOs. It confirms the biocidal effect of oils on the target pathogen, and reveals any phytotoxicity of oils on the plants. On the other hand, it enables the estimation of the required amounts in EOs for pathogen control in fields, to decide if the complete process of application of EOs is cost efficient.

2.3. Application limits of essential oils

In spite of considerable research effort throughout the world, and the ever increasing volume of scientific literature, the exploitation of EOs for management of plant pathogens in open fields or greenhouses hasn't been sufficient. Commercialized

pest control products based on essential oils are limited (Koul et al. 2008). Hence, there is noticeable delay towards the development end of the spectrum.

Several challenges hinder the commercialization of essential oils as biopesticides. First, there is the heavy regulatory process of approval for biopesticides, standardization and refinement of pesticide products, and protection of technology (patents). Several plant EOs are exempt from registration in the United States, however it is not the case for most countries (Isman 2005; Isman and Machial 2006). Solving this barrier requires the adjustment of regulatory systems to better accommodate these products (Isman and Machial 2006), which will clear a path for approval of more biopesticides, and enable development of EOs on commercial scale. On the other hand, there is an issue of efficacy. Essential oils often fell short in terms of efficacy in comparison with synthetic pesticides, although there are specific pest contexts where EOs produced the same level of control as conventional products (Koul et al. 2008). They may require great volumes to complete their action, or frequent reapplications when used in fields, which can be a challenge, as the availability of sufficient quantities of plant material is not always guarantied all year round. Many plant species have low yields and therefore can't be convenient for large-scale commercial application, as the latter requires great production of EOs (Koul et al. 2008). Appealing to farmers requires providing solutions that are not only effective but economical. Essential oil based pesticides (EOBP) often require greater volumes for use, consequently, significant application costs. Thus, they aren't able to compete in terms of cost with conventional chemical pesticides. To compensate for this, it is necessary to invest in innovative and more efficient extraction processes (e.g., microwave extraction and super critical fluid extraction), that enable increase of extraction yield. The choice of suitable chemotypes with high yields is also fundamental for practical use of EOs.

Moreover, frequent applications of EOBP may result in phytotoxicity if they are misused. Almost any oil can be phytotoxic if applied at concentrations exceeding 2% (as an aqueous emulsion), and in some cases at a concentration as low as 1% (Isman 2016). Creating formulations that combine EOs with other natural molecules like microbial substances can enhance EOBP, as it allows the reduction of volumes used in EOs while potentially improving the effectiveness of the product (Dimkić et al. 2015).

Other challenges include persistence, i.e., how long the product remains biologically active against target pests after application to the targeted area, and consistency in the performance, as the chemical profile of essential oils changes due to many intrinsic and extrinsic factors previously mentioned (Isman 2016). This will require regular testing of EOBP by their manufacturers and thus additional work and charges (Koul et al. 2008). Both issues could be mitigated through microencapsulation of EOs (Yang et al. 2009). Encapsulation is suitable for entrapping EOs with different chemical composition. This method reduces loss of the active principles (Moretti et al. 2002). It also offers the possibility of controlled release, thus, extending the residual activity of EOBP from hours to days (or even weeks) in the field (De Oliveira et al. 2014). Encapsulation in liposomes enables overcoming physicochemical stability concerns of EOs (sensibility to oxygen, light, temperature, and volatility) and their reduced bioavailability which is due to low solubility in water (Detoni et al. 2012).

The safety of a number of EO-based products has been reported on humans and other vertebrates. However, only moderate efforts have been carried out to shed light on the potential effects of EOs on non-target organisms, sharing the same ecological niche as the target pests (Pavela and Benelli 2016). In some cases, EOs were found to be toxic against non-target organisms. Essential oil of *Corymbia citriodora* caused high mortality of the pollinator bee *Tetragonisca angustula* Latreille (Ribeiro et al. 2018). Preventing this effect, requires following of the principles of ecological selectivity (Hull and Beers 1985), in which the application of botanical pesticides should be carried out at dusk in order to avoid periods of higher pollinator activity (i.e., warmer periods of the day) (De Bruijn and Sommeijer 1997). In the same context, EOs of *Melaleuca alternifolia, Myroxylon Pereira, Melaleuca linariifolia* and *Melaleuca quinquenervia*, have been proved to be toxic towards the non-target water flea, *Daphnia magna* Straus (Park et al. 2011; Seo et al. 2012; Conti et al. 2014). Thorough toxicological tests are needed on non-target organisms, such as earthworms, parasitoids and predators of moth pests, to ensure that potential botanical pesticides based on EOs are completely safe for the environment. This knowledge could be used to determine the optimal application dose of potential botanical pesticides based on EOs (Pavela and Govindarajan 2017; Benelli et al. 2018).

3. Lipopeptides

3.1. Lipopeptides, composition and ecological functions

Microorganisms produce surface and interface compounds that possess an antagonistic activity, namely lipopeptides, glycolipids, phospholipids, polysaccharides, fatty acids and protein complexes, of which

lipopeptides are the most renowned (Georgiou et al. 1992; Neu 1996; Ron and Rosenberg 2001; Kim et al. 2004). Their easy biodegradation in nature, minimal environmental toxicity and high stability towards extreme temperature, pH, and salinity makes them suitable for use as biological control agents (Ron and Rosenberg 2001; Inès and Dhouha 2015). They are produced by a wide range of bacteria such as species of genera *Bacillus, Pseudomonas, Enterobacter, Streptomyces* and *Erwinia* (Javaheri et al. 1985; Levy et al. 1992; Chernin et al. 1995; Bryk et al. 1998; Gomes et al. 2001). The focus in this review will be on the two genera *Bacillus* and *Pseudomonas*.

Having an amphiphilic nature, they consist of a cyclic oligopeptide linked to a lipid fraction (examples in Figure 3). Lipopeptides produced by the genus *Bacillus* are classified into three families according to their amino acid sequences: surfactins, iturins and fengycins (Ongena and Jacques 2008). These amphiphilic substances are composed of seven (surfactins, iturins) or ten α-amino acids (fengycins), linked to one unique β-hydroxy (surfactins, fengycins) or β-amino (iturins) fatty acid. The length of this fatty-acid chain may vary from C14 to C18 for fengycins, C14 to C17 for iturins and C13 to C16 for surfactins (Ongena et al. 2005). Lipopeptides produced by *Pseudomonas* spp. are classified in six groups: viscosin (Groupé et al. 1951), syringomycin (Segre et al. 1989), syringopeptin (Ballio et al. 1991), amphisin (Sørensen et al. 2001), tolaasin (Bassarello et al. 2004), and orfamide groups (Ma et al. 2016b). Discovery of new lipopeptides in numerous environments is ongoing. These can either be assigned to an existing group (Zachow et al. 2015; Ma et al. 2016b; Götze et al. 2017) or constitute a new group, such as the recently discovered xantholysins (Li et al. 2013) and bananamides (Nguyen et al. 2016).

Lipopeptides play important ecological roles in their ecosystems. They are involved in the process of plant root colonization by rhizobacteria. For example surfactins, which play a crucial role in the formation of biofilm by *Bacillus subtilis* 6051 around the roots of *Arabidopsis*, and thus the colonization of roots and their protection against *Pseudomonas syringae* pv tomato DC3000 (Bais et al. 2004). Arthrofactin produced by *Pseudomonas* sp. MIS38 also contributed to formation of biofilms (Roongsawang et al. 2003). The movement of bacteria on the roots during the production of biofilms is carried out by produced lipopeptides, such as surfactin (family of surfactins) and mycosubtilin (family of iturines) lipopeptides, which facilitate the propagation of a *B. subtilis* isolate (Leclère et al. 2006).

In addition to biofilm formation, lipopeptides destroy biofilms created by pathogenic bacteria. In fact, surfactin inhibits the biofilm formation for several bacteria such as *Salmonella enterica* serovar typhimurium, *Listeria monocytogenes* ATCC 7644 and ATCC 19112 and *Pseudomonas fluorescens* ATCC 13525 (Mireles et al. 2001; De Araujo et al. 2016). Moreover, putisolvins I and II lipopeptides produced by *Pseudomonas putida* PCL1445, inhibit biofilms formation of different species of *Pseudomonas* (Kuiper et al. 2004).

Lipopeptides also possess the chelating capacity for metal ions. Examples are lipopeptides iturin and gramicidin S, that have an affinity towards cations Rb^+, Na^+ and K^+(Rautenbach et al. 2000). This capacity is useful to the bacteria producing these lipopeptides, like siderophores, which exploit these metal ions as micronutrients (Raaijmakers et al. 2010). Further, lipopeptides that possess this capacity can detach metal ions from soil, which can be useful to treat soils contaminated with heavy metals (Mulligan et al. 2001).

Furthermore, they play a role in the induction of "induced systemic resistance" (ISR) in the host plant. It was shown that surfactin and fengycin produced by *Bacillus* spp. induce ISR in beans (Ongena et al. 2007), and massotolide A produced by *Pseudomonas fluorescens* SS101,which triggers ISR in tomato acts indirectly on the pathogen *P. infestans*, hence limiting its growth on the infected plant (Tran et al. 2007).

The process by which lipopeptides induce ISR has been detailed by many studies. The work of Ongena et al. (2005) showed that fengycins produced by *B. subtilis* M4 are involved in inducing ISR in potatoes, by stimulating the production of phenolic compounds by the plant (chlorogenic acid, ferulic acid, tyrosine, and cinnamic acid). Likewise, the inoculation of roots of cucumber by *Pseudomonas putida* BTP1 induced the production of antifungal compounds (phenols and aglycones), which contribute to the protection of the plant against *Pythium aphanidermatum* (Edson) Fitz. (Ongena et al. 1999). Jourdan et al. (2009) stated that lipopeptides are capable of inducing ISR by perturbation of the membrane, which triggers a cascade of reactions including alkalinization of the medium, ion flux, stimulation of the enzymes lipoxygenase and phenylalanine ammonia lyase, and the production of reactive species of oxygen. These changes are not irreversible, and are aimed only at the perturbation of the membrane, in order to trigger the ISR. Thus, the presence of lipopeptides is not associated with phytotoxicity or a repressive effect on plant growth. In the same context, lipopeptides mycosubtilin and surfactin produced by *B. subtilis* strains BBG131, BBG125 and Bs2504 stimulate grapevine innate immune responses, by stimulating

defense gene expression. Gene expression analyses suggest that mycosubtilin activates jasmonic acid and salicylic acid (SA) signaling pathways, whereas surfactin mainly induces an SA-regulated response. The two lipopeptides were efficient also at protecting grapevine plants against the fungus *B. cinerea*. The treatment of grapevine plants by mycosubtilin and surfactin separately prior to infection with *B. cinerea,* led to a local long-lasting enhanced tolerance to the fungus (Farace et al. 2015).

3.2. Biological activities of lipopeptides

The surfactin family compounds produced by *Bacillus* spp., are recognized mainly by their antimicrobial activity. They interfere with cell membranes in a proportional manner to their doses, due to their amphiphilic properties (Ongena and Jacques 2008). Surfactin produced by *B. subtilis* C4 allowed the inhibition of seven isolates of *L. monocytogenes* at a dose of 0.125 mg/ml (Sabaté and Audisio 2013). Similarly, surfactin produced by *B. subtilis* fmbj allowed the destruction of spores of *Bacillus cereus* (Huang et al. 2007). Some studies have shown that surfactins also possess antifungal activity. The example with surfactin produced by *Bacillus licheniformis* BC98, which allowed the inhibition of the fungus *Magnaporthe grisea* (Herbert) Barrat a minimal concentration of 1 μg/ml, in addition to the inhibition of other fungi (Tendulkar et al. 2007). Mycosubtilin produced by *B. subtilis* strains also showed potent *in vitro* and *in vivo* inhibitory activities, alone and in combination with surfactin against the fungus *F. oxysporum,* on rhizomes of *Iris germanica* odoratissima infected with the fungus. Activity of mycosubtilin results from its ability to inhibit spore formation and germination, and to damage the hyphal cell wall structures in an irreversible manner (Mihalache et al. 2018).

The fengycin family compounds are recognized by their antifungal properties (Deleu et al. 2005). They proved to be antifungal against a wide range of phytopathogenic fungi such as *B. cinerea, R. solani, R. stolonifer, Podosphaera fusca* SF48*, F. oxysporum* and *Fusarium graminearum* Schw. (Touré et al. 2004; Romero et al. 2007; Wang et al. 2007; Tao et al. 2011; Guo et al. 2014; Zhao et al. 2014). Fengycin A produced by *B. subtilis* IB inhibits the growth of the fungus *F. graminearum* by destroying the integrity of the pathogen's membrane, leading to disturbance of the metabolism and consequently disturbance of the fungal growth (Wang et al. 2007), and fengycin produced by *B. subtilis* fmbJ acts on cell membranes, cellular organs and inhibition of DNA synthesis on the fungus *R. stolonifer* (Tao et al. 2011).

The iturin family compounds are known for their antifungal and in some cases antimicrobial activities (Ongena and Jacques 2008). Iturins produced by *B. amyloliquefaciens* RC-2 allowed the inhibition of the fungus *Colletotrichum dematium* (Pers.: Fr.) Grove (Hiradate et al. 2002). Similarly, bacillomycin D produced by *B. subtilis* AU195, exerts antifungal activity against the fungus *A. flavus* (Moyne et al. 2001). The mechanism of action differs from those of surfactins and fengycins, which primarily disrupt the membrane. A study by Aranda et al. (2005) demonstrated that iturin A acts onosmotic perturbation, with the creation of ion-conducting pores.

From *Pseudomonas* spp., syringotoxin, syringomycin E, syringopeptin SP22A, syringopeptin SP25A, tolaasin I and II, white line inducing principle and putisolvin-like lipopeptides exert antifungal activity against the grey mold agent *B. cinerea* (Lavermicocca et al. 1997; Andolfi et al. 2008; Kruijt et al. 2009). Pseudophomins A and B isolated from *P. fluorescens* strain BRG100 displayed antifungal activity against the phytopathogens *Phoma lingam* (Tode ex Fr.) Desm. and *S. sclerotiorum,* the causal agents of black-leg and white mold diseases respectively (Pedras et al. 2003). Massetolide A was antifungal against *P. infestans* (Van de Mortel et al. 2009), and sringomycin E produced by *P. syringae* strains ESC-10 and ESC-11 suppressed *P. digitatum,* the agent of green mold of citrus (Bull et al. 1998). In the same context, tensin, viscosinamide, orfamide, unamycin, pseudophomins, poaeamide and putisolvin-like lipopeptides were antifungal against *R. solani* (Hansen et al. 2000; Nielsen et al. 2000; Pedras et al. 2003; Kruijt et al. 2009; Raaijmakers et al. 2010; Michelsen et al. 2015; Zachow et al. 2015; Ma et al. 2016b). Some lipopeptides were found to be antifungal only when used in combinations, the example of lipopeptides orfamide A and sessilin-(T) produced by *Pseudomonas* sp. CMR12, which were able to inhibit growth of *R. solani* when applied together (Olorunleke et al. 2015).

Other than their action on fungi and bacteria, few studies were reported on lipopeptides action on plant insects. From *Bacillus* spp., surfactin C14 and C15 purified from *B. subtilis* (S499 strain) showed insecticidal activity against the fruit fly *D. melanogaster*. Being incorporated to artificial diet of the insect at 100 ppm, surfactin C14 and C15 showed respectively 85.4 and 92.6% adults mortality after one-day exposure (Assie et al. 2002). *B. subtilis* SPB1 biosurfactant was evaluated against larvae of the Egyptian cotton leaf worm *Spodoptera littoralis* (Bosid.) and the Mediterranean flour moth *E. kuehniella*, and the obtained LC_{50} values were 251 ng/cm^2 and 257 µg/g respectively. Furthermore, histopathological changes were observed in the

larval midgut of both insects. These include vesicle formation in the apical region, cellular vacuolization and destruction of epithelial cells and their boundaries (Ghribi et al. 2012a, 2012b, 2012c).

From *Pseudomonas* spp., orfamide A produced by *Pseudomonas protegens* F6 exhibited insecticidal activity against green peach aphid *Myzus persicae* (Sulzer), producing an LC_{50} of 34.5 μg/mL (Jang et al. 2013). The same lipopeptide was required for full oral toxicity of *Pseudomonas protegens* strain Pf-5 against *D. melanogaster* (Loper et al. 2016). Similarly, orfamide produced by *P. protegens* CHA0 and *Pseudomonas* sp. CMR12a was important in oral infections of the cabbage moth *Plutella xylostella* (L.) (Flury et al. 2017). Moreover, xantholysines A and B isolated from *Pseudomonas* sp. DJ15 were insecticidal against *M. persicae* (Lim et al. 2017), and viscosin applied topically produced mortality of several aphids (Hashimoto 2002).

To our knowledge, lipopeptides have not been tested on nematodes. Thus, research must be oriented towards this axis. Further research is also required towards control of plant insects, for a global management approach.

Published studies on the biological efficacy of lipopeptides are limited to their *in vitro* or *in vivo* screening efficacy against target organisms. The work done so far on activities of lipopeptides against plant pathogens is thus only the first step in the development of lipopeptides based products. There is a knowledge gap on effects of lipopeptides on non-target organisms, while such research is important to prevent ecotoxicological effects. Hence the next step towards the development of products based on lipopeptides must include investigating the effects of lipopeptides on non-target organisms.

3.3. Application limits of lipopeptides

Production and application of lipopeptides at industrial scales is faced with many constraints. The main one is the high production cost, associated with the use of expensive commercial media (Makkar and Cameotra 2002). Thus, during the last decade, research has shifted towards finding cost-free or low-cost substrates for lipopeptides production (Zouari et al. 2014). Several by-products of agro-industrial origin have been reported as low cost alternative substrate, such as soybean (Abalos et al. 2001), rice straw (Zhu et al. 2012) and potato waste (Ayed et al. 2018). Other challenges include inefficient production and recovery methods. Improving the lipopeptide production process to become cost-competitive requires development of efficient multistep downstream processing methods, including optimization of the culture conditions, and separation processes for maximum production and recovery of lipopeptides. Reducing the final products cost also requires improving the production yield of the producer bacterial strains (Mukherjee et al. 2006). Using recombinant and mutant overproducing microbial strains, which are able to grow on a wide range of cheap substrates, could produce lipopeptides in high yields (Banat et al. 2010). Furthermore, the process byproducts should be minimal or managed as recycled products rather than as wastes (Makkar and Cameotra 2002).

New avenues of research on biosurfactant production are opening up, thanks to some emerging bioprocess intensification strategies currently being explored. These include coproduction of lipopeptides with other economically important compounds like enzymes, the use of immobilized cells and the use of nanoparticles. These techniques are promising to enhance industrial production of lipopeptides and consequently enable their commercial success (Singh et al. 2019).

Moving forward with research on lipopeptides also requires meaningful comparison of the effectiveness of lipopeptides or derivation of structure-activity relationships between studies. Yet, the comparison is limited by the diversity in investigated organisms, procedures used and concentration ranges tested, which causes hindrance for further development of lipopeptides as biological agents. It is necessary to define a common series of organisms, reference strains and assaying procedures, and make them available to characterize newly isolated lipopeptides. The data could then be added to existing databases or used to develop new ones, on the basis of using on molecular tools (Geudens et al. 2018).

Based on all what we cited above, lipopeptides and EOs have shown potential as biological control agents. Hence, it is noteworthy to test their combination for pathogen control. This is further expanded in Section 4.

4. Combined application of essential oils and antagonistic microorganisms and lipopeptides

Very few studies were performed to test the combined effect of EOs with antagonistic microorganisms against plant pathogens. Arrebola et al. (2010) tested the combination of EOs of *C. citrates* Stapf. and *T. vulgaris* with *B. amyloliquefaciens* PPCB004 on fungi *B. cinerea, P. expansum* and *R. stolonifer*. *In vitro*, a culture filtrate of *B. amyloliquefaciens* combined with each essential oil individually (5% (v/v)) provided complete inhibition of the three fungi at volumes ranging from 2 to 6 μl/petri dish. These volumes are lower than those required by the EOs applied alone, and which did not allow a total

inhibition. *In vivo*, the combination of the bacterial suspension (10^8 cfu/ml) and *C. citrates* essential oil at 75 µl was tested on peaches inoculated with the three fungi individually. Synergism has been defined by Richer (1987) as "the combined action of two or more agents that is greater than the sum of the action of each of the agents used alone".Limpel's formula, as described by Richer (1987), was used to determine synergistic interactions between EOs and the bacterial strain. Limpel 's formula is Ee = X + Y-(XY/100), in which Ee is the expected effect from additive response of two treatments and X and Y are the percentages of disease reduction relative to each agent used alone (Limpel 1962). Consequently, if the combination of the two agents produces values greater than Ee, then synergism is said to be exhibited. The combination of the bacterial strain and *C. citratus* essential oil produced a synergistic effect, as it gave higher results than those achieved by the essential oil and the bacterial strain applied alone resulting in a disease reduction of *B. cinerea*, *P. expansum* and *R. stolonifer* (50%, 42%and 82% respectively). Furthermore, the use of a modified atmosphere conditioning on the fruits having undergone the combined treatments, produced an optimum result by absence of infected fruit and preservation of fruit quality. In the same context, a combination of *Lactobacillus plantarum* A7 (10^8 cells/ml) with EOs of *T. vulgaris* at 0.5 µl/ml or *C. cyminum* at 3 µl/ml resulted in complete inhibition of *Botrytis* spp., with lower volumes in EOs than those required when used separately. The combinations *L. plantarum*/*T. vulgaris* (100 µl/l) and *L. plantarum*/*C. cyminum* (50 µl/l) were further tested *in vivo* on strawberries. An improvement in fruit infection control was observed in comparison with the unique application of EOs or the bacterial strain, in addition to the preservation of fruit quality (Zamani-Zadeh et al. 2014). The author referred to the effect resulting from the combined use of *L. plantarum* and thyme or cumin oils as a synergistic effect. Nevertheless, his reference wasn't based on any definition or equation.

As for combining EOs with lipopeptides, only one study addressed this type of combination to our knowledge. Dimkić et al. (2015) tested the effect of lipopeptides produced by *Bacillus* spp SS-12.6 in combination with EOs of *T. vulgaris* and *Satureja hortensis*, against seven *Fusarium* species. *In vitro*, lipopeptides produced a more significant inhibition of the fungi in combination with each essential oil, than that achieved by the lipopeptides applied alone. According to Limpel (1962) formula, a synergistic effect was noticed with the combination of lipopeptides with *T. vulgaris* against *Fusarium tricinctum, F. semitectum* and *F. solani*, and with the combination of lipopeptides with *S. hortensis* against *F. equiseti*. For the remaining species of *Fusarium*, the effect produced was additive. These combinations were also tested *in vivo* on marigold seeds, and a reduction in infection was noticed, without a synergistic effect. The essential oil of *T. vulgaris* produced an inhibition of 80% of seed infection when coupled with lipopeptides, compared to 50% inhibition when the oil is used alone, without an adverse effect on germination. Similarly, *S. hortensis* essential oil coupled with lipopeptides produced higher inhibition (75%) than that produced by the oil applied alone (46%) (Dimkić et al. 2015).

According to the authors of this study, the synergistic effect between lipopeptides and EOs can be related to their chemical structures, and may be oriented towards cytoplasmic membranes. In addition to enhancing antifungal activity, the combination of these substances reduces the required concentrations in each, which is very useful in *in vivo* projection for crop treatments, on economic and environmental scale. It is important though to establish the chemical compatibility between EOs and lipopeptides prior to their combination in formulations.

More studies need to be performed in this direction. Further, similar combinations must be tested against plant attacking insects and nematodes. Both lipopeptides and EOs have proved to be insecticidal and nematicidal. Thus, research must be oriented towards discovering possible additive and synergistic effects, which can be produced as a result of their combination. Creating formulations using both substances at affordable prices will provide farmers with solutions that are eco-friendly but also effective, which will ultimately give them a more favorable view on bio pesticides in the future.

5. Conclusion and further direction

This review highlights essential oils and lipopeptides as biocontrol agents of plant pathogens. Both have showed promising activities against post-harvest pathogens. Nevertheless, their consideration in the future for possible applications in crop protection requires overcoming several limitations. The combination of essential oils and lipopeptides in plant pathogens control is also discussed, for the possible synergistic effect resulting from this combination. More evaluations and tests are required to fully understand the mechanism of this synergy. The synergy between plants and other community members (bacteria, fungi, nematodes and insects) is highly important. It results in the development of 'coping' strategies for community members within the soil. To make use of this interaction in fields for crop protection, we need to measure the elements and

factors that control this synergy, and that requires system approaches.

Essential oils and lipopeptides link the formation of distinct communities and their responses in the soil environment. Future approaches should center on further refining the classes (qualities) to be considered. The recommended qualitative approach contributes to form approximated rules by which interactions take place within synergy. A more highly refined systems approach will lead to greater measurement of the defined system, potentially enabling scenario formation and prediction of synergy with 100% certainty. Exploration of hybrid mathematic and combinatorial areas enable expansion of the effect of the groups identified here, throughout all related community members in the soil environment. Resolving the scales on which interaction takes place is another important step towards a measured predictive model. First, the main classes for example essential oils and lipopeptides must be quantified, and their antifungal, nematicidal, insecticidal effects must be measured. The latter will develop cause-effect, process based and combinatorial models of synergy and thus apply our intuition in crop development with agroecological and wider ecological impact.

Disclosure statement

The authors report no conflict of interest.

Authors' contributions

Bouchra Chebli and El Hassan Mayad provided guidance throughout the process of creating this review, they created the concept for this review, formed the plan for it, and emphasized the main areas of discussion in detail (format of presentation of precedent work, cited references, etc.), Rachid Bouharroud, François Krier, Timothy Paulitz and Mustapha Barakate read the article and provided feedback before the manuscript's submission, and James N Furze contributed subjectively and helped in refining the review.

References

Abalos A, Pinazo A, Infante MR, Casals M, Garcia F, Manresa A. 2001. Physicochemical and antimicrobial properties of new rhamnolipids produced by *Pseudomonas aeruginosa* AT10 from soybean oil refinery wastes. Langmuir. 17(5):1367–1371.

Abbassy MA, Abdel-Rasoul MA, Nassar AM, Soliman BS. 2017. Nematicidal activity of silver nanoparticles of botanical products against root-knot nematode, *Meloidogyne incognita*. Arch Phytopathol Plant Protect. 50(17-18):909–926.

Abdelgaleil SAM, Badawy MEI, Mahmoud NF, Marei A. 2019. Acaricidal activity, biochemical effects and molecular docking of some monoterpenes against two-spotted spider mite (*Tetranychus urticae* Koch). Pest Biochem Physiol. 156:105–115.

Abdelgaleil SAM, Mohamed MIE, Shawir MS, Abou-Taleb HK. 2016. Chemical composition, insecticidal and biochemical effects of essential oils of different plant species from Northern Egypt on the rice weevil, *Sitophilus oryzae* L. J Pest Sci. 89(1):219–229.

Abou-Taleb HK, Mohamed MIE, Shawir MS, Abdelgaleil S. 2016. Insecticidal properties of essential oils against *Tribolium castaneum* (Herbst) and their inhibitory effects on acetylcholinesterase and adenosine triphosphatases. Nat Prod Res. 30(6):710–714.

Aghel N, Yamini Y, Hadjiakhoondi A, Pourmortazavi SM. 2004. Supercritical carbon dioxide extraction of *Mentha pulegium* L. essential oil. Talanta. 62(2): 407–411.

Aharoni A, Galili G. 2011. Metabolic engineering of the plant primary–secondary metabolism interface. Curr Opin Biotechnol. 22(2):239–244.

Alilou H, Akssira M, Idrissi Hassani LM, Chebli B, El Hakmoui A, Mellouki F, Rouhi R, Boira H, Blázquez MA. 2008. Chemical composition and antifungal activity of Bubonium imbricatum volatile oil. Phytopathol Mediterranea. 47:3–10. https://www.jstor.org/stable/26463292.

Al-Mousawi AH, Al-Naib F. 1975. Allelopathic effects of *Eucalyptus microtheca* F. *Muell*. J. Univ. Kuwait (Science). 2:59–66.

Amzouar S, Boughdad A, Maatoui A, Allam L. 2016. Comparison of the chemical composition and the insecticidal activity of essential oils of *Mentha suaveolens* Ehrh. collected from two different regions of Morocco, against *Bruchus rufimanus* (Bohman) (Coleoptera: Chrysomelidae). Int J Innov Appl Stud. 18:836–845.

Andolfi A, Cimmino A, Cantore PL, Iacobellis NS, Evidente A. 2008. Bioactive and structural metabolites of Pseudomonas and *Burkholderia* species causal agents of cultivated mushrooms diseases. Perspect Med Chem. 2:81–112.

Andrés MF, Rossa GE, Cassel E, Vargas RMF, Santana O, Díaz CE, González-Coloma A. 2017. Biocidal effects of *Piper hispidinervum* (Piperaceae) essential oil and synergism among its main components. Food Chem Toxicol. 109:1086–1092.

Angioni A, Barra A, Coroneo V, Dessi S, Cabras P. 2006. Chemical composition, seasonal variability, and antifungal activity of *Lavandla stoechas* L. ssp. *stoechas* essential oils from stem/leaves and flowers. J Agric Food Chem. 54(12):4364–4370.

Aranda FJ, Teruel JA, Ortiz A. 2005. Further aspects on the hemolytic activity of the antibiotic lipopeptide iturin A. Biochim Biophys Acta (BBA)-Biomembr. 1713:51–56.

Arasu MV, Viayaraghavan P, Ilavenil S, Al-Dhabi NA, Choi KC. 2019. Essential oil of four medicinal plants and protective properties in plum fruits against the spoilage bacteria and fungi. Indus Crops Prod. 133: 54–62.

Arrebola E, Sivakumar D, Bacigalupo R, Korsten L. 2010. Combined application of antagonist *Bacillus amyloliquefaciens* and essential oils for the control of peach postharvest diseases. Crop Protect. 29(4):369–377.

Asano K, Shinagawa K, Hashimoto N. 1982. Characterization of haze-forming proteins of beer and their roles in chill haze formation. J Am Soc Brew Chem. 40(4):147–154.

Assie LK, Deleu M, Arnaud L, Paquot M, Thonart P, Gaspar CH, Haubruge E. 2002. Insecticide activity of surfactins and iturins from a biopesticide *Bacillus subtilis* Cohn (S499 strain). Mededelingen (Rijksuniversiteit Te Gent Fakulteit Van De Landouwkundige En Toegepaste Biologische Wetenschappen). 67:647–655.

Avato P, Laquale S, Argentieri MP, Lamiri A, Radicci V, D'Addabbo T. 2017. Nematicidal activity of essential oils from aromatic plants of Morocco. J Pest Sci. 90(2): 711–722.

Ayed HB, Azabou MC, Hmidet N, Triki MA, Nasri M. 2018. Economic production and biocontrol efficiency of lipopeptide biosurfactants from *Bacillus mojavenis* A21. Biodegradation. 1–14.

Ayvaz A, Sagdic O, Karaborklu S, Ozturk I. 2010. Insecticidal activity of the essential oils from different plants against three stored-product insects. J Insect Sci. 10(21):1–13. 10.1673/031.010.2101.

Badi HN, Yazdani D, Ali SM, Nazari F. 2004. Effects of spacing and harvesting time on herbage yield and quality/quantity of oil in thyme, *Thymus vulgaris* L. Indus Crops Prod. 19(3):231–236.

Bais HP, Fall R, Vivanco JM. 2004. Biocontrol of *Bacillus subtilis* against infection of Arabidopsis roots by *Pseudomonas syringae* is facilitated by biofilm formation and surfactin production. Plant Physiol. 134(1): 307–319.

Bakkali F, Averbeck S, Averbeck D, Idaomar M. 2008. Biological effects of essential oils–a review. Food Chem Toxicol. 46(2):446–475.

Ballio A, Barra D, Bossa F, Collina A, Grgurina I, Marino G, Moneti G, Paci M, Pucci P, Segre A, et al. 1991. Syringopeptins, new phytotoxic lipodepsipeptides of *Pseudomonas syringae* pv. *syringae*. FEBS Lett. 291(1): 109–112.

Banat I M, Franzetti A, Gandolfi I, Bestetti G, Martinotti M G, Fracchia L, Smyth T J, Marchant R. 2010. Microbial biosurfactants production, applications and future potential. Appl Microbiol Biotechnol. 87(2): 427–444.

Barkai-Golan R. 2001. Postharvest diseases of fruits and vegetables: development and control. Amsterdam, The Netherland: Elsevier.

Basile A, Jiménez-Carmona MM, Clifford AA. 1998. Extraction of rosemary by superheated water. J Agric Food Chem. 46(12):5205–5209.

Bassarello C, Lazzaroni S, Bifulco G, Lo Cantore P, Iacobellis NS, Riccio R, Gomez-Paloma L, Evidente A. 2004. Tolaasins A – E, five new lipodepsipeptides produced by *Pseudomonas tolaasii*. J Nat Prod. 67(5): 811–816.

Beckman CH. 2000. Phenolic-storing cells: keys to programmed cell death and periderm formation in wilt disease resistance and in general defence responses in plants? Physiol Mol Plant Pathol. 57(3):101–110.

Benelli G, Govindarajan M, Rajeswary M, Vaseeharan B, Alyahya SA, Alharbi NS, Kadaikunnan S, Khaled JM, Maggi F. 2018. Insecticidal activity of camphene, zerumbone and α-humulene from *Cheilocostus speciosus* rhizome essential oil against the Old-World bollworm, *Helicoverpa armigera*. Ecotoxicol Environ Saf. 148: 781–786.

Benelli G, Pavela R, Canale A, Nicoletti M, Petrelli R, Cappellacci L, Galassi R, Maggi F. 2017. Isofuranodiene and germacrone from *Smyrnium olusatrum* essential oil as acaricides and oviposition inhibitors against *Tetranychus urticae:* impact of chemical stabilization of isofuranodiene by interaction with silver triflate. J Pest Sci. 90(2):693–699.

Berger S, Sinha AK, Roitsch T. 2007. Plant physiology meets phytopathology: plant primary metabolism and plant–pathogen interactions. J Exp Bot. 58(15-16):4019–4026.

Brahmi F, Abdenour A, Bruno M, Silvia P, Alessandra P, Danilo F, Drifa Y-G, Fahmi E M, Khodir M, Mohamed C. 2016. Chemical composition and in vitro antimicrobial, insecticidal and antioxidant activities of the essential oils of *Mentha pulegium* L. and *Mentha rotundifolia* (L.) huds growing in Algeria. Indus Crops Prod. 88:96–105.

Bryk H, Sobiczewski P, Dyki B. 1998. Antagonistic effect of *Erwinia herbicola* on in vitro spore germination and germ tube elongation of *Botrytis cinerea* and *Penicillium expansum*. BioControl. 43(1):97–106.

Bull CT, Wadsworth ML, Sorensen KN, Takemoto JY, Austin RK, Smilanick JL. 1998. Syringomycin E produced by biological control agents controls green mold on lemons. Biol Control. 12(2):89–95.

Burt S. 2004. Essential oils: their antibacterial properties and potential applications in foods—a review. Int J Food Microbiol. 94(3):223–253. 2004.03.022

Cabras P, Schirra M, Pirisi FM, Garau VL, Angioni A. 1999. Factors affecting imazalil and thiabendazole uptake and persistence in citrus fruits following dip treatments. J Agric Food Chem. 47(8):3352–3354.

Chebli B, Achouri M, Idrissi Hassani LM, Hmamouchi M. 2003a. Antifungal activity of essential oils from several medicinal plants against four postharvest citrus pathogens. Phytopathol Mediterranea. 42:251–256. https://www.jstor.org/stable/26456671.

Chebli B, Hmamouchi M, Achouri M, Idrissi Hassani LM. 2004. Composition and in vitro fungitoxic activity of 19 essential oils against two post-harvest pathogens. J Essential Oil Res. 16(5):507–511.

Chebli B, Achouri M, Idrissi Hassani LM, Hmamouchi M. 2003b. Chemical composition and antifungal activity of essential oils of seven Moroccan Labiatae against *Botrytis cinerea* Pers: Fr. J Ethnopharmacol. 89:165–169.

Chernin L, Ismailov Z, Haran S, Chet I. 1995. Chitinolytic *Enterobacter agglomerans* antagonistic to fungal plant pathogens. Appl Environ Microbiol. 61(5): 1720–1726.

Cid-Pérez TS, Torres-Muñoz JV, Nevárez-Moorillón GV, Palou E, López-Malo A. 2016. Chemical characterization and antifungal activity of *Poliomintha longiflora* Mexican oregano. J Essential Oil Res. 28(2):157–165.

Conner DE, Beuchat LR. 1984. Effects of essential oils from plants on growth of food spoilage yeasts. J Food Sci. 49(2):429–434.

Conti B, Flamini G, Cioni PL, Ceccarini L, Macchia M, Benelli G. 2014. Mosquitocidal essential oils: are they safe against non-target aquatic organisms? Parasitol Res. 113(1):251–259.

Da Cruz Cabral L, Pinto VF, Patriarca A. 2013. Application of plant derived compounds to control fungal spoilage and mycotoxin production in foods. Int J Food Microbiol. 166(1):1–14.

Daferera DJ, Ziogas BN, Polissiou MG. 2000. GC-MS Analysis of essential oils from some Greek aromatic plants and their fungitoxicity on *Penicillium digitatum*. J Agric Food Chem. 48(6):2576–2581.

Dangl JL, Jones J. 2001. Plant pathogens and integrated defence responses to infection. Nature. 411(6839): 826–833.

Davis EL, Haegeman A, Kikuchi T. 2011. Degradation of the plant cell wall by nematodes. In: Jones J, Gheysen G, Fenoll C, editors. Genomics and molecular genetics of plant-nematode interactions. Dordrecht: Springer; p. 255–272.

De Andrade Dutra K, de Oliveira JV, Navarro DMdAF, Barbosa DReS, Santos JPO. 2016. Control of *Callosobruchusmaculatus* (FABR.)(Coleoptera: Chrysomelidae: Bruchinae) in *Vigna unguiculata* (L.) WALP. with essential oils from four *Citrus* spp. plants. J Stored Prod Res. 68:25–32.

De Araujo LV, Guimarães CR, Da Silva Marquita RL, Santiago VMJ, De Souza MP, Nitschke M, Freire D. 2016. Rhamnolipid and surfactin: Anti-adhesion/anti-biofilm and antimicrobial effects. Food Control. 63: 171–178.

De Bruijn LLM, Sommeijer MJ. 1997. Colony foraging in different species of stingless bees (Apidae, Meliponinae) and the regulation of individual nectar foraging. Insectes Sociaux. 44(1):35–47.

De Oliveira JL, Campos EVR, Bakshi M, Abhilash PC, Fraceto LF. 2014. Application of nanotechnology for the encapsulation of botanical insecticides for sustainable agriculture: prospects and promises. Biotechnol Adv. 32(8):1550–1561.

Deleu M, Paquot M, Nylander T. 2005. Fengycin interaction with lipid monolayers at the air–aqueous interface—implications for the effect of fengycin on biological membranes. J Colloid Interface Sci. 283(2): 358–365.

Detoni CB, de Oliveira DM, Santo IE, Pedro AS, El-Bacha R, da Silva Velozo E, Ferreira D, Sarmento B, De Magalhães Cabral-Albuquerque EC. 2012. Evaluation of thermal-oxidative stability and antiglioma activity of *Zanthoxylumtingoassuiba* essential oil entrapped into multi-and unilamellar liposomes. J Liposome Res. 22(1):1–7.

Dimkić I, Berić T, Stević T, Pavlović S, Šavikin K, Fira D, Stanković S. 2015. Additive and synergistic effects of *Bacillus* spp. isolates and essential oils on the control of phytopathogenic and saprophytic fungi from medicinal plants and marigold seeds. Biol Control. 87:6–13.

Dixon RA. 1999. Plant natural products: the molecular genetic basis of biosynthetic diversity. Curr Opin Biotechnol. 10(2):192–197.

Dorman HJD, Deans SG. 2000. Antimicrobial agents from plants: antibacterial activity of plant volatile oils. J Appl Microbiol. 88(2):308–316.

Ebadollahi A, Jalali-Sendi J, Razmjou J. 2016. Toxicity and phytochemical profile of essential oil from Iranian *Achilleamellifolium* L. against *Tetranychus urticae* Koch (Acari: Tetranychidae). Toxin Rev. 35(1-2):24–28.

El Ouadi Y, Manssouri M, Bouyanzer A, Majidi L, Bendaif H, Elmsellem H, Shariati M, Melhaoui A, Hammouti B. 2017. Essential oil composition and antifungal activity of *Melissa officinalis* originating from North-Est Morocco, against postharvest phytopathogenic fungi in apples. Microb Pathogenesis. 107:321–326.

El-Mogy MM, Alsanius BW. 2012. Cassia oil for controlling plant and human pathogens on fresh strawberries. Food Control. 28(1):157–162.

Eloh K, Kpegba K, Sasanelli N, Koumaglo HK, Caboni P. 2019. Nematicidal activity of some essential plant oils from tropical West Africa. Int J Pest Manage. 1–11.

Enan EE. 2005. Molecular and pharmacological analysis of an octopamine receptor from American cockroach and fruit fly in response to plant essential oils. Arch Insect Biochem Physiol. 59(3):161–171.

Farace G, Fernandez O, Jacquens L, Coutte F, Krier F, Jacques P, Clément C, Barka E A, Jacquard C, Dorey S. 2015. Cyclic lipopeptides from *Bacillus subtilis* activate distinct patterns of defence responses in grapevine. Mol Plant Pathol. 16(2):177–187.

Ferhat MA, Meklati BY, Chemat F. 2007. Comparison of different isolation methods of essential oil from citrus fruits: cold pressing, hydrodistillation and microwave 'dry' distillation. Flavour Fragr J. 22(6):494–504.

Flury P, Vesga P, Péchy-Tarr M, Aellen N, Dennert F, Hofer N, Kupferschmied KP, Kupferschmied P, Metla Z, Ma Z, et al. 2017. Antimicrobial and Insecticidal: Cyclic lipopeptides and hydrogen cyanide produced by plant-beneficial *Pseudomonas strains* CHA0, CMR12a, and PCL1391 contribute to insect killing. Front Microbiol. 8:100.

Fraternale D, Flamini G, Ricci D. 2016. Essential oil composition of *Angelica archangelica* L. (Apiaceae) roots and its antifungal activity against plant pathogenic fungi. Plant Biosyst. 150(3):558–563.

Georgiou G, Lin SC, Sharma MM. 1992. Surface–active compounds from microorganisms. Nat Biotechnol. 10(1):60–65.

Geudens N, Sinnaeve D, Martins JC. 2018. Cyclic lipodepsipeptides: time for a concerted action to unlock their application potential? Future Med Chem. 10(5): 479–481.

Ghribi D, Abdelkefi-Mesrati L, Boukedi H, Elleuch M, Ellouze-Chaabouni S, Tounsi S. 2012a. The impact of the *Bacillus subtilis* SPB1 biosurfactant on the midgut histology of *Spodoptera littoralis* (Lepidoptera: Noctuidae) and determination of its putative receptor. J Invertebr Pathol. 109(2):183–186.

Ghribi D, Elleuch M, Abdelkefi L, Ellouze-Chaabouni S. 2012b. Evaluation of larvicidal potency of *Bacillus subtilis* SPB1 biosurfactant against *Ephestia kuehniella* (Lepidoptera: Pyralidae) larvae and influence of abiotic factors on its insecticidal activity. J Stored Prod Res. 48:68–72.

Ghribi D, Elleuch M, Abdelkefi-Mesrati L, Boukadi H, Ellouze-Chaabouni S. 2012c. Histopathological effects of *Bacillussubtilis* SPB1 biosurfactant in the midgut of Ephestia kuehniella (Lepidoptera: Pyralidae) and improvement of its insecticidal efficiency. J Plant Dis Protect. 119(1):24–29.

Gomes RC, Sêmedo L, Soares RMA, Linhares LF, Ulhoa CJ, Alviano CS, Coelho RR. 2001. Purification of a thermostable endochitinase from *Streptomyces* RC1071 isolated from a cerrado soil and its antagonism against phytopathogenic fungi. J Appl Microbiol. 90(4):653–661.

Götze S, Herbst-Irmer R, Klapper M, Görls H, Schneider KRA, Barnett R, Burks T, Neu U, Stallforth P. 2017. Structure, biosynthesis, and biological activity of the cyclic lipopeptide anikasin. ACS Chem Biol. 12(10): 2498–2502.

Groupé V, Pugh LH, Weiss D, Kochi M. 1951. Observations on antiviral activity of viscosin. Proceedings of the Society for. Exp Biol Med. 78:354–358.

Guo Q, Dong W, Li S, Lu X, Wang P, Zhang X, Wang Y, Ma P. 2014. Fengycin produced by *Bacillus subtilis* NCD-2 plays a major role in biocontrol of cotton seedling damping-off disease. Microbiol Res. 169(7-8): 533–540.

Guo Y, Ni J, Denver R, Wang X, Clark SE. 2011. Mechanisms of molecular mimicry of plant CLE

peptide ligand by the parasitic nematode *Globodera rostochiensis*. Plant Physiol. 157(1):476–484.
Haegeman A, Mantelin S, Jones JT, Gheysen G. 2012. Functional roles of effectors of plant-parasitic nematodes. Gene. 492(1):19–31.
Haider S. Z, Mohan M, Pandey A K, Singh P. 2017. Use of *Tanacetum tomentosum* and Ta. *dolichophyllum*essential oils as botanical repellents and insecticidal agents against storage pest *Tribolium castaneum* (Coleoptera: Tenebrionidae). Entomol Res. 47(5): 318–327.
Hansen M, Thrane C, Olsson S, Sørensen J. 2000. Confocal imaging of living fungal hyphae challenged with the fungal antagonist viscosinamide. Mycologia. 92(2):216–221.
Hartmann T. 2007. From waste products to ecochemicals: Fifty years research of plant secondary metabolism. Phytochemistry. 68(22-24):2831–2846.
Hashimoto Y. 2002. Study of the bacteria pathogenic for aphids, isolation of bacteria and identification of insecticidal compound. Rep Hokkaido Prefectural Agric Exp Station (Japan). 102:1–48.
Hewezi T, Baum TJ. 2013. Manipulation of plant cells by cyst and root-knot nematode effectors. MPMI. 26(1): 9–16.
Hiradate S, Yoshida S, Sugie H, Yada H, Fujii Y. 2002. Mulberry anthracnose antagonists (iturins) produced by *Bacillus amyloliquefaciens* RC-2. Phytochemistry. 61(6):693–698. (02)00365-5
Hori M. 2003. Repellency of essential oils against the cigarette beetle, *Lasioderma serricorne* (Fabricius) (Coleoptera: Anobiidae). Appl Entomol Zool. 38(4): 467–473.
Hossain F, Follett P, Vu KD, Harich M, Salmieri S, Lacroix M. 2016. Evidence for synergistic activity of plant-derived essential oils against fungal pathogens of food. Food Microbiol. 53:24–30.
Huang X, Lu Z, Bie X, Lu F, Zhao H, Yang S. 2007. Optimization of inactivation of endospores of *Bacillus cereus* by antimicrobial lipopeptides from *Bacillus subtilis* fmbj strains using a response surface method. Appl Microbiol Biotechnol. 74(2):454–461.
Hull LA, Beers EH. 1985. Ecological selectivity: modifying chemical control practices to preserve natural enemies. In: Hoy MA, Herzog DC, editors. Biological control in Agriculture IPM System. Florida: Academic Press; p. 103–122.
Hummelbrunner LA, Isman MB. 2001. Acute, sublethal, antifeedant, and synergistic effects of monoterpenoid essential oil compounds on the tobacco cutworm, *Spodoptera litura* (Lep., Noctuidae). J Agric Food Chem. 49(2):715–720.
Inès M, Dhouha G. 2015. Lipopeptide surfactants: production, recovery and pore forming capacity. Peptides. 71:100–112.
Isman MB. 2000. Plant essential oils for pest and disease management. Crop Protect. 19(8-10):603–608.
Isman MB. 2005. Problems and opportunities for the commercialization of botanical insecticides. Biopest Plant Origin. 283–291. In: Lavoisier, Paris.
Isman MB. 2016. Pesticides based on plant essential oils: phytochemical and practical considerations. Med Aromatic Crops: Prod, Phytochem Utilization. 13–26.
Isman MB, Machial CM. 2006. Pesticides based on plant essential oils: from traditional practice to commercialization. Adv Phytomed. 3:29–44.
Isman MB, Wan AJ, Passreiter CM. 2001. Insecticidal activity of essential oils to the tobacco cutworm, *Spodoptera litura*. Fitoterapia. 72(1):65–68.
Jang JY, Yang SY, Kim YC, Lee CW, Park MS, Kim JC, Kim IS. 2013. Identification of Orfamide A as an insecticidal metabolite produced by *Pseudomonas protegens* F6. J Agric Food Chem. 61(28):6786–6791.
Javaheri M, Jenneman GE, McInerney MJ, Knapp RM. 1985. Anaerobic production of a biosurfactant by *Bacillus licheniformis* JF-2. Appl Environ Microbiol. 50(3):698–700.
Jeon JH, Ko HR, Kim SJ, Lee JK. 2016. Chemical compositions and nematicidal activities of essential oils on *Meloidogyne hapla* (Nematoda: Tylenchida) under laboratory conditions. KJPS. 20(1):30–34. http://dx.doi.org/10.7585/kjps.2016.20.1.30.
Ji H, Li YC, Wen ZY, Li XH, Zhang HX, Li HT. 2016. GC-MS analysis of nematicidal essential oil of *Mentha canadensis* aerial parts against *Heterodera avenae* and *Meloidogyne incognita*. J Essential Oil Bearing Plants. 19(8):2056–2064.
Jones JDG, Dangl JL. 2006. The plant immune system. Nature. 444(7117):323–329.
Jourdan E, Henry G, Duby F, Dommes J, Barthelemy JP, Thonart P, Ongena M. 2009. Insights into the defense-related events occurring in plant cells following perception of surfactin-type lipopeptide from *Bacillus subtilis*. MPMI. 22(4):456–468.
Kaloustian J, Chevalier J, Mikail C, Martino M, Abou L, Vergnes MF. 2008. Étude de six huiles essentielles: composition chimique et activité antibactérienne. Phytotherapie. 6(3):160–164.
Khanavi M, Laghaei P, Isman MB. 2017. Essential oil composition of three native Persian plants and their inhibitory effects in the cabbage looper, *Trichoplusia ni*. J Asia-Pacific Entomol. 20(4):1234–1240.
Kim PI, Bai H, Bai D, Chae H, Chung S, Kim Y, Park R, Chi YT. 2004. Purification and characterization of a lipopeptide produced by *Bacillus thuringiensis* CMB26. J Appl Microbiol. 97(5):942–949.
Kim NS, Lee DS. 2002. Comparison of different extraction methods for the analysis of fragrances from *Lavandla* species by gas chromatography–mass spectrometry. J Chromatogr A. 982(1):31–47.
Kim SW, Lee HR, Jang MJ, Jung CS, Park IK. 2016a. Fumigant toxicity of Lamiaceae plant essential oils and blends of their constituents against adult rice weevil *Sitophilus oryzae*. Molecules. 21(3):361.
Kim E, Oh CS, Koh SH, Kim HS, Kang KS, Park PS, Jang MJ, Lee HR, Park IK. 2016b. Antifungal activities after vaporization of ajowan (*Trachyspermum ammi*) and allspice (*Pimenta dioica*) essential oils and blends of their constituents against three *Aspergillus* species. J Essential Oil Res. 28(3):252–259.
Kim J, Seo SM, Lee SG, Shin SC, Park IK. 2008. Nematicidal activity of plant essential oils and components from coriander (*Coriandum sativum*), oriental sweetgum (*Liquidambar orientalis*), and valerian (*Valeriana wallichii*) essential oils against pine wood nematode (*Bursaphelenchus xylophilus*). J Agric Food Chem. 56(16):7316–7320.
Kimbaris A C, González-Coloma A, Andrés M F, Vidali V P, Polissiou M G, Santana-Méridas O. 2017. Biocidal compounds from *Mentha* sp. essential oils and their structure-activity relationships. Chem Biodivers. 14(3): e1600270.

Koul O, Walia S, Dhaliwal GS. 2008. Essential oils as green pesticides: potential and constraints. Biopest Int. 4:63–84.

Koutsaviti A, Antonopoulou V, Vlassi A, Antonatos S, Michaelakis A, Papachristos DP, Tzakou O. 2018. Chemical composition and fumigant activity of essential oils from six plant families against *Sitophilus oryzae* (Col: Curculionidae). J Pest Sci. 91(2):873–886.

Kruijt M, Tran H, Raaijmakers JM. 2009. Functional, genetic and chemical characterization of biosurfactants produced by plant growth-promoting *Pseudomonas putida* 267. J Appl Microbiol. 107(2):546–556.

Kuiper I, Lagendijk EL, Pickford R, Derrick JP, Lamers GE, Thomas-Oates JE, Lugtenberg BJ, Bloemberg GV. 2004. Characterization of two *Pseudomonas putida* lipopeptide biosurfactants, putisolvin I and II, which inhibit biofilm formation and break down existing biofilms. Mol Microbiol. 51(1):97–113.

Kurkin VA. 2003. Phenylpropanoids from medicinal plants: distribution, classification, structural analysis, and biological activity. Adv Biol Chem. 39:123–153.

Lahlou M. 2004. Methods to study the phytochemistry and bioactivity of essential oils. Phytother Res. 18(6): 435–448.

Laquale S, Avato P, Argentieri MP, Bellardi MG, D'Addabbo T. 2018. Nematotoxic activity of essential oils from *Monarda* species. J Pest Sci. 91(3):1115–1125.

Lavermicocca P, Sante Iacobellis NS, Simmaco M, Graniti A. 1997. Biological properties and spectrum of activity of *Pseudomonas syringae* pv. *syringae* toxins. Physiol Mol Plant Pathol. 50(2):129–140.

Leclère V, Marti R, Béchet M, Fickers P, Jacques P. 2006. The lipopeptides mycosubtilin and surfactin enhance spreading of *Bacillus subtilis* strains by their surface-active properties. Arch Microbiol. 186(6):475–483.

Lee C, Chronis D, Kenning C, Peret B, Hewezi T, Davis EL, Baum TJ, Hussey R, Bennett M, Mitchum MG. 2011. The novel cyst nematode effector protein 19C07 interacts with the Arabidopsis auxin influx transporter LAX3 to control feeding site development. Plant Physiol. 155(2):866–880.

Lee YS, Kim J, Shin SC, Lee SG, Park IK. 2008. Antifungal activity of Myrtaceae essential oils and their components against three phytopathogenic fungi. Flavour Fragr J. 23(1):23–28.

Levy E, Gough F. J, Berlin K. D, Guiana P. W, Smith J. T. 1992. Inhibition of *Septoria tritici* and other phytopathogenic fungi and bacteria by *Pseudomonas fluorescens* and its antibiotics. Plant Pathol. 41(3):335–341.

Li YC, Ji H, Li XH, Zhang HX, Li HT. 2017. Isolation of nematicidal constituents from essential oil of *Kaempferia galanga* L rhizome and their activity against *Heterodera avenae* Wollenweber. Trop J Pharm Res. 16(1):59–65. http://dx.doi.org/10.4314/tjpr.v16i1.8.

Li W, Rokni-Zadeh H, De Vleeschouwer M, Ghequire MG, Sinnaeve D, Xie GL, Rozenski J, Madder A, Martins JC, De Mot R. 2013. The antimicrobial compound xantholysin defines a new group of *Pseudomonas* cyclic lipopeptides. PLoS One. 8(5): e62946.

Lim DJ, Yang SY, Noh MY, Lee CW, Kim JC, Kim IS. 2017. Identification of lipopeptide xantholysins from *Pseudomonas* sp. DJ15 and their insecticidal activity against *Myzus persicae*. Entomol Res. 47(6):337–343.

Limpel LE. 1962. Weed control by dimethyl tetrachloroterephthalate alone and in certain combinations. Proceedings of the Northeast Weed Control Conference, New York. 16. p. 48–53.

Loper J E, Henkels M D, Rangel L I, Olcott M H, Walker F L, Bond K L, Kidarsa T A, Hesse C N, Sneh B, Stockwell V O, et al. 2016. Rhizoxin analogs, orfamide A and chitinase production contribute to the toxicity of *Pseudomonasprotegens* strain Pf-5 to *Drosophila melanogaster*. Environ Microbiol. 18(10):3509–3521.

López-Meneses AK, Sánchez-Mariñez RI, Quintana-Obregón EA, Parra-Vergara NV, González-Aguilar GA, López-Saiz CM, Cortez-Rocha MO. 2017. In vitro antifungal activity of essential oils and major components against fungi plant pathogens. J Phytopathol. 165(4): 232–237.

Lu H, Xu S, Zhang W, Xu C, Li B, Zhang D, Mu W, Liu F. 2017. Nematicidal Activity of trans-2-hexenal against Southern root-knot nematode (*Meloidogyne incognita*) on tomato plants. J Agric Food Chem. 65(3):544–550.

Lucchesi ME, Smadja J, Bradshaw S, Louw W, Chemat F. 2007. Solvent free microwave extraction of *Elletaria cardamomum* L.: a multivariate study of a new technique for the extraction of essential oil. J Food Eng. 79(3):1079–1086.

Lucini EI, Zunino MP, López ML, Zygadlo JA. 2006. Effect of monoterpenes on lipid composition and sclerotial development of *Sclerotium cepivorum* Berk. J Phytopathol. 154(7-8):441–446.

Ma BX, Ban XQ, He JS, Huang B, Zeng H, Tian J, Chen YX, Wang YW. 2016a. Antifungal activity of *Ziziphoraclinopodioides* Lam. essential oil against *Sclerotinia sclerotiorum* on rapeseed plants (*Brassica campestris* L.). Crop Protect. 89:289–295.

Ma Z, Geudens N, Kieu NP, Sinnaeve D, Ongena M, Martins JC, Höfte M. 2016b. Biosynthesis, chemical structure, and structure-activity relationship of orfamide lipopeptides produced by *Pseudomonas protegens* and related species. Front Microbiol. 7:382.

Makkar R, Cameotra S. 2002. An update on the use of unconventional substrates for biosurfactant production and their new applications. Applied microbiology and biotechnology. 58:428–434.

Mansour SA, El-Sharkawy AZ, Abdel-Hamid NA. 2015. Toxicity of essential plant oils, in comparison with conventional insecticides, against the desert locust, *Schistocerca gregaria* (Forskål). Indus Crops Prod. 63: 92–99.

Marei GIK, Abdelgaleil S. 2018. Antifungal potential and biochemical effects of monoterpenes and phenylpropenes on plant pathogenic fungi. Plant Protect Sci. 54: 9–16.

Martinez JA. 2012. Natural fungicides obtained from plants. In: Dhanasekaran D, editor. Fungicides for plant and animal diseases. Croatia: IntechOpen; p. 3–28.

Mejdoub K, Benomari FZ, Djabou N, Dib MEA, Benyelles NG, Costa J, Muselli A. 2019. Antifungal and insecticidal activities of essential oils of four *Mentha* species. Jundishapur J Nat Pharm Prod. 14:e64165.

Michelsen CF, Watrous J, Glaring MA, Kersten R, Koyama N, Dorrestein PC, Stougaard P. 2015. Nonribosomal peptides, key biocontrol components for *Pseudomonas fluorescens* In5, isolated from a Greenlandic suppressive soil. MBio. 6(2):e00079–15.

Mihalache G, Balaes T, Gostin I, Stefan M, Coutte F, Krier F. 2018. Lipopeptides produced by *Bacillus subtilis* as new biocontrol products against fusariosis in ornamental plants. Environ Sci Pollut Res. 25(30): 29784–29793.

Mireles JR, Toguchi A, Harshey RM. 2001. Salmonella enterica serovar *typhimurium* swarming mutants with altered biofilm-forming abilities: surfactin inhibits biofilm formation. J Bacteriol. 183(20):5848–5854.

Moghaddam M, Mehdizadeh L. 2017. Chemistry of essential oils and factors influencing their constituents. In: Grumezescu AM, Holban AM, editors. Soft chemistry and food fermentation. Cambridge: Academic press; p. 379–419.

Mohammadifar M, Norabadi MT, Hasanzadeh M, Dashtipoor S, Etebarian HR, Sahebani N. 2012. Study of antifungal activities of seven essential oils from some Iranian medicinal plants against various postharvest phytopathogenic fungi. Arch Phytopathol Plant Protect. 45(17):2046–2056.

Moretti MDL, Sanna-Passino G, Demontis S, Bazzoni E. 2002. Essential oil formulations useful as a new tool for insect pest control. AAPS PharmSciTech. 3(2):64–74.

Moyne AL, Shelby R, Cleveland TE, Tuzun S. 2001. Bacillomycin D: an iturin with antifungal activity against *Aspergillusflavus*. J Appl Microbiol. 90(4): 622–629.

Mukherjee S, Das P, Sen R. 2006. Towards commercial production of microbial surfactants. Trends Biotechnol. 24(11):509–515.

Mulligan CN, Yong RN, Gibbs BF. 2001. Heavy metal removal from sediments by biosurfactants. J Hazard Mater. 85(1-2):111–125.

Nasiou E, Giannakou IO. 2017. The potential use of carvacrol for the control of *Meloidogyne javanica*. Eur J Plant Pathol. 149(2):415–424.

Nasiou E, Giannakou IO. 2018. Effect of geraniol, a plant-based alcohol monoterpene oil, against *Meloidogyne javanica*. Eur J Plant Pathol. 152(3): 701–710.

Neu TR. 1996. Significance of bacterial surface-active compounds in interaction of bacteria with interfaces. Microbiol Rev. 60(1):151–166.

Nguyen DD, Melnik A, Koyama N, Lu X, Schorn M, Fang J, Aguinaldo K, Lincecum TL, Jr Ghequire MGK, Carrion VJ, et al. 2016. Indexing the *Pseudomonas* specialized metabolome enabled the discovery of poaeamide B and the bananamides. Nat Microbiol. 2(1): 16197. https://www.nature.com/articles/nmicrobiol2016197#supplementary-information.

Nielsen TH, Thrane C, Christophersen C, Anthoni U, Sørensen J. 2000. Structure, production characteristics and fungal antagonism of tensin – a new antifungal cyclic lipopeptide from *Pseudomonas fluorescens* strain 96-578. J Appl Microbiol. 898:992–1001.

Oka Y. 2001. Nematicidal activity of essential oil components against the root-knot nematode *Meloidogyne javanica*. Nematology. 3(2):159–164.

Oka Y, Nacar S, Putievsky E, Ravid U, Yaniv Z, Spiegel Y. 2000. Nematicidal activity of essential oils and their components against the root-knot nematode. Phytopathology. 90(7):710–715.

Olorunleke FE, Hua GKH, Kieu NP, Ma Z, Höfte M. 2015. Interplay between orfamides, sessilins and phenazines in the control of Rhizoctonia diseases by *Pseudomonas* sp. *CMR12a.* Environ Microbiol Rep. 7(5):774–781.

Ongena M, Daayf F, Jacques P, Thonart P, Benhamou N, Paulitz TC, Cornelis P, Koedam N, Bélanger RR. 1999. Protection of cucumber against Pythium root rot by fluorescent pseudomonads: predominant role of induced resistance over siderophores and antibiosis. Plant Pathol. 48:66–76.

Ongena M, Jacques P. 2008. *Bacillus* lipopeptides: versatile weapons for plant disease biocontrol. Trends Microbiol. 16(3):115–125.

Ongena M, Jacques P, Toure Y, Destain J, Jabrane A, Thonart P. 2005. Involvement of fengycin-type lipopeptides in the multifaceted biocontrol potential of *Bacillus subtilis*. Appl Microbiol Biotechnol. 69(1):29–38.

Ongena M, Jourdan E, Adam A, Paquot M, Brans A, Joris B, Arpigny JL, Thonart P. 2007. Surfactin and fengycin lipopeptides of *Bacillus subtilis* as elicitors of induced systemic resistance in plants. Environ Microbiol. 9(4):1084–1090.

Onifade A K, Fatope M O, Deadman M L, Al-Kindy S M.Z. 2008. Nematicidal activity of *Haplophyllum tuberculatum* and *Plectranthus cylindraceus* oils against *Meloidogyne javanica*. Biochem Syst Ecol. 36(9): 679–683.

Pandey R, Kalra A, Tandn S, Mehrotra N, Singh HN, Kumar S. 2000. Essential Oils as potent source of nematicidal compounds. J Phytopathol. 148:501–502.

Papachristos DP, Stamopoulos DC. 2002. Repellent, toxic and reproduction inhibitory effects of essential oil vapours on *Acanthoscelides obtectus* (Say) (Coleoptera: Bruchidae). J Stored Prod Res. 38(2):117–128.

Park H-M, Kim J, Chang K-S, Kim B-S, Yang Y-J, Kim G-H, Shin S-C, Park I-K. 2011. Larvicidal activity of Myrtaceae essential oils and their components against *Aedes aegypti*, acute toxicity on *Daphnia magna*, and aqueous residue. Jnl Med Entom. 48(2):405–410.

Pavela R, Benelli G. 2016. Essential oils as ecofriendly biopesticides? Challenges and constraints. Trends Plant Sci. 21(12):1000–1007.

Pavela R, Govindarajan M. 2017. The essential oil from *Zanthoxylum monophyllum* a potential mosquito larvicide with low toxicity to the non-target fish *Gambusia affinis*. J Pest Sci. 90(1):369–378.

Pedras MSC, Ismail N, Quail JW, Boyetchko SM. 2003. Structure, chemistry, and biological activity of pseudophomins A and B, new cyclic lipodepsipeptides isolated from the biocontrol bacterium *Pseudomonas fluorescens*. Phytochemistry. 62(7):1105–1114.

Pichersky E, Gershenzon J. 2002. The formation and function of plant volatiles: perfumes for pollinator attraction and defense. Curr Opin Plant Biol. 5(3): 237–243.

Prakash P, Gupta N. 2005. Therapeutic uses of *Ocimum sanctum* Linn (Tulsi) with a note on eugenol and its pharmacological actions: A short review. Indian J Physiol Pharmacol. 49:125–131.

Pusey PL, Wilson CL, Wisniewski ME. 2018. Management of postharvest diseases of fruits and vegetables: strategies to replace vanishing fungicides. In: Altman J, editor. Pesticide interactions in crop production. Boca Raton: CRC Press; p. 477–492.

Raaijmakers JM, De Bruijn I, Nybroe O, Ongena M. 2010. Natural functions of lipopeptides from *Bacillus* and *Pseudomonas*: more than surfactants and antibiotics. FEMS Microbiol Rev. 34(6):1037–1062.

Ramezanian A, Azadi M, Mostowfizadeh-Ghalamfarsa R, Saharkhiz MJ. 2016. Effect of *Zataria multiflora* Boiss and *Thymus vulgaris* L. essential oils on black rot of 'Washington Navel' orange fruit. Postharvest Biol Technol. 112:152–158.

Rattan RS. 2010. Mechanism of action of insecticidal secondary metabolites of plant origin. Crop Protect. 29(9): 913–920.

Rautenbach M, Swart P, Vvan der Merwe MJ. 2000. The interaction of analogues of the antimicrobial lipopeptide, iturin A2, with alkali metal ions. Bioorg Med Chem. 8:2539–2548.

Reddy SGE, Dolma SK. 2018. Acaricidal activities of essential oils against two-spotted spider mite, Tetranychus Urticae Koch. Toxin Rev. 37(1):62–66.

Regnault-Roger C, Hamraoui A. 1995. Fumigant toxic activity and reproductive inhibition induced by monoterpenes on *Acanthoscelides obtectus* (Say) (coleoptera), a bruchid of kidney bean (*Phaseolus vulgaris* L.). J Stored Prod Res. 31(4):291–299.

Regnier T, Combrinck S, Veldman W, Du Plooy W. 2014. Application of essential oils as multi-target fungicides for the control of *Geotrichum citri-aurantii* and other postharvest pathogens of citrus. Indus Crops Prod. 61:151–159.

Ribeiro AV, de Sá Farias E, Santos AA, Filomeno CA, dos Santos IB, Barbosa LCA, Picanço MC. 2018. Selection of an essential oil from Corymbia and Eucalyptus plants against *Ascia monuste* and its selectivity to two non-target organisms. Crop Protect. 110: 207–213.

Richer DL. 1987. Synergism—a patent view. Pest Sci. 19(4):309–315.

Romero D, De Vicente A, Rakotoaly RH, Dufour SE, Veening JW, Arrebola E, Cazorla FM, Kuipers OP, Paquot M, Pérez-García A. 2007. The iturin and fengycin families of lipopeptides are key factors in antagonism of *Bacillus subtilis* toward *Podosphaera fusca*. MPMI. 20(4):430–440.

Ron EZ, Rosenberg E. 2001. Natural roles of biosurfactants. Environ Microbiol. 3(4):229–236.

Roongsawang N, Hase K, Haruki M, Imanaka T, Morikawa M, Kanaya S. 2003. Cloning and characterization of the gene cluster encoding arthrofactin synthetase from *Pseudomonas* sp. MIS38. Chem Biol. 10: 869–880.

Sabaté DC, Audisio MC. 2013. Inhibitory activity of surfactin, produced by different *Bacillus subtilis* subsp. *subtilis* strains, against *Listeria monocytogenes* sensitive and bacteriocin-resistant strains. Microbiol Res. 168(3): 125–129.

Sacchetti G, Maietti S, Muzzoli M, Scaglianti M, Manfredini S, Radice M, Bruni R. 2005. Comparative evaluation of 11 essential oils of different origin as functional antioxidants, antiradicals and antimicrobials in foods. Food Chem. 91(4):621–632.

Segre A, Bachmann RC, Ballio A, Bossa F, Grgurina I, Iacobellis NS, Marino G, Pucci P, Simmaco M, Takemoto JY. 1989. The structure of syringomycins A1, E and G. FEBS Lett. 255(1):27–31.

Seo S-M, Park H-M, Park I-K. 2012. Larvicidal activity of ajowan (*Trachyspermum ammi*) and Peru balsam (*Myroxylon pereira*) oils and blends of their constituents against mosquito, *Aedes aegypti,* acute toxicity on water flea, *Daphnia magna,* and aqueous residue. J Agric Food Chem. 60(23):5909–5914.

Sharma N, Tripathi A. 2008. Effects of Citrus sinensis (L.) Osbeck epicarp essential oil on growth and morphogenesis of *Aspergillus niger* (L.) Van Tieghem. Microbiol Res. 163(3):337–344.

Shoda M. 2000. Bacterial control of plant diseases. J Biosci Bioeng. 89(6):515–521.

Sikkema J, de Bont JA, Poolman B. 1995. Mechanisms of membrane toxicity of hydrocarbons. Microbiol Rev. 59(2):201–222.

Singh P, Patil Y, Rale V. 2019. Biosurfactant production: emerging trends and promising strategies. J Appl Microbiol. 126(1):2–13.

Soliman KM, Badeaa RI. 2002. Effect of oil extracted from some medicinal plants on different mycotoxigenic fungi. Food Chem Toxicol. 40(11):1669–1675.

Sørensen D, Nielsen T H, Christophersen C, Sørensen J, Gajhede M. 2001. Cyclic lipoundecapeptide amphisin from *Pseudomonas* sp. strain DSS73. Acta Crystallogr C Cryst Struct Commun. 57(9):1123–1124.

Soylu EM, Kose F. 2015. Antifungal activities of essential oils against citrus black rot disease agent *Alternaria alternata*. J Essential Oil Bearing Plants. 18(4):894–903.

Stević T, Berić T, Šavikin K, Soković M, Gođevac D, Dimkić I, Stanković S. 2014. Antifungal activity of selected essential oils against fungi isolated from medicinal plant. Indus Crops Prod. 55:116–122.

Stewart D. 2005. The chemistry of essential oils made simple: God's love manifest in molecules. Marble Hill: Care publications.

Tak JH, Jovel E, Isman MB. 2016a. Comparative and synergistic activity of *Rosmarinus officinalis* L. essential oil constituents against the larvae and an ovarian cell line of the cabbage looper, *Trichoplusia ni* (Lepidoptera: Noctuidae). Pest Manag Sci. 72(3):474–480.

Tak JH, Jovel E, Isman MB. 2016b. Contact, fumigant, and cytotoxic activities of thyme and lemongrass essential oils against larvae and an ovarian cell line of the cabbage looper, *Trichoplusia ni*. J Pest Sci. 89(1): 183–193.

Tang X, Shao Y-L, Tang Y-J, Zhou W-W. 2018. Antifungal activity of essential oil compounds (geraniol and citral) and inhibitory mechanisms on grain pathogens (*Aspergillus flavus* and *Aspergillus ochraceus*). Molecules. 23(9):2108.

Tao Y, Bie XM, Lv FX, Zhao HZ, Lu ZX. 2011. Antifungal activity and mechanism of fengycin in the presence and absence of commercial surfactin against *Rhizopus stolonifer*. J Microbiol. 49(1):146–150.

Tendulkar SR, Saikumari YK, Patel V, Raghotama S, Munshi TK, Balaram P, Chattoo BB. 2007. Isolation, purification and characterization of an antifungal molecule produced by *Bacillus licheniformis* BC98, and its effect on phytopathogen *Magnaporthe grisea*. J Appl Microbiol. 103(6):2331–2339.

Thompson DP. 1989. Fungitoxic activity of essential oil components on food storage fungi. Mycologia. 81(1): 151–153.

Thompson JD, Chalchat JC, Michet A, Linhart YB, Ehlers B. 2003. Qualitative and quantitative variation in monoterpene co-occurrence and composition in the essential oil of *Thymus vulgaris* chemotypes. J Chem Ecol. 29(4):859–880.

Tomazoni EZ, Pauletti GF, Da Silva Ribeiro RT, Moura S, Schwambach J. 2017. In vitro and in vivo activity of essential oils extracted from *Eucalyptus staigeriana, Eucalyptus globulus* and *Cinnamomum camphora* against *Alternaria solani* Sorauer causing early blight in tomato. Sci Horticul. 223:72–77.

Touré Y, Ongena M, Jacques P, Guiro A, Thonart P. 2004. Role of lipopeptides produced by *Bacillus subtilis* GA1 in the reduction of grey mould disease caused by *Botrytis cinerea* on apple. J Appl Microbiol. 96: 1151–1160.

Tran H, Ficke A, Asiimwe T, Höfte M, Raaijmakers JM. 2007. Role of the cyclic lipopeptide massetolide A in biological control of *Phytophthora infestans* and in colonization of tomato plants by *Pseudomonas fluorescens*. New Phytol. 175(4):731–742.

Valadares ACF, Alves CCF, Alves JM, De Deus IPB, DO F.J.G, Dos Santos TCL, Dias HJ, Crotti AEM, Mirand M. 2018. Essential oils from *Piper aduncum* inflorescences and leaves: chemical composition and antifungal activity against *Sclerotinia sclerotiorum*. An Acad Bras Ciênc. 90(3):2691–2699. http://dx.doi.org/10.1590/0001-3765201820180033.

Van de Mortel JE, Tran H, Govers F, Raaijmakers JM. 2009. Cellular responses of the late blight pathogen *Phytophthorainfestans* to cyclic lipopeptide surfactants and their dependence on G Proteins. Appl Environ Microbiol. 75(15):4950–4957.

Verma RK, Chaurasia L, Kumar M. 2011. Antifungal activity of essential oils against selected building fungi. Indian J Nat Prod Resour. 2:448–451. http://nopr.niscair.res.in/handle/123456789/13343.

Vickers CE, Gershenzon J, Lerdau MT, Loreto F. 2009. A unified mechanism of action for volatile isoprenoids in plant abiotic stress. Nat Chem Biol. 5(5):283–291.

Vila R, Mundina M, Tomi F, Furlan R, Zacchino S, Casanova J, Cañigueral S. 2002. Composition and antifungal activity of the essential oil of *Solidago chilensis*. Planta Med. 68(2):164–167.

Vitoratos A, Bilalis D, Karkanis A, Efthimiadou A. 2013. Antifungal activity of plant essential oils against *Botrytis cinerea*, *Penicillium italicum* and *Penicillium digitatum*. Not Bot Hort Agrobot Cluj. 41(1):86–92.

Wang K, Jiang S, Pu T, Fan L, Su F, Ye M. 2019. Antifungal activity of phenolic monoterpenes and structure-related compounds against plant pathogenic fungi. Nat Prod Res. 33(10):1423–1430.

Wang J, Liu J, Chen H, Yao J. 2007. Characterization of *Fusarium graminearum* inhibitory lipopeptide from *Bacillus subtilis* IB. Appl Microbiol Biotechnol. 76(4):889–894.

Wedge DE, Galindo JCG, Macías FA. 2000. Fungicidal activity of natural and synthetic sesquiterpene lactone analogs. Phytochemistry. 53(7):747–757.

Wisniewski ME, Wilson CL. 1992. Biological control of post-harvest diseases of fruits and vegetables: recent advances. HortSci. 27(2):94–98.

Xie Y, Huang Q, Wang Z, Cao H, Zhang D. 2017. Structure-activity relationships of cinnamaldehyde and eugenol derivatives against plant pathogenic fungi. Indus Crops Prod. 97:388–394.

Yang F-L, Li X-G, Zhu F, Lei C-L. 2009. Structural characterization of nanoparticles loaded with garlic essential oil and their insecticidal activity against *Tribolium castaneum* (Herbst)(Coleoptera: Tenebrionidae). J Agric Food Chem. 57(21):10156–10162.

Yazdanpanah L, Mohamadi N. 2014. Antifungal activity of *Satureja hortensis* L. essential oil against *Alternaria citri*. Eur J Exp Biol. 4:399–403.

Zachow C, Jahanshah G, de Bruijn I, Song C, Ianni F, Pataj Z, Gerhardt H, Pianet I, Lämmerhofer M, Berg G, et al. 2015. The novel lipopeptide poaeamide of the endophyte *Pseudomonas poae* RE*1-1-14 is involved in pathogen suppression and root colonization. MPMI. 28(7):800–810.

Zamani-Zadeh M, Soleimanian-Zad S, Sheikh-Zeinoddin M, Goli S. 2014. Integration of *Lactobacillus plantarum* A7 with thyme and cumin essential oils as a potential biocontrol tool for gray mold rot on strawberry fruit. Postharvest Biol Technol. 92:149–156.

Zhang H, Ma L, Wang L, Jiang S, Dong Y, Zheng X. 2008. Biocontrol of gray mold decay in peach fruit by integration of antagonistic yeast with salicylic acid and their effects on postharvest quality parameters. Biol Control. 47(1):60–65.

Zhang Z, Pang X, Guo S, Cao J, Wang Y, Chen Z, Feng Y, Lei N, Du S. 2019. Insecticidal activity of *Artemisia frigida* willd. essential oil and its constituents against three stored product insects. Rec Nat Prod. 13(2):176–181.

Zhang JH, Sun HL, Chen SY, Zeng L, Wang TT. 2017. Anti-fungal activity, mechanism studies on α-phellandene and nonanal against *Penicillium cyclopium*. Bot Stud. 58(1):13–21.

Zhang Z, Yang T, Zhang Y, Wang L, Xie Y. 2016. Fumigant toxicity of monoterpenes against fruit fly, *Drosophila melanogaster*. Indus Crops Prod. 81:147–151.

Zhao P, Quan C, Wang Y, Wang J, Fan S. 2014. *Bacillus amyloliquefaciens* Q-426 as a potential biocontrol agent against *Fusarium oxysporum* f. sp. *spinaciae*. J Basic Microbiol. 54(5):448–456.

Zhu Z, Zhang G, Luo Y, Ran W, Shen Q. 2012. Production of lipopeptides by *Bacillus amyloliquefaciens* XZ-173 in solid state fermentation using soybean flour and rice straw as the substrate. Bioresour Technol. 112:254–260.

Zouari R, Ellouze-Chaabouni S, Ghribi-Aydi D. 2014. Optimization of *Bacillus subtilis* SPB1 biosurfactant production under solid-state fermentation using by-products of a traditional olive mill factory. Achieve Life Sci. 8(2):162–169.