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To cite this version:

Roman Pavela, Raul Narciso C Guedes, Filippo Maggi, Nicolas Desneux, Giovanni Benelli. Essential oil antifeedants against armyworms: promises and challenges. Entomologia Generalis, 2023, 43 (4), pp.689-704. 10.1127/entomologia/2023/1887 . hal-04292029

HAL Id: hal-04292029
https://hal.inrae.fr/hal-04292029

Submitted on 17 Nov 2023

Entomologia Generalis, Volume 43 (2023), Issue 4, 689–704

Open Access Review Article

Essential oil antifeedants against armyworms: promises and challenges

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With 2 tables

Abstract: Plant secondary metabolites are fascinating weapons in the fight against herbivores. Of note, products of the plant secondary metabolism can be highly useful in developing insecticides for insect pest management. In this framework, the present review focuses on a group of plant secondary metabolites, i.e., essential oils (EOs), and a major group of insect pest species, armyworms, *Spodoptera* spp. (Lepidoptera: Noctuidae), with a major focus on antifeeding responses. Among all tested EOs, only the ones extracted from *Angelica archangelica, Artemisia nakaii, Piper hispidinervum, P. sanctifelicis, Pulegium vulgare* and *Tanacetum parthenium* showed good antifeedant efficacy (i.e., $ED_{50}<10$ μg/cm^2) against *Spodoptera littoralis* or *S. litura*. EO major constituents showing promising antifeedant activity include pulegone, 11α-epoxyeremophil-9-en-8-one (ligudicin A), piperitone epoxide and thujone, all showing $ED_{50}<1$ μg/cm^2. Other promising compounds are dehydrofukinone, germacrone, piperitenone and piperitenone oxide, showing $ED_{50}<5$ μg/cm^2. Overall, considering the sparse literature on the topic and the lack of standardized methods for testing EOs and their major constituents as antifeedants on armyworms, a call for standardization of armyworm antifeedant tests is presented.

Keywords: armyworms, green insecticide, ingestion toxicity, moth pest, Noctuidae, *Spodoptera frugiperda*, *Spodoptera litura*, *Spodoptera littoralis*

1 Introduction

The Lilliputian realm of insects imposes focus on these organism’s small body size transferring our biased understanding away from the human scale. As size permeates all aspects of insect ecology and physiology, it largely drives the interactions of these organisms with their physical substrate mainly through the forces of cohesion, adhesion and friction rather than through gravity (Chown & Gaston 2010, Clapham & Karr 2012). This scenario of small organisms living in close association with a substrate drives the need to understand the dynamics of this interaction (Backus et al. 2020), and phytophagous insects interacting with their host plants is an illustration of that (Bernays 1991).

Insect-plant interactions provide a multilayered level of intricacies that serves as a relevant driver of both insect and plant diversification (Cogni et al. 2022, Coolen et al. 2022, Sharma et al. 2021). Constitutive and induced plant defenses, including physical traits and volatile and non-volatile compounds, challenge insect herbivory countered by a range of tactics including evasion of plant defenses, manipulation of plant parts, and sequestration and detoxification of toxic plant defense compounds (Bernays 1991, Giron et al. 2018, Naorem & Karthi 2021). Besides the eco-evolutionary importance of the subject, insect-plant interactions are also important within a more applied framework, both when crop pollinators are involved and when insect crop pests are considered (Naorem & Karthi 2021, Shree et al. 2021).

DOI: 10.1127/entomologia/2023/1887
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Plant secondary metabolism is particularly frequent as a defense against herbivory driving insect specialization. It affords a generous array of study possibilities ranging from the understanding of how plants manipulate herbivore insects, how herbivore insects manipulate plants, and how these two processes interact generating the respective plant and insect responses (Giron et al. 2018, Riffell 2020, Sharma et al. 2021). Furthermore, products of the plant secondary metabolism are also useful in developing chemical tools for insect pest management and several modern insecticide molecules were developed from such basic structures (Loso et al. 2017, Sparks et al. 2020). However, phytochemicals produced from this metabolism are also potentially important as insecticidal and deterrent compounds (Sparks et al. 2001, Gerwick & Sparks 2014, Pavela & Benelli 2016, Isman 2020, Kavallieratos et al. 2021, Umesh et al. 2021, Collares et al. 2023).

In this scenario, the present review focuses on a group of them, essential oils, and a major group of insect pest species, armyworms, particularly focusing on antifeeding responses. Of note, considering the sparse literature on the topic and the lack of standardized methods for testing these substances on *Spodoptera* pest species, a call for standardization of insecticide test methods has been put forward.

2 Chemoreception, host location and selection

Lepidoptera pest species possesses chemoreceptors essential for spatial orientation necessary for their survival, development and reproduction (Pitre et al. 1983, Whitford et al. 1988). Such chemoreceptors are usually abundant on the antennae and mouthparts allowing the reliable recognition of various substances in the environment guiding the organism behavior (Koul 2005). Besides spatial orientation of males mediated by female pheromone molecules during partner search in the mating period (Koul 2008, Benelli et al. 2019a), the chemoreceptor-based mechanism of searching for suitable food is undoubtedly the second most important one (Wanner & Robertson 2009).

Host searching and selection are important not only for specialist insect species (i.e., monophagous and oligophagous species) (Koul 2008), but also for polyphagous species such as moths of *Spodoptera frugiperda* Smith (da Silva et al. 2017). Individuals of the latter are able to select suitable hosts for feeding and egg-laying, and sex-specific differences in macronutrient regulation were also detected in *S. litura* Fab, with consequences for development, migration and reproduction (Lee 2010).

Numerous examples show that Lepidoptera can actively orient toward volatiles from their host plants (Carroll & Berenbaum 2002, Castrejon et al. 2006, Becher & Guerin 2009), toward plants attacked by conspecific larvae (Carroll et al. 2008, Mooney et al. 2009), or selectively move away from odors of non-host plants (Piesik et al. 2009), and even detect the conspecific adult female pheromone (Poivet et al. 2012). Several species can learn the odor of their host plant on which they feed (Rojas & Wyatt 1999), and they are capable of associative learning with tastants (Salloum et al. 2011) or with noxious stimuli associated with feeding on a noxious host plant (Dethier 1980). Thus, Lepidoptera species have a very elaborate olfactory system which enables them to make ecologically relevant choices.

In Lepidoptera, the olfactory system has been mostly studied in the adult stage, which is important but can't overshadow the relevance of such system for the larval stage. Regardless, the complexity of the adult olfactory system makes it difficult to understand how sensory inputs are detected at the peripheral level and translated into behaviors. In contrast, the caterpillar olfactory system is much simpler and consists of two olfactory organs, the antennae that bear only three olfactory basiconica sensilla and the maxillary palps that bear 8 sensilla, 4–5 of which are olfactory (Roessingh et al. 2007). Together, 16 olfactory neurons are found on the antennae (Dethier & Schoonhoven 1969). In *S. littoralis*, the larvae express 22 out of 47 identified olfactory receptors; 15 of them are expressed in both the antennae and the palps, one is expressed only in the palps and 6 are expressed only in the antennae (Poivet et al. 2013). Even with such a reduced olfactory system, caterpillars have astonishing discrimination capabilities (Mooney et al. 2009, Piesik et al. 2013), which change according to experience, particularly through associative learning (Salloum et al. 2011).

The chemoreceptors in insects are primary sense cells and thus true neurons generally protected from the deleterious effects of secondary plant compounds (Simmonds et al. 1990). If some receptor cells have retained their primordial sensitivity to different kinds of secondary plant compounds, they are ideally suited to signal the presence of chemicals to be avoided. The above-mentioned cells, in addition to show basic sensitivity to secondary plant substances been preserved, are also connected to the action potential generating system, resulting in a change of impulse frequency upon stimulation (Schoonhoven 1991). Thus, in contrast to sugar and salt receptors, deterrent receptors have preserved their general sensitivity, which has been linked to a neural response mechanism. In fact, all lepidopteran larvae possess a pair of maxillary palps that "drum" the surface of foods during feeding. It has been hypothesized that some plant compounds elicit rejection through stimulating (1) olfactory receptor cells, (2) taste receptor cells, (3) oral mechanoreceptors, and (4) a post-ingestion response mechanism (Koul 2005).

Insects may also use other codes for taste quality, such as assessment of the temporal sequence of firing, which gives a continuous evaluation of the activity of individual neurons.

It is also likely that simultaneous evaluation of inputs from different neurons allows contradictory signals, indicating the presence of phagostimulants or antifeedants, and is assessed concurrently (Koul 2008). In addition to these neural mechanisms, other targets are also vulnerable to antifeedants, like gamma-aminobutyric acid (GABA) antagonistic mechanisms, and biogenic amine inhibition (Schoonhoven 1982, Jankowska et al. 2017, 2019).

In this framework, it is important to study plant antifeedant compounds and their mechanisms of action on phytophagous insects, not only to deepen our understanding of the plant-insect interactions, but also for their practical application. If plant chemicals can effectively prevent leaf-eating pests from food intake, they can be potentially used in plant protection, or respectively, in the development of botanical insecticides (Koul 2008, Pavela & Benelli 2016, Collares et al. 2023).

3 Phytochemical mediators of insect response

Botanical insecticides, fully recognized today as a fully-fledged alternative for synthetic insecticides, utilize secondary metabolites of plant defense mechanisms as active substances (Pavela 2016, Isman 2020a, 2020b, Haddi et al. 2020, Turchen et al. 2020, Collares et al. 2023). They contain plant metabolites commonly present in nature and their residues promptly decompose, posing no burden to the environment (Isman 2015). Additionally, they contain mixtures of bioactive substances that often exhibit potentiation and even synergistic action (Pavela 2010), which can help to delay the development of resistant pest populations (EC 2009), a highly positive aspect of these products compared to synthetic insecticides (Cloyd 2010). Moreover, as the consumption of active substances of synthetic insecticides is being restricted (e.g. Jactel et al. 2019, Verheggen et al. 2022) because of their potential negative impact on environmental and human health (EFSA 2018, Lucchi & Benelli 2018, Ricupero et al. 2020), there is an urgent need for new bioactive substances, particularly of natural or plant origin to effectively prevent insect pest damage caused by phytophagous insects (Callaghan 1991, Jankowska et al. 2017, 2019, Mantzoukas et al. 2022). Novel modes and mechanisms of action are particularly welcome in that regard, and they also include deterrents or inhibitors of chemosensory cells. Any impairment of chemoreceptor response in insects causes a subsequent change in insect behavior, with special reference to repellent, antiovipositional or antifeedant behavior, and a range of addition sublethal effects (Desneux et al. 2007, Koul 2008, Ribeiro et al. 2015, Borzoui et al. 2016, Benelli et al. 2019b, 2022, Devrnja et al. 2020, Rizzo et al. 2021).

4 Plant essential oils

Plant metabolites with an ability to mediate communication with insects and change their behavior include, among others, the group of essential oils (EOs). EOs are complex mixtures of up to several tens of compounds, predominantly oxygenated and non-oxygenated monoterpenes, sesquiterpenes and other aromatic substances such as phenypropanoids. While responsible for plant smell and taste (Tisserand & Young 2013), EOs also form part of their natural defense mechanisms (Pavela & Benelli 2016). EOs exhibit insecticidal and antioviposition, repellent or antifeedant effects (Pavela et al. 2009, Koul 2005, Benelli & Pavela 2018). They are therefore viewed as phytochemicals with good prospects for the development of new botanical insecticides (Pavela & Benelli 2016).

Considering that EOs exhibit diverse mechanisms of action (Mossa 2016), the study of their antifeedant potential is also important, and also their potential use in plant protection against phytophagous insects. Rather than relying on insect mortality, antifeedants minimizes plant yield losses by discouraging insect herbivory by deterring feeding, which is a frequent response sparked by plant defensive compounds and particularly of EO (Barik 2021, Isman 2002). Antifeedant activity may be reached by either stimulating specialized deterrent receptors in insect, or by distorting the normal functions of sensory nerve cells that perceive phagostimulating compounds (Koul 2008). The former mode of action, by affecting specific sensory cells (i.e., antifeedant receptors), may either prevent insect feeding or interrupt or slow down further feeding (Koul 2008, Purrington 2016). In contrast, the blocking of the herbivore feeding-stimulant receptors or directly binding to its usual feeding cues, may also lead to antifeeding activity (Purrington 2016), although compounds exhibiting this mode of action may not be regarded as antifeedant by some authors (Isman 2002).

5 *Spodoptera* armyworms, cutworms and leafworms

Among Lepidoptera, the night moths belonging to Noctuidae family include key pests of many crops of economic importance. Among them, the genus *Spodoptera* holds prominence. For example, *S. litura,* known as tobacco cutworm or cotton leafworm, is one of the most harmful and polyphagous moths in Asia, Oceania and Indian subcontinent where more than 112 host species are grown including tobacco, cotton, soybean, beet, cabbage, and chickpeas (Munir eta al. 2009). *S. litura* is often mistaken for its close relative, *S. littoralis* Boisd., also referred to as the African cotton leafworm or Egyptian cotton leafworm, or even Mediterranean brocade. *S. littoralis* is abundant particularly in Africa, Mediterranean Europe and Middle East countries. It is a highly polyphagous organism harmful to many cultural plants and crops, as *S. litura*. Consequently, this species has been identified as an A2 quarantine pest by the European Plant Protection Organization (EPPO) and recognized to be a highly invasive species in the United States (OEPP/EPPO 2015). Also, the fall armyworm, *S. frugiperda*, is a widely spread polyphagous species, especially in eastern and central North America and in South America wherefrom it has spread to most warm regions of the world (Kenis et al. 2023). The armyworm's diet consists mainly of grasses and grain crops such as corn, but this species can consume over 80 different plants (De Groote et al. 2020).

The above-mentioned representatives of the *Spodoptera* genus pests not only cause considerable economic damage (OEPP/EPPO 2015), but owing to their rapid reproduction, polyphagous nature, and development of resistant populations, are becoming ever more difficult threat to agricultural crops (Gutirrez-Moreno et al. 2019). The global range expansion of the fall armyworm further emphasizes the concern with the *Spodoptera* genus, whose common control methods face drastic challenges. Pheromones, for example, tend to be not specific enough for effective monitoring while biocontrol agents have limited distribution or disputable impact at least in some scenarios. On the other hand, considering genetically modified plants and chemical insecticides, their efficacy is affected by the quick development and spread of resistant populations of this group of pest species, as is well illustrated by the difficult management of the fall armyworm (Kenis et al. 2023). Thus, new methods of protection against these insect pests are necessary, and antifeedants seem to provide an option worth considering.

The purpose of this review was to undertake a critical evaluation of what is known today about the antifeedant efficacy of plant EOs against the highly polyphagous *Spodoptera* spp. larvae. As we intended to obtain information that would be as objective as possible and that would provide evidence of the primary antifeedant response, the following criteria of selection were determined for publications: use of standard choice or non-choice tests in leaf discs; known dose and EO composition, or use of pure compounds contained in EOs. Publications of WoS and Scopus databases (accessed: January 2022) were searched using the following key words: "*Spodoptera*", "essential oil", and "antifeedant".

6 Essential oils as antifeedants against *Spodoptera* spp. pests

Concerning the antifeedant tests of EOs for managing *Spodoptera* spp., our database search retrieved a total of 51 research items. However, only 17 articles satisfied the selection criteria and contained relevant information on antifeedant efficacy of EOs against *Spodoptera* spp. larvae (Table 1). In total, EOs of 33 plant species were tested. Of these, only EOs obtained from *Angelica archangelica, Artemisia nakaii, Piper hispidinervum, P. sanctifelicis, Pulegium vulgare* and *Tanacetum parthenium* showed significant antifeedant efficacy against *S. littoralis* or *S. litura,* where the estimated median effective dose (ED_{50}) was lower than 10 µg/cm^2. In general, the efficacy of EOs depends on their chemical composition, particularly on the mutual ratios and synergistic relationships among the major compounds (Pavela 2010). Based on the content of major compounds in selected EOs with the highest efficacy, substances such as phellandrene, sabinene, α-pinene, β-pinene, safrole, terpinolene, bicyclogermacrene, ocimene, δ-3-carene, limonene, *p*-cymene, nerolidol, pulegone or camphor are the likely candidates for the antifeedant activity.

To understand the antifeedant efficacy of EOs, we need to test not only the EOs but also their individual component compounds. So far, only 20 publications have tested the total of 45 aromatic compounds for antifeedant activity against *Spodoptera* spp. larve, a frequent shortcoming of botanical insecticides and their phytochemical components. By comparing relevant results, it was possible to select several compounds with very good antifeedant activity (Table 2). Those with the highest efficacy include pulegone, 11α-epoxyeremophil-9-en-8-one (ligudicin A), piperitone epoxide and thujone which showed ED_{50} below 1 µg/cm^2. Other promising compounds include dehydrofukinone, germacrone, piperitenone and piperitenone oxide with ED_{50} estimated as lower than 5 µg/cm^2.

7 A call for standardization of methods to assess antifeedant activity in moths

Although the antifeedant response can be studied using electrophysical methods focused predominantly on measuring the neuronal response of B2 sensilla in caterpillars (Roessingh et al. 2007), from the practical point of view it is more convenient to use standard methods of treated and untreated leaf discs. These methods are faster, technically less demanding, can provide more information about the importance of antifeedant efficacy in practice, and if applied in a standard way, the results of individual authors can be compared.

In our opinion, standard antifeedant activity tests can be characterized as follows.

1. These tests can be used to compare the amount of contaminated food received by larvae in a given time period compared to untreated control. Therefore, it is strongly encouraged to calculate the so-called Feeding Deterrent Index (FDI), which provides information on the % reduction rate of contaminated food intake (T) compared to untreated food: FDI (%) = ((C-T)/(C+T)) *100 (Koul 2005, 2008)

Table 1. Antifeedant efficacy of plant essential oils tested on larvae of species belonging to the genus *Spodoptera*. Plant parts used for essential oil extraction: S: seeds, L: leaves, F: flowers, B: berries, AP: aerial parts; -: not specified (commercial essential oil).

Plants	Family	Plant part	Majority compounds	Test used	Species (instar)	Dose	FDI (%)	EC$_{50}$ ($\mu g/cm^2$)	References
Angelica archangelica L.	Apiaceae	S	β-Phellandrene, sabinene, α-pinene, α-phellandrene	No-choice	*S. littoralis* (3rd instar)			ED50 = 7.12 (6.76–7.25)	Pavela & Vrchotova 2013
Acanthospermum hispidum DC.	Asteraceae	L, F	β-caryophyllene, α-bisabolol, germacrene D, β-elemene, bicyclogermacrene	Choice	*S. frugiperda* (2nd instar)	250 μg/g	53.3 ± 0.25	x	Alva et al. 2012
Artemisia absinthium L. (E4)	Asteraceae	AP	(Z)-2,6-dimethylocta-5,7-dien-2,3-diol, chrysanthenol, diterpene $C_{20}H_{28}O$, $C_{10}H_{18}O$ sesquiterpene	Choice	*S. littoralis* (6th instar)	100 μg/cm^2	21 ± 9	x	Bailen et al. 2013
Artemisia absinthium L. (H1)	Asteraceae	AP	β-Thujone, sabinyl acetate, α-thujone, limonene	Choice	*S. littoralis* (6th instar)	100 μg/cm^2	89 ± 3	x	Bailen et al. 2013
Artemisia absinthium L. (Sierra Nevada) – HD extraction	Asteraceae	AP	(−)-(Z)-Epoxyocimene, (−)-cis-chrysanthenol, (5Z)-2,6-dimethylocta-5,7-diene-2,3-diol, linalool	Choice	*S. littoralis* (6th instar)	100 μg/cm^2	47.8 (40.8–53.2)	x	Julio et al. 2015
Artemisia absinthium L. (SNC)	Asteraceae	AP	Chrysanthenol, bornyl acetate, cis-epoxyocimene, caryophyllene	Choice	*S. littoralis* (6th instar)	100 μg/cm^2	48 ± 10	x	Bailen et al. 2013
Artemisia absinthium L. (Teruel) - HD extraction	Asteraceae	AP	(−)-(Z)-epoxyocimene, (5Z)-2,6-dimethylocta-5,7-diene-2,3-diol, (−)-cis-chrysanthenol, linalool	Choice	*S. littoralis* (6th instar)	100 μg/cm^2	52.9 (40.1–64.6)	x	Julio et al. 2015
Artemisia herba-alba Asso	Asteraceae	L, F	Camphor, α-thujone, β-thujone, 1,8-cineole	Choice	*S. littoralis* (6th instar)	100 μg/cm^2	93.7 ± 2.2	14.6 (8.0, 24.5)	Santana et al. 2014
Artemisia nakaii Pamp.	Asteraceae	AP	Feropodin, (+)-camphor, 1,8-cineole, rishitin	Choice	*S. litura* (3rd instar)			3.76 ± 0.73	Liu et al. 2021
Artemisia pedemontana subsp. *assoana* (Willk.) Rivas Mart. (aeroponia)	Asteraceae	AP	Camphor, 1,8-cineole, p-cymene, camphene	Choice	*S. littoralis* (6th instar)	100 μg/cm^2	53.0 ± 8.9	x	Sainz et al. 2019
Artemisia pedemontana subsp. *assoana* (Willk.) Rivas Mart. (greenhouse)	Asteraceae	AP	Camphor, 1,8-cineole, terpinen-4-ol, borneol	Choice	*S. littoralis* (6th instar)	100 μg/cm^2	85.6 ± 7.9	x	Sainz et al. 2019
Artemisia pedemontana subsp. *assoana* (Willk.) Rivas Mart. (greenhouse)	Asteraceae	AP	Camphor, 1,8-cineole, terpinen-4-ol, borneol	Choice	*S. littoralis* (6th instar)	50 μg/cm^2	43.3 ± 19.2	x	Sainz et al. 2019
Santolina chamaecyparissus L.	Asteraceae	AP	1,8-Cineole, 8-methylene-3-oxatricyclo[5.2.0.02,4]nonane, viridiflorol, neo-allo-ocimene	Choice	*S. littoralis* (6th instar)	100 μg/cm^2	68.67 ± 7.4	x	de Elguea-Culebras et al. 2018
Tanacetum parthenium (L.) Sch. Bip.	Asteraceae	AP	Camphor, trans-chrysanthenyl acetate, (Z)-spiroether, camphene	No-choice	*S. littoralis* (4th instar)			0.31 (0.29–0.36) μL/cm^2	Pavela et al. 2010

Table 1. continued.

Plants	Family	Plant part	Majority compounds	Test used	Species (instar)	Dose	FDI (%)	EC_{50} (µg/cm^2)	References
Jatropha curcas L.	Euphorbiaceae	L	Dibutyl phthalate, diisooctyl phthalate, phytol, carvacrol	Choice	*S. littoralis* (6th instar)	10 µL/cm^2	71.31 ± 27.662	x	Soto-Armenta et al. 2019
Ricinus communis L.	Euphorbiaceae	-	Dotriacontane, thujone, 1,8 cineole, cynaropicrin	Choice	*S. littoralis* (4th instar)	72.0 µg/mL	6.62 ± 0.95	x	Ali et al. 2018
Geranium macrorrhizum L. (GH)	Geraniaceae	AP	β-elemenone, thymol, germacrone, nerolidol acetate	Choice	*S. littoralis* (6th instar)	100 µg/cm^2	87.8 ± 9.7	22 (14–34)	Navarro-Rocha et al. 2018
Geranium macrorrhizum L. (VB)	Geraniaceae	AP	Linalool, linalyl acetate, geranyl acetate, cis-linalool oxide	Choice	*S. littoralis* (6th instar)	100 µg/cm^2	55.5 ± 16.1	x	Navarro-Rocha et al. 2018
Hyssopus officinalis L.	Lamiaceae	AP	1,8-Cineole, β-pinene, pinocarvone, sabinene	Choice	*S. littoralis* (6th instar)	100 µg/cm^2	78.99 ± 8.1	49 (31 – 67)	de Elguea-Culebras et al. 2018
Lavandula (*luisieri*) *stoechas* (Portuguese population, Casal da Fraga)	Lamiaceae	L	trans-α-Necrodyl acetate, trans-α-necrodol, sesquiterpene acetate C17H28O3, viridiflorol	Choice	*S. littoralis* (6th instar)	100 µg/cm^2	73 ± 10	x	González-Coloma et al. 2011
Lavandula (*luisieri*) *stoechas* (Portuguese population, Casal da Fraga)	Lamiaceae	F	Trans-α-necrodyl acetate, trans-α-necrodol, sesquiterpene acetate, viridiflorol	Choice	*S. littoralis* (6th instar)	100 µg/cm^2	66 ± 10	x	González-Coloma et al. 2011
Lavandula (*luisieri*) *stoechas* (Portuguese population, Castelo Branco 2006)	Lamiaceae	L	trans-α-Necrodyl acetate, p-cymene, cis-α-necrodyl acetate, linalool	Choice	*S. littoralis* (6th instar)	100 µg/cm^2	90 ± 3	x	González-Coloma et al. 2011
Lavandula (*luisieri*) *stoechas* (Portuguese population, Castelo Branco 2006)	Lamiaceae	F	trans-α-Necrodyl acetate, viridiflorol, 1,8-cineole, camphor, 2,3,4,4-tetramethyl-5-methylen-2-cyclopenten-1-one	Choice	*S. littoralis* (6th instar)	100 µg/cm^2	51 ± 6	x	González-Coloma et al. 2011
Lavandula (*luisieri*) *stoechas* (Portuguese population, Castelo Branco 2007)	Lamiaceae	L	trans-α-Necrodyl acetate, fenchone, cis-α-necrodyl acetate, camphor	Choice	*S. littoralis* (6th instar)	100 µg/cm^2	97 ± 1	x	González-Coloma et al. 2011
Lavandula (*luisieri*) *stoechas* (Portuguese population, Castelo Branco 2007)	Lamiaceae	F	Camphor, 2,3,4,4-tetramethyl-5-methylen-2-cyclopenten-1-one, 1,8-cineole, bornyl acetate	Choice	*S. littoralis* (6th instar)	100 µg/cm^2	90 ± 7	x	González-Coloma et al. 2011
Lavandula (*luisieri*) *stoechas* L. (Portuguese population, Penamacor)	Lamiaceae	L	trans-α-Necrodyl acetate, β-selinene, trans-α-necrodol, fenchone	Choice	*S. littoralis* (6th instar)	100 µg/cm^2	96 ± 2	x	González-Coloma et al. 2011

Table 1. continued.

Plants	Family	Plant part	Majority compounds	Test used	Species (instar)	Dose	FDI (%)	EC_{50} (μg/cm²)	References
Lavandula (*luisieri*) *stoechas* L. (Portuguese population, Penamacor)	Lamiaceae	F	trans-α-Necrodyl acetate, β-selinene, trans-α-necrodol, fenchone	Choice	*S. littoralis* (6th instar)	100 μg/cm²	97 ± 1	x	González-Coloma et al. 2011
Lavandula x *intermedia* var. Super Emeric ex Loisel.	Lamiaceae	AP	Linalyl acetate, linalool, camphor, borneol	Choice	*S. littoralis* (6th instar)	100 μg/cm²	89.11 ± 6.7	25 (22 – 28)	de Elguea-Culebras et al. 2018
Mentha pulegium L. (Orestiada - Pul1)	Lamiaceae	L, F	Piperitone, limonene, 3-octanol, menthone	Choice	*S. littoralis* (6th instar)	100 μg/cm²	80.8 ± 4.6	x	Kimbaris et al. 2017
Mentha pulegium L. (Samothraki Island – Pul2)	Lamiaceae	L, F	Pulegone, isomenthone, piperitenone, menthone	Choice	*S. littoralis* (6th instar)	100 μg/cm²	75.1 ± 2.7	x	Kimbaris et al. 2017
Mentha spicata L.	Lamiaceae	L, F	Carvone, limonene, trans-caren-4-ol isomer, β-bourbonene	Choice	*S. littoralis* (6th instar)	100 μg/cm²	41.8 ± 24.5	x	Santana et al. 2014
Mentha spicata L. (Sparti – SP)	Lamiaceae	L, F	Piperitenone epoxide, piperitone epoxide, carvone, limonene	Choice	*S. littoralis* (6th instar)	100 μg/cm²	51.2 ± 8.8	x	Kimbaris et al. 2017
Pogostemon cablin (Blanco) Benth.	Lamiaceae	L	Patchouli alcohol, α-bulnesene, α-guaiene	No-choice	*S. litura* (3rd instar)	500 μg/mL	91.3 ± 1.0		Manjesh et al. 2022
Pulegium vulgare Mill.	Lamiaceae	L, F	Pulegone, 1,3,4-trimethyl-3-cyclohexene-1-carboxaldehyde, piperitenone	Choice	*S. littoralis* (6th instar)	100 μg/cm²	100.0 ± 0.0	1.3 (0.4, 4.1)	Santana et al. 2014
Rosmarinus officinalis L.	Lamiaceae	L, F	1,8-cineole, α-pinene, camphor, β-pinene, camphene	Choice	*S. littoralis* (6th instar)	100 μg/cm²	24.2 ± 19.4	x	Santana et al. 2014
Thymus satureioides Coss.	Lamiaceae	AP	Borneol, thymol, p-cymene, camphene	Choice	*S. littoralis* (6th instar)	100 μg/cm²	36.9 ± 22.7	x	Santana et al. 2014
Thymus linearis Benth.	Lamiaceae	AP	thymol, p-cymene	No-choice	*S.litura* (2nd instar)	8.0 μL/mL	95.8	x	Kabdal et al. 2022
Cinnamomum camphora (L.) J. Presl	Lauraceae	-	Cynaropicrin, D-camphor, 1,8-cineole, dotriacontane	Choice	*S. littoralis* (6th instar)	62.0 mg/mL	12.69 ± 1.48	x	Ali et al. 2018
Laurus novocanariensis Rivas Mart., Lousã, Fern. Prieto, E.Días, J.C.Costa & C.Aguiar (fall leaves)	Lauraceae	L, B	α-pinene, β-pinene, 1,8-cineole, α-terpinyl acetate	Choice	*S. littoralis* (6th instar)	100 μg/cm²	36	x	Rodila et al. 2008
Myrtus communis L.	Myrtaceae	L, F	1,8-Cineole + limonene, α-pinene, myrtenyl acetate, linalool	Choice	*S. littoralis* (6th instar)	100 μg/cm²	25.6 ± 19.4	x	Santana et al. 2014
Piper dilatatum L.C. Rich.	Piperaceae	L	Apiol, trans-caryophyllene, spathulenol, β-eudesmol	Choice	*S. littoralis* (6th instar)	100 μg/cm²	65.3 ± 1.3	x	Jaramillo-Colorado et al. 2019

Table 1. continued.

Plants	Family	Plant part	Majority compounds	Test used	Species (instar)	Dose	FDI (%)	EC_{50} (μg/cm^2)	References
Piper divaricatum G.Mey.	Piperaceae	L	Eugenol, methyl eugenol, γ-elemene, asarone	Choice	*S. littoralis* (6th instar)	100 μg/cm^2	70.7 ± 5.2	x	Jaramillo-Colorado et al. 2019
Piper hispidinervum C. DC. (Ph 1.5)	Piperaceae	AP	Safrole, terpinolene, bicyclogermacrene, (E)-β-ocimene	Choice	*S. littoralis* (6th instar)	100 μg/cm^2	97.7 ± 1.0	3.1 (1.1, 8.4)	Andres et al. 2017
Piper hispidum Sw.	Piperaceae	L	Limonene, δ-3-carene, p-cymene, elemol, spathulenol	Choice	*S. littoralis* (6th instar)	100 μg/cm^2	76.2 ± 2.5	48.0 (47.8–48.2)	Jaramillo-Colorado et al. 2019
Piper marginatum Jacq. (Acandi)	Piperaceae	L	cis-p-anethole, estragole, safrole	Choice	*S. littoralis* (6th instar)	10 μg/cm^2	64.3 ± 17.9	x	Jaramillo-Colorado et al. 2015
Piper marginatum Jacq. (Turbaco)	Piperaceae	L	Germacrene D, β-elemene, germacren-D-4-ol	Choice	*S. littoralis* (6th instar)	10 μg/cm^2	80.6 ± 12.1	x	Jaramillo-Colorado et al. 2015
Piper sanctifelicis Trel.	Piperaceae	L	δ-3-carene, limonene, p-cymene, β-pinene, nerolidol	Choice	*S. littoralis* (6th instar)	100 μg/cm^2	96.9 ± 0.9	4.5 (4.3–4.7)	Jaramillo-Colorado et al. 2019
Chloroxylon swietenia DC.	Rutaceae	L	Limonene, geijerene, germacrene D, pregeijerene	Choice	*S. litura* (3rd instar)			72.2 (60.5–83.9)	Kiran et al. 2006
Aloysia citriodora Palau	Verbenaceae	L, F	Limonene, sulcatone, trans-caryophyllene, sabinene, α-citral	Choice	*S. littoralis* (6th instar)	100 μg/cm^2	36.6 ± 22.6	x	Santana et al. 2014
Bulnesia sarmientoi Lorentz ex Griseb.	Zygophyllaceae	AP	Bulnesol, guaiol, α-eudesmol, γ-eudesmol	Choice	*S. littoralis* (6th instar)	100 μg/cm^2	28	x	Rodilla et al. 2011

Table 2. Antifeedant efficacy of selected essential oil constituents tested on larvae of species belonging to the genus *Spodoptera*.

Substance	Test used	Species (instar)	Dose (µg/cm²)	FDI (%)	EC_{50} (µg/cm²)	References
Monoterpene hydrocarbons						
Limonene	Choice	*S. littoralis* (6th instar)	100	44.8 ± 14.5	x	Valcárcel et al. 2021
Limonene	Choice	*S. littoralis* (6th instar)	50	55.6 ± 19.0	x	Santana et al. 2014
Limonene	Choice	*S. litura* (3rd instar)			110.4 (94.8–126.0)	Kiran et al. 2006
p-Cymene	Choice	*S. littoralis* (6th instar)	100	8.61 ± 6.09	x	Valcárcel et al. 2021
Terpinolene	Choice	*S. littoralis* (6th instar)	50	73.0 ± 12.6	53.80 (26.8, 99.4)	Andres et al. 2017
α-Pinene	Choice	*S. littoralis* (6th instar)	100	67.3 ± 8.9	x	Valcárcel et al. 2021
α-Pinene	Choice	*S. littoralis* (6th instar)	50	67.3	x	Rodilla et al. 2008
α-Pinene	No-choice	*S. litura* (3rd instar)			1.13 (0.65, 1.78)*	Rani et al. 2014
(*E*)-β-Ocimene	Choice	*S. littoralis* (6th instar)	50	92.7	10.6 (7.1, 15.9)	Rodilla et al. 2008
β-Pinene	Choice	*S. littoralis* (6th instar)	50	78.7	32.0 (26.5, 38.8)	Rodilla et al. 2008
Oxygenated monoterpenes						
Borneol	Choice	*S. littoralis* (6th instar)	50	40.4 ± 13.0	x	Santana et al. 2014
Camphor	Choice	*S. littoralis* (6th instar)	100	22.6 ± 6.0	x	Valcárcel et al. 2021
Camphor	Choice	*S. littoralis* (6th instar)	50	22.6 ± 6.0	x	Santana et al. 2014
Camphor	Choice	*S. littoralis* (6th instar)	50	59.9 ± 12.6	x	Sainz et al. 2019
Camphor	Choice	*S. littoralis* (6th instar)	50	22.64 ± 6.0	x	Julio et al. 2015
Carvacrol	Choice	*S. littoralis* (6th instar)	100	55.8 ± 11.8	x	Valcárcel et al. 2021
Carvacrol	Choice	*S. litura* (5th instar)			115.1 (109.3–121.3)	Hummelbrunner & Isman 2001
Carvone	Choice	*S. littoralis* (6th instar)	100	52.9 ± 12.7	x	Valcárcel et al. 2021
Carvone	Choice	*S. littoralis* (6th instar)	50	52.9 ± 12.7	x	Santana et al. 2014
1,8-Cineole	Choice	*S. littoralis* (6th instar)	100	36.0 ± 8.7	x	Valcárcel et al. 2021
1,8-Cineole	Choice	*S. littoralis* (6th instar)	50	36.0 ± 8.7	x	Santana et al. 2014
1,8-Cineole	Choice	*S. littoralis* (6th instar)	50	54.5	x	Rodilla et al. 2008
1,8-Cineole	Choice	*S. littoralis* (6th instar)	50	12.3 ± 7.6	x	Sainz et al. 2019
Fenchone	Choice	*S. littoralis* (6th instar)	50	27.16 ± 5.1	x	Julio et al. 2014
Linalool	Choice	*S. littoralis* (6th instar)	100	45.3 ± 7.2	x	Valcárcel et al. 2021
Linalool	Choice	*S. littoralis* (6th instar)	50	45	x	Rodilla et al. 2008
Linalool	Choice	*S. littoralis* (6th instar)	50	45.3 ± 7.2	x	Navarro-Rocha et al. 2018
Linalool	No-choice	*S. litura* (3rd instar)			1.13 (0.86, 1.25)*	Rani et al. 2014
Linalool oxide	Choice	*S. littoralis* (6th instar)	50	35	x	Rodilla et al. 2008

Table 2. continued.

Substance	Test used	Species (instar)	Dose (μg/cm²)	FDI (%)	EC_{50} (μg/cm²)	References
Menthol	Choice	*S. littoralis* (6th instar)	100	35.6 ± 14.3	x	Valcárcel et al. 2021
Menthone	Choice	*S. littoralis* (6th instar)	100	29.2 ± 9.8	x	Valcárcel et al. 2021
trans + *cis*-α-Necrodyl acetate (2 substances tested together)	Choice	*S. littoralis* (6th instar)	50	9.2 ± 9.2	x	Julio et al. 2016
Piperitenone	Choice	*S. littoralis* (6th instar)	100	91.8 ± 4.9	1.45 (0.2–9.9)	Valcárcel et al. 2021
Piperitenone oxide	Choice	*S. littoralis* (6th instar)	100	90.1 ± 3.7	5.0 (1.8–13.5)	Valcárcel et al. 2021
Piperitone	No-choice	*S. littoralis* (3rd instar)	500 / 1000 μg/ml	84.0 / 100.0	x	Abdelgaleil et al. 2008
Piperitone epoxide	Choice	*S. littoralis* (6th instar)	100	Not specified	0.18 (0.01, 3.0)	Kimbaris et al. 2017
Pulegone	Choice	*S. littoralis* (6th instar)	50	100.0 ± 0.0	0.2 (0.1, 0.4)	Santana et al. 2014
Pulegone	Choice	*S. littoralis* (6th instar)	100	Not specified	0.25 (0.1, 0.4)	Kimbaris et al. 2017
Thujone	Choice	*S. littoralis* (6th instar)	50	100.0 ± 0.0	0.2 (0.1, 0.4)	Santana et al. 2014
Thymol	Choice	*S. littoralis* (6th instar)	100	52.4 ± 10.1	x	Valcárcel et al. 2021
Thymol	Choice	*S. littoralis* (6th instar)	50	78.5 ± 8.0	21.0 (14.5, 27.1)	Santana et al. 2014
Thymol	Choice	*S. littoralis* (6th instar)	50	52.4 ± 13.0	x	Navarro-Rocha et al. 2018
Thymol	Choice	S. *litura* (5th instar)			85.6 (69.2–105.8)	Hummelbrunner & Isman 2001
Sesquiterpene hydrocarbons						
β-Caryophyllene	Choice	*S. littoralis* (6th instar)	50	90.7	26.2 (21.7, 31.6)	Rodilla et al. 2008
β-Caryophyllene	Choice	*S. littoralis* (6th instar)	50	91	26.2 (21.7, 31.6)	Rodilla et al. 2011
Germacrene D	Choice	*S. litura* (3rd instar)			144.4 (125.5, 163.4)	Kiran et al. 2006
Oxygenated sesquiterpenes						
11-Hydroxy-eremophila-6,9-dien-8-one[1]	Choice	*S. littoralis* (6th instar)	50	21 ± 7	x	Ruiz-Vasquez et al. 2017
11α-Epoxy-eremophil-9-en-8-one (ligudicin A)[1]	Choice	*S. littoralis* (6th instar)	50	89 ± 3	0.08 (0.04, 0.18)	Ruiz-Vasquez et al. 2017
Dehydrofukinone (SO)	Choice	*S. littoralis* (6th instar)	50	95 ± 1	1.68 (1.38, 2.04)	Ruiz-Vasquez et al. 2017
β-Caryophyllene oxide (SO)	Choice	*S. littoralis* (6th instar)	50	65.2	x	Rodilla et al. 2008
β-Elemenone (SO)	Choice	*S. littoralis* (6th instar)	50	25.2 ± 8.1	x	Navarro-Rocha et al. 2018
β-Eudesmol (SO)	Choice	*S. littoralis* (6th instar)	50	17	x	Rodilla et al. 2011
γ-Eudesmol (SO)	Choice	*S. littoralis* (6th instar)	50	29	x	Rodilla et al. 2011
Germacrone (SO)	Choice	*S. littoralis* (6th instar)	50 ug	90.5 ± 9.8	1.9 (0.1, 3.6)	Navarro-Rocha et al. 2018

Table 2. continued.

Substance	Test used	Species (instar)	Dose (µg/cm²)	FDI (%)	EC_{50} (µg/cm²)	References
Phenylpropanoids						
trans-Anethole	Choice	*S. litura* (5. instar)			103.1 (82.3, 129.2)	Hummelbrunner & Isman 2001
trans-Ethyl cinnamate	No-choice	*S. littoralis* (3rd instar)	500 / 1000	86.7 / 100.0	x	Abdelgaleil et al. 2008
Eugenol	Choice	*S. litura* (5th instar)			141.8 (122.8, 163.8)	Hummelbrunner & Isman 2001
Geijerene	Choice	*S. litura* (3rd instar)	192	100	82.5 (69.7, 95.2)	Kiran et al. 2006
Pregeijerene	Choice	*S. litura* (3rd instar)	225	100	95.1 (83.3, 107.0)	Kiran et al. 2006
Safrole	Choice	*S. littoralis* (6th instar)	50	80.5 ± 7.2	5.25 (1.3, 20.7)	Andres et al. 2017
4′,5-Dihydroxy-3,7-dimethoxyflavone[1]	Choice	*S. littoralis* (6th instar)	50	20 ± 8	x	Ruiz-Vasquez et al. 2017
5-Hydroxy-3,4′,7-trimethoxyflavone[1]	Choice	*S. littoralis* (6th instar)	50	48 ± 4	x	Ruiz-Vasquez et al. 2017

[1] these compounds are flavonoids isolated from an ethanol extract of *Senecio adenotrichius* DC. (Asteraceae).

2. A choice test that utilizes the principle of larval ability to naturally choose food with a better nutritional potential, not burdened with hazardous compounds. To a certain extent, larvae can enzymatically inactivate some indigestible or poisonous substances. However, this inactivation requires energy. Additionally, some substances may inhibit their food utilization ability, and thus plants without such substances are more convenient for the larvae. Nevertheless, even without a choice they can feed on food contaminated with growth inhibiting substances. The choice test thus answers the question whether a substance can discourage the larvae from food intake, and the results suggest whether the larvae respond to such substances as inappropriate for feeding or whether, on the contrary, food contaminated with these substances becomes more attractive for them.
3. A non-choice test is more rigorous and provides more input for potential use in practice. If no other but contaminated food is presented to the larvae, they are either able to feed with a time delay compared to untreated control or the treated food is inacceptable. Generally, if FDI is below 90%, the tested substance(s) probably only reduce the rate of food intake without posing insurmountable barrier to food intake. However, an FDI value above 90% indicates that the tested compound may be a true antifeedant substance as it can significantly inhibit the response of (1) olfactory receptor cells, (2) taste receptor cells, (3) oral mechanoreceptors, and/or (4) a post-ingestion response mechanism.

8 Conclusions and challenges for future research

In polyphagous insect species, including *Spodoptera* spp. larvae, it is very difficult to find an appropriate antifeedant because the larvae have a high capacity to inactivate various plant chemicals. Still, some compounds such as pulegone, 11α-epoxyeremophil-9-en-8-one (ligudicin A), piperitone epoxide and thujone showing ED_{50} below 1 µg/cm² can be viewed as highly promising for the development of botanical insecticides with an antifeedant activity. Some EOs (e.g., from *Piper aduncum, P. divaricatum, Melaleuca leucadendra, M. alternifolia, Syzygium aromaticum, Citrus aurantium* var. *amara* and *C. limon*) can exhibit antifeedant activity when tested at LC_{30} estimated in acute toxicity assays against *S. frugiperda* larvae, among others. In contrast, other EOs tested in the same study, e.g., *Eucalyptus citriodora, E. globulus, Citrus aurantium* var. *dulcis*, elicited attraction or neutral responses (Camara et al. 2022). Nevertheless, we are currently in the initial phases of research of the antifeedant efficacy against caterpillars provided by EOs, and the research should be intensified in order to achieve a level of progress comparable to that seen, for example, in the case of repellent EOs used against mosquitoes and ticks (Pavela & Benelli 2016a,b, Benelli & Pavela 2018).

Nevertheless, like the above-mentioned repellent compounds used in protection against mosquitoes, EOs also provide a limited residual activity due to evaporation and natural biodegradation (Tisserand & Young 2013). Therefore, it is important to study EO persistence from the implementation point of view. In this respect, specific reviews dealing with the encapsulation of EOs enabling to overcome several issues concerning their environmental dispersion and persistence, and efficacy at the target site of pest species are useful and should be referred to (Pavoni et al. 2019, Pavela et al. 2019, 2021, Benelli et al. 2020). However, comprehensive information on the duration of EO antifeedant effects remains lacking. Logically, though, unlike mosquitoes, larvae cannot fly away to seek other food items. Although they can disperse, their movement is limited in space. The persistence of EO antifeedant effect depends mainly on the applied concentration, on larval ability to overcome resistance to feeding on contaminated food, and on the environmental stability of active substances (Skuhrovec et al. 2020).

In conclusion, we believe that future research should focus on the following issues: (*i*) deeper investigation of EO modes of action, particularly those exhibiting high antifeedant potential; (*ii*) residual activity and the possibility of extending EO efficacy through time e.g. using modern encapsulation techniques (see Pavoni et al. 2019, Manjesh et al. 2022); and (*iii*) development of formulation exploring synergic effects of several EOs components and techniques that extend the post-application persistence of EOs.

Acknowledgements: Financial support was provided by the Ministry of Agriculture of the Czech Republic (Project MZE-RO0423) to R. Pavela, and by the ADOPT-IPM project from HORIZON Europe program (Grant Number 101060430) to N. Desneux.

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Manuscript received: 26 October 2022
Revisions requested: 16 January 2023
Modified version received: 4 February 2023
Accepted: 15 March 2022