frontiers | Frontiers in Horticulture

TYPE Review
PUBLISHED 28 November 2024
DOI 10.3389/fhort.2024.1379997

OPEN ACCESS

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RECEIVED 31 January 2024
ACCEPTED 29 October 2024
PUBLISHED 28 November 2024

CITATION
Favaro R, Berka M, Pettersson M, Thöming G, Arce CCM, Inácio ML, Turlings TCJ, Faria JMS, Jung T, Bazin D, Pozzebon A, Angeli S and Cappellin L (2024) The use of volatile organic compounds in preventing and managing invasive plant pests and pathogens. *Front. Hortic.* 3:1379997. doi: 10.3389/fhort.2024.1379997

The use of volatile organic compounds in preventing and managing invasive plant pests and pathogens

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Invasive pests and plant pathogens pose a significant threat to ecosystems and economies worldwide, prompting the need of anticipatory strategies. Preventing their introduction by detection at the ports of entry has been proven extremely difficult. This review explores the potential of biogenic volatile detection as a reliable preventive solution. It underscores the importance of early detection and rapid response as integral components of effective invasive pest management, and it discusses the limitations of current control measures and the increasing globalization that facilitates the spread of pests and pathogens. Through a synthesis of existing literature, this review analyzes the Volatile Organic Compound (VOC) emissions in five invasive model species: three insects, *Halyomorpha halys*, *Spodoptera frugiperda*, *Helicoverpa armigera*, a nematode, *Bursaphelenchus xylophilus*, and an oomycete, *Phytophthora ramorum*. The review focuses on the specific volatiles, released by both the invasive organisms and the infested host plants. If available, the volatiles emitted from similar species were considered for comparison. Ultimately, this review highlights specific pest volatile and shared Herbivore Induced Plant Volatiles (HIPVs) as a reliable and innovative solution in pest detection. If possible, candidate compounds are provided, whilst the lack of some emphasizes the urge of expanding the information available.

KEYWORDS

headspace, VOC collection, detection, *Halyomorpha halys*, *Spodoptera frugiperda*, *Helicoverpa armigera*, *Bursaphelenchus xylophilus*, *Phytophthora ramorum*

1 Introduction

In the global context of agriculture, the continuous threat posed by quarantine and severe pest species has become a pressing concern for researchers, policymakers, and farmers. The expansion of international trade and travel has facilitated the inadvertent spread of invasive pests, resulting in substantial economic losses and ecological imbalances worldwide. Management of these pests can be achieved through several approaches, but the most used ones are harmful chemicals, such as insecticides and fungicides in plant protection. The reduction by 50% of pesticide use is among the proposals adopted by the European Commission, in line with the EU's Farm to Fork and Biodiversity strategies (EC, 2020b). To achieve this goal, it is important to control new pest invasions and already established pests. The detection of invasive pests is a fundamental aspect of contemporary agricultural practices and ecological conservation. Swift and accurate detection allows for the implementation of timely control measures, preventing the establishment and spread of invasive species, minimizing economic and ecological impacts (MacDougall et al., 2022). One innovative approach to enhance the detection of invasive pests involves exploiting the volatile organic compounds (VOCs) released by the target pests or induced in attacked plants (Cui et al., 2018). Insects and pathogens produce VOCs as a mean of communication (semiochemicals in insects) or as metabolic derivatives (Bos et al., 2013; Gullan and Cranston, 2014; Fennine et al., 2024). Plants use VOCs to interact with other plants and insects, by luring pollinators, recruiting an herbivore's adversaries, camouflaging other plants, spotting invading plants, alerting other plants to impending danger, and exhibiting allelopathy (Baldwin, 2010; Heil, 2014; Karban et al., 2014; Turlings and Erb, 2018; MacDougall et al., 2022; Schuman, 2023). Once attacked by an enemy (either animals, fungi, bacteria, virus or nematodes), plants change their volatile profile induced volatiles (Dicke et al., 2009). They are a plant defense mechanism released by plants attacked by herbivores as a signal for higher trophic levels or other plants (Paré and Tumlinson, 1999; Gebreziher, 2018; Turlings and Erb, 2018; War et al., 2011).

The unique chemical signatures of these VOCs serve as indirect early warning signals, enabling to identify the presence of invasive pests before establishment and significant damage occur (Cui et al., 2018). These volatile signals can be used as valuable cues for monitoring and identifying pest infestations, enabling timely interventions, reducing potential crop damage and optimizing pest management strategies (MacDougall et al., 2022). Nixon et al. (2018), proposed to use the compounds released by *Halyomorpha halys* to detect the diapausing insects in shipments and selected possible target VOCs after a Gas Chromatography - Mass Spectrometry (GC-MS) analysis. Similarly, pest VOCs were taken into consideration to detect the presence of bed bugs (Akhoundi et al., 2023), a serious human health-related issue. Forty-nine compounds emitted by *Cimex lectuarius L.* and *C. hemipterus Fabricius* through their life stages were considered as valuable indicators of the bug presence. The same approach has also been proposed for the detection of a pine fungal pathogen, *Fusarium circinatum Nirenberg & O'Donnell* (Nordström et al., 2022), where through VOCs collection, GC-MS and automated data analysis, they managed to correctly distinguish infested and healthy seedlings of *Pinus radiata Don* and *P. sylvestris L.*

Volatiles can be collected in various ways (Brezolin et al., 2018; Tholl et al., 2021). Pre-concentration of VOCs on solid adsorbents followed by thermal desorption has become one of the standard methods for both field and laboratory studies. The type of adsorbent must be carefully selected to match the physicochemical characteristics of the target compounds. Additionally, the time from sampling to analysis must be minimized to prevent sample degradation due to reactive gases like ozone. However, most commercially available adsorbents work well, and they can be stored for a long time in a freezer without severely affect the outcomes of the analysis (Chu et al., 2016; Ho et al., 2018, authors personal observation). Among the different analytical techniques available for VOC analysis, including Proton Transfer Reaction Mass Spectrometry (PTR-MS) or electronic e-nose, Gas chromatography-Mass Spectrometry (GC-MS) has proven to efficiently separate and identify trace levels of VOCs in complex mixtures. However, both PTR-MS and GC-MS requires the use of large, expensive laboratory equipment that is unsuitable for use in the field. Moreover, the collection, processing, and analysis of the samples is time consuming and requires trained people. Therefore, for timely detection of pest, rapid and accurate diagnostic techniques that can be applied in the field are required. Efforts to achieve this goal have focused on the employment of so-called electronic noses to identify plant diseases and pests. An electronic nose uses a variety of gas sensors in conjunction with techniques for feature extraction and pattern recognition to identify and differentiate between distinct odors. The work of Fundurulic et al. (2023) provides an overview of the most recent developments in the field and emphasizes the application of cutting-edge methods for the prompt, non-destructive identification and control of harmful plant pests. Still, deploying e-nose for accurate and reliable characterization of specific VOCs in the field requires addressing challenges like sensor stability, specificity and reproducibility.

This review provides a context on the biology and, importantly, summarizes the current knowledge on the signature VOCs of five invasive pest model species: the brown marmorated stink bug (*Halyomorpha halys*), the fall armyworm (*Spodoptera frugiperda*), the cotton bollworm (*Helicoverpa armigera*), the pinewood nematode (*Bursaphelenchus xylophilus*) and *Phytophthora ramorum*. They are three insects, a nematode and an oomycete, and they were chosen because of their relevance to the EU pest surveillance programs. Induced volatiles released by attacked plants are also reported. The purpose of this review goes beyond the evaluation of the scientific soundness of the reference works, as they span a time of decades and a wide array of VOC collection techniques. It aims instead at presenting the current state of available information on VOCs of some relevant key pests, defining, when possible, a list of candidate VOCs for the pest identification to be used in pest surveillance and monitoring. The candidate VOCs were selected following the criteria of specificity and consistency. Specificity refers to the quality of clearly define or identify the target pest, whilst reducing unrelated false positive signals. Consistency on the other hand is crucial for scientific reproducibility and defines uniformity and stability of measurements over time and across different conditions or experiment. Therefore, findings that were confirmed by multiple studies were accounted as reliable. Each pest is presented in a dedicated section, reporting the biology, the management and its related VOCs.

2 Volatile organic compounds produced and induced by *Halyomorpha halys*

2.1 The brown marmorated stink bug: distribution, biology and management

Halyomorpha halys (Stål) (Hemiptera: Pentatomidae), known as the Brown Marmorated Stink Bug (BMSB) (Figures 1A, B), is an insect native to eastern Asia, and is now considered one of the most harmful invasive pests in North America and Europe (Zobel et al., 2016).

Halyomorpha halys consumes plant juices for nutrition feeding on the green parts of the plant, such as leaves and stems, but fruits are typically preferred (Figure 1C). The most significant crop damage comes from piercing fruiting structure on pome, stone and other fruit crops as well as seeds in legume pods such as soybeans (Leskey and Nielsen, 2018). The fruits are Highly deformed in cases of severe infestations, and there may be significant financial losses (Zobel et al., 2016). Fruit attacked by *H. halys* showed also increase in damage by fruit pathogens (Rice et al., 2014; Moore et al., 2019). The economic implications in the agricultural production are considerable, reaching billions of euros in crops worldwide (Rice et al., 2014). From a detailed estimation conducted in Northern Italy, it has emerged that it causes damages in the production of pears, apples, peaches, and kiwis for an estimated economic loss of 740 million euros (Fornasiero et al., 2023). In the eastern USA, the effects on apple and peach orchards reached up to total loss in 2010 (Leskey et al., 2012).

Due to its extreme polyphagia, *H. halys* has roughly 40 hosts among domesticated plants and much more (around 300) wild hosts (EPPO Global Database, 2023). *Halyomorpha halys* has one or two generations per year in the USA and Europe, but there have been reports up to 5–6 generations per year in the species' native range (Lee et al., 2013; Haye et al., 2014; Costi et al., 2017). In its adult stage, the stink bug spends the winter in natural shelters or anthropogenic structures. On the underside of the leaves, in clusters of 20–30 eggs, females lay 50–150 eggs, but they can also lay up to 400 eggs per female. There are five nymphal stages before reaching the adult stage (Lee et al., 2013) (Figure 1B). The control of *H. halys* relies on insecticides (Leskey et al., 2012). Recently, adventive populations of Asian egg parasitoid *Trissolcus* spp. (Hymenoptera: Scelionidae), in particular *Trissolcus japonicus* Ashmead and *Trissolcus mitsukurii* Ashmead were discovered in America and Europe (Talamas et al., 2019; Abram et al., 2019; Stahl et al., 2019; Sabbatini Peverieri et al., 2018; Scaccini et al., 2020) and may serve as viable antagonists. Other management options for the control of *H. halys* are staking, trap crops, perimeter reshaping in orchards, push-pull, exclusion nets, and behavioral manipulation. These had the potential to drastically minimize fruit loss (e.g., Blaauw et al., 2015; Candian et al., 2020; Falagiarda et al., 2023; Fornasiero et al., 2023; Carnio et al., 2024).

The use of semiochemicals plays an important role in the management of this pest. The discovery of the pest aggregation pheromone (Khrimian et al., 2014) opened for further pest control strategies. It is solely produced by adult males, and it attracts both adult males, adult females, and nymphs (Weber, 2015). For this reason, the pheromone lures are employed in traps for monitoring, early detection (Vandervoet et al., 2019) and for pest management decision making.

2.2 Summary of literature on *Halyomorpha halys* VOCs

Numerous studies have identified and characterized the volatile compounds emitted by *H. halys* (Table 1). These volatiles primarily consist of a diverse array of aldehydes, alcohols, esters, terpenes, and sulphur-containing compounds. Some of the most notable compounds include the aldehydes (*E*)-2-decenal, (*E*)-2-octenal, (*E*)-2-hexenal, sesquiterpenes and alkanes. The composition and ratios of these volatiles can vary depending on factors such as developmental stage, sex, feeding status, and environmental conditions.

Stink bugs, including *H. halys*, possess specialized scent glands located on their thorax and abdomen that release volatiles when disturbed or threatened (Kitamura et al., 1984). The emission of volatiles is primarily a passive process, relying on the release of pressure built up within the scent gland reservoir. These defense compounds are shared among many species and (*E*)-2-decenal, (*E*)-2-octenal, (*E*)-2-hexenal, (*E*)-2-decenyl acetate are reported in not only *H. halys* (Harris and Webber, 2016; Zhong et al., 2017; Nixon et al., 2018, Nixon et al., 2019, 2021; Karimi and Gross, 2024), but also in a cosmopolitan species, the green stink bug *Nezara viridula* L (Aldrich et al., 1987).These volatiles were collected from either full insect after immersion in solvent (Zhong et al., 2017) or from headspace by using different adsorption materials: Super-Q (Khrimian et al., 2014; Harris and Webber, 2016; Nixon et al., 2018, 2019, 2021), Tenax (Karimi and Gross, 2024), activated charcoal (Aldrich et al., 1987).

Generally, these (*E*)-2-aldehydes are reported as defensive compounds inducing avoidance by predators (Noge et al., 2012), and likely connected to the disturbance level the insects are exposed (Nixon et al., 2021). It was showed that they function also as alarm pheromones (Harris and Webber, 2016), acting as warning signal to conspecifics, indicating the presence of threats, and as dispersal signals, causing other stink bugs to disperse quickly, reducing the likelihood of multiple individuals being preyed upon simultaneously (Nixon et al., 2018, 2021). The implication of these VOCs in an intraspecific context is supported by the data reported in Nixon et al. (2021), in which the proportion of samples that released these defensive odors was null in singularly agitated insects, whilst increased proportionally to the number of insects in the group. Khrimian et al (2014) characterized the male-produced

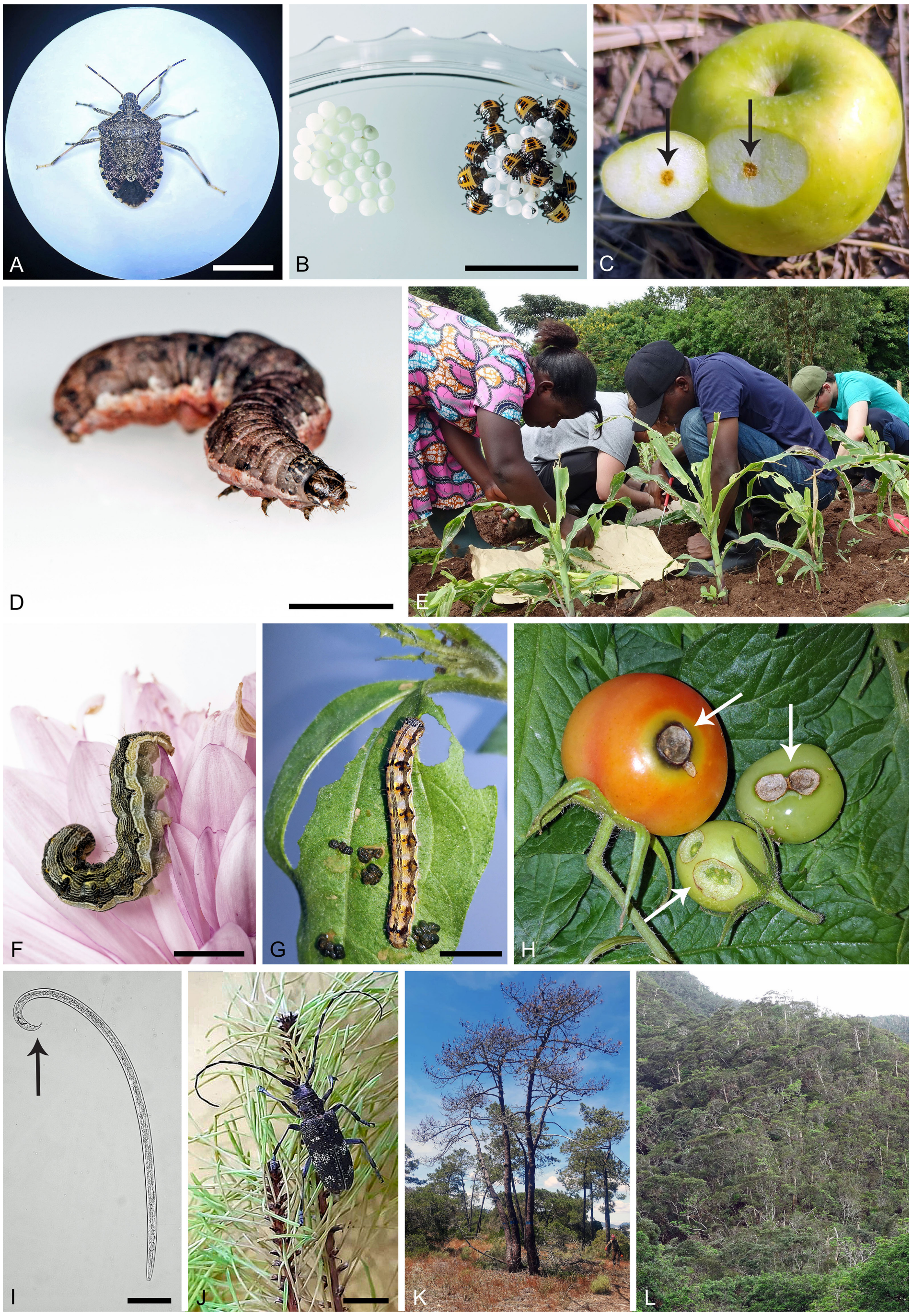

FIGURE 1
Pests and representative disease symptoms. **(A–C)** Brown marmorated stink bug (*Halyomorpha halys*). Scale bar = 1 cm. **(A)** Adult bug (photo courtesy: Diana La Forgia, Agroscope, Switzerland). **(B)** Eggs (left) and newly hatched nymphs (right) (photo courtesy: Carole Paroli, Agroscope, Switzerland). **(C)** Apple with sucking damage (arrows) (photo courtesy: Veronica Carnio, Free University of Bolzano, Italy). **(D, E)** Fall armyworm (*Spodoptera frugiperda*). **(D)** Mature caterpillar with distinctive inverted Y suture on the forehead (photo courtesy: Neil Villard, University of Neuchâtel, Switzerland). Scale bar = 1 cm. **(E)** Fall armyworm frass and feeding damage in a maize field in Rwanda (photo courtesy: Stefan Toepfer, CABI, Switzerland). **(F–H)** Cotton bollworm (*Helicoverpa armigera*). Scale bar = 1 cm. **(F)** Mature caterpillar on *Chrysanthemum* flower (photo courtesy: Erling Fløistad, NIBIO, Norway). **(G)** Mature caterpillar with frass and feeding damage on a sunflower leaf (photo: Gunda Thöming). **(H)** Damage caused by caterpillar frass on tomato fruits (arrows) (photo: Gunda Thöming). **(I)** Male Pinewood Nematode (PWN; *Bursaphelenchus xylophilus*) with characteristic pointed tale. Scale bar = 100 nm (photo courtesy: INIAV, Portugal). **(J)** *Monochamus galloprovincialis*, main vector of the PWN in Europe. Scale bar = 1 cm (photo courtesy: INIAV, Portugal). **(K)** Mature *Pinus pinaster* tree in Portugal showing acute wilting and mortality caused by the PWN (photo courtesy: INIAV, Portugal). **(L)** Natural *Pinus densiflora* forest on Amami Island, Japan with high mortality due to PWN damage (photo: Thomas Jung).

TABLE 1 List of Volatile Organic Compounds (VOCs) released by *Halyomorpha halys* and *Nezara viridula* (A), and list of Herbivore Induced Plant Volatiles (HIPVs) released by *H. halys*-infested plants (B) described in the literature.

A. Insect volatiles				
Plant species	VOC name	CAS-Nr	ID level	Reference
H. halys, adult male	(3*S*,6*S*,7*R*,10*S*)-10,11-Epoxy-1-bisabolen-3-ol	–	1	Khrimian et al., 2014; Harris and Webber, 2016; Weber, 2015
H. halys, adult male	(3*R*,6*S*,7*R*,10*S*)-10,11-Epoxy-1-bisabolen-3-ol	–	1	Khrimian et al., 2014; Harris and Webber, 2016; Weber, 2015
H. halys, adult, nymph, male genital capsule; *N. viridula*, adult	Tridecane	629-50-5	1	Aldrich et al., 1987; Tognon et al., 2017; Harris and Webber, 2016; Fraga et al., 2017; Zhong et al., 2017; Nixon et al., 2018;
H. halys, adult, eggs; *N. viridula*, adult	(*E*)-2-Decenal	3913-81-3	1	Aldrich et al., 1987; Sturaro et al., 1994; Harris and Webber, 2016; Tognon et al., 2017; Zhong et al., 2017; Nixon et al., 2018
H. halys, adult	(*E*)-2-Decen-1-ol	22104-80-9	1	Kitamura et al., 1984
H. halys, adult; *N. viridula*, adult	(*E*)-2-Decenyl acetate	19487-61-7	1	Aldrich et al., 1987; Zhong et al., 2017
H. halys, adult; *N. viridula*, adult	(*E*)-2-Hexenal	6728-26-3	1	Aldrich et al., 1987; Solomon et al., 2013; Zhong et al., 2017
H. halys, adult	(*E*)-2-Octenal	2548-87-0	2	Kitamura et al., 1984
H. halys, adult	(*E*,*E*)-2,4-Hexadienal	142-83-6	1	Solomon et al., 2013
H. halys, adult	(*Z*)-Cyclodecene	935-31-9	1	Solomon et al., 2013
H. halys, adult	1-Ethyl-1,5-cycloctadiene	5194-50-5	1	Solomon et al., 2013
H. halys, adult	3-Hepten-2-one	1119-44-4	1	Solomon et al., 2013
H. halys, adult, eggs	2,4-Decadienal	25152-84-5	1	Kitamura et al., 1984; Tognon et al., 2017
H. halys, adult	4-Oxo-(*E*)-2-hexenal	2492-43-5	2,1	Zhong et al., 2017; Nixon et al., 2018
H. halys, adult	5-Ethyl-2(5H)-furanone	2407-43-4	1	Solomon et al., 2013
H. halys, adult; *N. viridula*, adult	Dodecane	112-40-2	1	Kitamura et al., 1984; Aldrich et al., 1987; Borges et al., 1987; Zhong et al., 2017; Nixon et al., 2018
H. halys, adult	Pentadecane	629-62-9	1	Kitamura et al., 1984
H. halys, adult	Tetradecane	629-59-4	1	Kitamura et al., 1984
H. halys, adult	Undecane	1120-21-4	1	Kitamura et al., 1984
H. halys, eggs	Hexadecanal	629-80-1	1	Tognon et al., 2017
H. halys, eggs	Octadecanal	638-66-4	1	Tognon et al., 2017
H. halys, eggs	Eicosanal	2400-66-0	1	Tognon et al., 2017
H. halys, eggs	Nonanal	124-19-6	1	Tognon et al., 2017
H. halys, eggs	2-Undecenal	53448-07-0	1	Tognon et al., 2017
N. viridula, adult	Nonadecane	629-92-5	2,1	Aldrich et al., 1987; Borges et al., 1987
N. viridula, adult	(*Z*)-α-Bisabolene	29837-07-8	1	Aldrich et al., 1987
N. viridula, adult	(*E*)-Nerolidol	40716-66-3	1	Aldrich et al., 1987
N. viridula, adult	(*E*,*Z*)-α-Bisabolene epoxide	20767-74-6	1	Aldrich et al., 1987
N. viridula, adult	(*Z*,*Z*)-α-Bisabolene epoxide	1746-04-3	1	Aldrich et al., 1987

(Continued)

TABLE 1 Continued

B. Herbivore induced plant volatiles (HIPVs) after *Halyomorpha halys* infestation				
Plant species	VOC name	CAS-Nr	ID level	Reference
Peach (*Prunus persica* L.)	4'-Ethylacetophenone	937-30-4	2	Peterson et al., 2022
Peach	(*E*)-β-Caryophyllene	87-44-5	2	Peterson et al., 2022
Peach	(*Z*)-3-Hexenyl acetate	3681-71-8	2	Peterson et al., 2022
Peach	4-Hexenyl, acetate	72237-36-6	2	Peterson et al., 2022
Peach	Benzaldehyde	100-52-7	2	Peterson et al., 2022
Tree of heaven (*Ailanthus altissima* (Mill.) Swingle)	2,4-Di-*tert*-butylphenol	96-76-4	2	Peterson et al., 2022
Tree of heaven	(*E*)-β-Ocimene	3779-61-1	2	Peterson et al., 2022
Tree of heaven	Methyl palmitate	112-39-0	2	Peterson et al., 2022
Tree of heaven	(*E*)-Nerolidol	40716-66-3	2	Peterson et al., 2022
Tree of heaven	Sesquirosefuran	39007-93-7	2	Peterson et al., 2022
Tree of heaven	(3*E*)-4,8-Dimethyl-1,3,7-nonatriene	19945-61-0	2	Peterson et al., 2022
Tree of heaven	Alloocimene	3016-19-1	2	Peterson et al., 2022
Tree of heaven	Cinerone	-	2	Peterson et al., 2022
Tree of heaven	(*E*)-Farnesene epoxide	-	2	Peterson et al., 2022
Tree of heaven	Linalool	78-70-6	2	Peterson et al., 2022
Tree of heaven	Nonanal	124-19-6	2	Peterson et al., 2022
Tree of heaven	*p*-Mentha-1,3,8-triene	18368-95-1	2	Peterson et al., 2022

The ID level reports the VOCs identification levels reported by the literature (1= identified compound, 2= putatively identified compound, based upon physiochemical properties of a chemical class and/or by spectral similarities). The CAS number is a compound-specific unique identification number assigned by the Chemical Abstracts Service (CAS).

aggregation pheromone of *H. halys* as a 3.5:1 mixture of two stereoisomers, (3*S*,6*S*,7*R*,10*S*)-10,11-epoxy-1-bisabolen-3-ol and (3*S*,6*S*,7*R*,10*S*)-10,11-epoxy-1-bisabolen-3-ol. According to Harris and Webber (2016), mature males started producing pheromone at a mean age of 13 days. Males who were housed alone produced a mean of 843 ng of pheromone per day, in daily volatile collections in levels that ranged fivefold. Males in groups emitted <10% pheromone per bug per day than lone males due to a strong negative reaction to male density. The pheromone is mainly emitted during the day and it is effective to both adult sexes and nymphs (Weber, 2015).

An array of linear hydrocarbons has been detected in *H. halys*: undecane, dodecane, tridecane and pentadecane (Kitamura et al., 1984; Baldwin, 2010; Harris and Webber, 2016; Zhong et al., 2017). Among them, tridecane was the most frequently found. Linear hydrocarbons are also reported among the emissions of *N. viridula*: dodecane, tridecane and nonadecane (Borges et al., 1987). It is unclear whether these volatiles might play a role as bioactive compounds (Weber, 2015). A likely explanation proposed that such hydrocarbons serve as solvents or carriers (Calam and Youdeowei, 1968), as they would facilitate the efficient evaporation of active substances such as aldehydes on the scent gland system in a variety of pentatomid species (Kment and Vilimova, 2010). However, behavioral studies showed that the exposure of adult *H. halys* to the insect most abundant alkane, tridecane, led to an increased speed (Lockwood and Story 1985, 1987; Nixon et al., 2018), total distance and mean angular velocity (Nixon et al., 2021), and it also significantly reduced the emission of pheromones in adult males (Harris and Webber, 2016). This evidence might reveal a possible biological function of tridecane, but its mechanisms have yet to be understood. As addressed by Weber (2015), the data proposed by Harris and Webber (2016) lack statistical significance and should be considered carefully. On the other hand, the more recent work from Nixon et al. (2021) shows statistically sound evidence of an actual tridecane effect on the stink bugs behavior. It is worth considering however, that tridecane has always been found in all samples of *H. halys* VOCs studies, despite a more occasional presence of the *E*-2-aldehydes (Aldrich et al., 1987; Tognon et al., 2017; Harris and Webber, 2016; Zhong et al., 2017; Nixon et al., 2018), opening up a question on the biological relevance of an ubiquitous compound.

2.3 Summary of literature on *Halyomorpha halys* - induced plant VOCs

Despite the relevance of *H. halys* on crops worldwide, only one study has so far explored the HIPVs released after infestation. Peterson et al. (2022), analyzed direct and systemic emissions of potted peach (*Prunus persica* L.) and tree of heaven (*Ailanthus altissima* (Mill.) Swingle) plants following insect feeding and oviposition. The VOCs were collected from the headspace of a bag-enclosed branch for 24 hours by using a Hayesep adsorbent (Sigma-Aldrich, St. Louis, MO) and later eluted in dichloromethane and analyzed in GC-MS. The study showed a species-specific response in the VOCs released. Nerolidol was released at a greater rate by tree of heaven branches that were directly exposed to *H. halys* oviposition and feeding than by branches exposed to only feeding and control trees. In comparison to plants exposed to oviposition and feeding or control trees, tree of heaven leaves treated to *H. halys* feeding alone emitted greater rates of (*E*)-4,8-dimethyl-1,3,7-nonatriene. On the other hand, when peaches were subjected to *H. halys* oviposition, there was a reduction in (*Z*)-3-hexenyl acetate in both the directly and systemically exposed branches. Other compounds in peach plants varied between treatments: 4'-ethylacetophenone, (*E*)-β-caryophyllene, 4-hexenyl acetate and benzaldehyde. Similarly in tree of heaven plants, differences appeared between treatments: 2,4-di-tert-butylphenol, (*E*)-β-ocimene, methyl palmitate, sesquirosefuran, alloocimene, cinerone, (*E*)-farnesene epoxide, linalool, nonanal, *p*-mentha-1,3,8-triene.

2.4 Candidate VOCs for *Halyomorpha halys* detection

So far, the most unique compounds are the two stereoisomers (3*S*,6*S*,7*R*,10*S*)-10,11-epoxy-1-bisabolen-3-ol and (3*R*,6*S*,7*R*,10*S*)-10,11-epoxy-1-bisabolen-3-ol, identified as the main components of the aggregation pheromone released by adult males. All the other VOCs (Table 2) are generic of stink bugs or other organisms. It is however worth considering the aldehydes (*E*)-2-decenal, (*E*)-2-octenal, (*E*)-2-hexenal and the ester (*E*)-2-decenyl acetate, the unpleasant odors released by stink bugs when disturbed (alarm/defense pheromones). These VOCs, even if very generic, can at least indicate presence of stink bugs. Tridecane, the most frequently compound detected from *H. halys* and other stink bugs, occurs commonly in the environment as it is largely emitted by biotic and abiotic sources. The candidate VOCs here selected should answer to a specificity requirement, and therefore tridecane, due to its ubiquitous nature, has not been considered. The question on whether plants may respond in a similar way after an insect attack is crucial to increase the number of candidate HIPVs. Induced compounds that would be shared among a considerable number of host plant species following *H. halys* infestation would be extremely valuable as candidates for detection. However, the scarce literature available does not provide enough confidence to select any HIPVs, and more plant species need to be tested.

TABLE 2 List of candidate Volatile Organic Compounds (VOCs) for *Halyomorpha halys* detection.

VOC name	CAS-Nr	Biological relevance
(3*S*,6*S*,7*R*,10*S*)-10,11-Epoxy-1-bisabolen-3-ol	–	Aggregation pheromone
(3*R*,6*S*,7*R*,10*S*)-10,11-Epoxy-1-bisabolen-3-ol	–	Aggregation pheromone
(*E*)-2-Decenal	3913-81-3	Defense/alarm pheromone
(*E*)-2-Decenyl acetate	19487-61-7	Defense/alarm pheromone
(*E*)-2-Hexenal	6728-26-3	Defense/alarm pheromone
(*E*)-2-Octenal	2548-87-0	Defense/alarm pheromone

The CAS number is a compound-specific unique identification number assigned by the Chemical Abstracts Service (CAS).

3 Volatile organic compounds produced and induced by *Spodoptera frugiperda*

3.1 The fall armyworm: distribution, biology and management

The Fall Armyworm (FAW), *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae), is native to the Americas (Todd and Poole, 1980) and has been reported to attack a wide range of host plants and causes serious damage to many economical plants (Kenis et al., 2022). Although the larvae (Figure 1D) are known to feed on many host plants, they exhibit a preference for grasses and cereal crops like maize (Figure 1E), rice, sorghum, and wheat (Sparks, 1979; Pitre and Hogg, 1983). The high invasiveness potential of *S. frugiperda* is attributed to the exceptional capacity of the adult moths to migrate (Johnson, 1987; Westbrook et al., 2019). *Spodoptera frugiperda* has invaded all of sub-Saharan Africa after it was first observed in Nigeria in 2016 (Cock et al., 2017; Day et al., 2017) and also made its way from Africa to Asia (Sharanabasappa et al., 2018; Liu et al., 2020). More recently it was found in Oceania (Day et al., 2017; Lamsal et al., 2020) and entered continental Europe in 2024 (https://www.fao.org/fall-armyworm/monitoring-tools/faw-map/en/). It is now one of the biggest threats to food security on multiple continents (FAO, 2020), causing tremendous yield losses, especially in maize (Day et al., 2017; Baudron et al., 2019; Hruska and Gould, 1997; Rwomushana et al., 2018; Wan et al., 2021), threatening the livelihoods of millions of farmers and the food security of over 65 million people in Africa alone (Day et al., 2017; Rwomushana et al., 2018; Babendreier et al., 2020) (Figure 1E). According to estimates, it causes in maize up to 73% of global economic losses (Guo et al., 2018). In Africa, *S. frugiperda* alone results in annual yield losses of 9.4 billion US dollars (Eschen et al., 2021). Between 2017 and 2019, the pest reduced Ethiopia's grain yield by 0.225 million tons, with an average yearly loss of 36% in maize production (Abro et al., 2021). According to De Groote et al. (2020), the pest results in losses of around one-third of Kenya's yearly maize crop, or one million tons, with significant regional variations.

As a consequence of the *S. frugiperda* invasion, the use of pesticides has dramatically increased (Tambo et al., 2020; Yang et al., 2021), potentially causing health problems, harming the environment, and threatening biodiversity. The FAO considers *S. frugiperda* one of the most important threats to food security in these regions (http://www.fao.org/fall-armyworm/en/). Management of *S. frugiperda* involves, however, not only chemical insecticides but a wide array of integrated pest management strategies (Kenis et al., 2022). Many pathogens (bacteria, fungi, viruses), parasitoids (Diptera and Hymenoptera), and predators (Coleoptera, Dermaptera, Hemiptera, Hymenoptera) attack it throughout its natural habitat. Of all the natural enemies, egg parasitoids are the simplest to raise in high quantities for augmentative releases, and several studies are testing its viability (Vieira et al., 2017; Firake and Behere, 2020). Experiments on host plant choice have been carried out throughout the pest invasive range, mostly to look at the viability of intercropping and push-pull control techniques (Tay et al., 2023). Biopesticides involving entomopathogenic fungi, baculoviruses, entomopathogenic bacteria and nematodes have also been extensively explored (Kenis et al., 2022).

Research on the chemical ecology of *S. frugiperda* has focused on two aspects: the pheromone produced by the female moths to attract males, and the caterpillar-induced plant volatiles that attract natural enemies of the caterpillars. The sex pheromone of *S. frugiperda* is a blend of several volatile acetates, dominated by (*Z*)-9-tetradecenyl acetate (*Z*9-14:Ac). A combination of *Z*9-14:Ac with (*Z*)-7-dodecenyl acetate (*Z*7-12:Ac) is highly attractive to males in the field (Tumlinson et al., 1986), also to invasive populations in Japan (Wakamura et al., 2021). In a study in China a pheromone lure was optimized by still adding (*Z*)-11-hexadecenyl acetate (*Z*11-16:Ac) to the blend that was initially identified. Indeed, the *S. frugiperda* pheromone blend has been shown to be different for different geographic regions (Batista-Pereira et al., 2006; Groot et al., 2008). *Spodoptera. frugiperda* was one of the first insects studied in the context of herbivore-induced plant volatiles (HIPVs). Maize plants in particular are very responsive to caterpillar attacks and have been shown to emitted large amounts of mainly terpenoids, but also indole in response to such attacks (Tumlinson et al., 1990, Turlings et al., 1993). The emissions of the truly inducible compounds are systemic and not just limited to the damaged site (Turlings and Tumlinson, 1992), enhancing their detectability. The fatty acid-amino acid conjugate volicitin (N-[17-hydroxylinolenoyl]-L glutamine) present in the caterpillar oral secretions was found to be the main elicitor that triggers this response (Alborn et al., 1997; Turlings et al., 2000). *Spodoptera frugiperda* also emits such volatiles (Turlings et al., 1993), but to a lesser extent, possibly because it is able to somewhat suppress the emissions (De Lange et al., 2020). There is tremendous variation among maize genotypes in the amounts of volatiles that they release upon caterpillar attack (Degen et al., 2004), yet the overall volatile profile shows clear consistencies in their caterpillar-induced emissions (Hoballah et al., 2002; Gouinguené and Turlings, 2002; Gouinguené et al., 2003). Studying the *S. frugiperda*-maize model is therefore has not only a great economic importance, but also an ideal model to demonstrate the potential of odor-based detection technologies (Turlings and Erb, 2018; Turlings and Degen, 2022).

3.2 Summary of literature on *Spodoptera frugiperda* - related VOCs

The literature on volatiles directly emitted by *S. frugiperda* is limited to publications on the identification of the sex pheromone blend emitted by female moths. The first identification was done by extracting the pheromone directly from the female moth glands (Sekul and Sparks, 1967), which composition is different from the pheromone released by the moths (Tumlinson et al., 1986). The female moths were found to release (*Z*)-7-dodecenyl acetate (*Z*7-12:Ac), dodecanyl acetate (12:Ac), 11-dodecenyl acetate (11-12:Ac), (*Z*)-9-tetradecenyl acetate (*Z*9-14:Ac), and (*Z*)-11-hexadecen-yl acetate (*Z*11-16:Ac). To the best of our knowledge, this latter publication is the only one that used the dynamic headspace technique to collect and identify the sex pheromone of *Spodoptera*, including *S. frugiperda*. The composition of the sexual pheromone of two closely related species, *S. exigua* and *S. frugiperda*, can be distinguished by the exclusive presence of the 12:Ac, *Z*7-12:Ac and 11-12:Ac in the *S. frugiperda* sex pheromone blend. Tests on the biological function of *Z*7-12:Ac have shown that it is the main compound responsible for the attraction of males (Tumlinson et al., 1986; Andrade et al., 2000; Cruz-Esteban et al., 2018). Their concentration is not very accurate, and composition and ratios of volatiles can vary depending on factors such as developmental stage, sex, feeding status, and environmental conditions. In subsequent studies it was shown that *Z*9-14:Ac and *Z*7-12:Ac are universal pheromone components of *S. frugiperda*, but other compounds, such as *Z*9-12:Ac, *Z*11-16:Ac and *E*7-12:Ac were also found to be released in different geographic populations (Tumlinson et al., 1986; Descoins et al., 1988; Fleischer et al., 2005; Batista-Pereira et al., 2006; Groot et al., 2008; Lima and McNeil, 2009; Jiang et al., 2022). In addition to the pheromone work, considerable information is available on plant volatiles induced by the caterpillars of *S. frugiperda* and other *Spodoptera* species have been extensively studied (Turlings and Erb, 2018; Turlings and Degen, 2022). In Table 3 we list the most relevant papers on inducible volatiles emitted by maize plants. It is important to note that different varieties of maize were used in different studies and they were also conducted under varying conditions ranging for the laboratory to the field. It can be concluded that different induction techniques and *Spodoptera* species induce similar volatile profiles. *S. frugiperda* does not appear to differ from other species in the volatile profile that they induce in maize plants, but there are quantitative differences, resulting in differences in ratios among VOCs that may facilitate the detection of specific pest species. For maize plants attacked by *S. frugiperda* and other *Spodoptera* species about 25 different volatiles have been reported. These include a diverse array of green leaf volatiles (GLV's), monoterpenes, sesquiterpenes and aromatic compounds. Some of the most notable compounds include (*Z*)-3-hexenyl acetate, linalool, indole, (3*E*)-4,8-dimethyl-1,3,7-nonatriene (DMNT), (3*E*, 7*E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene (TMTT) and (*E*)-β-farnesene. The release of the GLVs is induced within seconds, whereas the others are released after 4 to 6 hours after *S. frugiperda* attack (terpenoids and indole) small maize plants typically release these compounds at rates of 50-200 ng per hour.

TABLE 3 List of Volatile Organic Compounds (VOCs) released by *Spodoptera frugiperda* and *S. exigua* adult females (A), and list of Herbivore Induced Plant Volatiles (HIPVs) released by damaged plants (B) described in the literature.

A. Insect volatiles				
Pest developmental stage	**VOC name**	**CAS-Nr**	**ID level**	**Reference**
S. frugiperda, adult female	Dodecanyl acetate	112-66-3	1	Tumlinson et al., 1986
S. frugiperda, adult female	7-Dodecenyl acetate	16677-06-8	1	Tumlinson et al., 1986
S. frugiperda, adult female	11-Dodecenyl acetate	35153-10-7	1	Tumlinson et al., 1986
S. frugiperda, adult female; *Spodoptera exigua*, adult female	(*Z*)-9-Tetradecenol	53939-27-8	1	Tumlinson et al., 1986; Tumlinson et al., 1990
S. frugiperda, adult female; *Spodoptera exigua*, adult female	(*Z*)-9-Tetradecenol acetate	16725-53-4	1	Tumlinson et al., 1986; Tumlinson et al., 1990
S. frugiperda, adult female	(*Z*)-1l-Hexadecenal	53939-28-9	1	Tumlinson et al., 1986
S. frugiperda, adult female; *Spodoptera exigua*, adult female	(*Z*)-11-Hexadecenyl acetate	34010-21-4	1	Tumlinson et al., 1986; Tumlinson et al., 1990
Spodoptera exigua, adult female	(*Z,E*)-9,12-Tetradecadienyl acetate	31654-77-0	1	Tumlinson et al., 1990
B. Herbivore induced plant volatiles (HIPVs) after *Spodoptera frugiperda* infestation				
Plant species	**VOC name**	**CAS-Nr**	**ID level**	**Reference**
Maize (*Zea mays* L.)	(*Z*)-3-Hexenol	928-96-1	1,2	Turlings et al., 1998b; Turlings et al., 1998a; Hoballah et al., 2002; Carroll et al., 2006; Pinto-Zevallos et al., 2016; De Lange et al., 2020
Maize	Indole	120-72-9	1,2	Turlings et al., 1993; Turlings et al., 1998b; Turlings et al., 1998a; Turlings et al., 2000; Hoballah et al., 2002; Peñaflor et al., 2011; Carroll et al., 2006; Robert et al., 2013; De Lange et al., 2016; Pinto-Zevallos et al., 2016
Maize	Cycloisosativene	22469-52-9	2	Pinto-Zevallos et al., 2016
Maize	(3*E*)-4,8-Dimethyl-1,3,7-nonatriene	19945-61-0	1,2	Turlings et al., 1993; Turlings et al., 1998b; Turlings et al., 1998a; Turlings et al., 2000; Hoballah et al., 2002; Carroll et al., 2006; Peñaflor et al., 2011; Peñaflor et al., 2011; Robert et al., 2013; De Lange et al., 2016; Pinto-Zevallos et al., 2016; De Lange et al., 2020; Yactayo-Chang et al., 2021
Maize	(3*E*, 7*E*)-4,8,12-Trimethyl-1,3,7,11-tridecatetraene	62235-06-7	1,2	Turlings et al., 1993; Hoballah et al., 2002; Carroll et al., 2006; De Lange et al., 2016; Pinto-Zevallos et al., 2016; De Lange et al., 2020
Maize	(*E*)-2-Hexenol	928-95-0	1	Hoballah et al., 2002
Maize	(*E*)-2-Hexenal	6728-26-3	1,2	Hoballah et al., 2002; Carroll et al., 2006; Peñaflor et al., 2011; Robert et al., 2013; Pinto-Zevallos et al., 2016; De Lange et al., 2020
Maize	(*E*)-2-Hexenyl acetate	2497-18-9	1	De Lange et al., 2020
Maize	(*E*)-3-Hexenol	928-97-2	1,2	Peñaflor et al., 2011; Robert et al., 2013
Maize	(*E*)-α-Bergamotene	13474-59-4	1,2	Turlings et al., 1993; Turlings et al., 1998a; Turlings et al., 2000; Hoballah et al., 2002; Carroll et al., 2006; Peñaflor et al., 2011; Robert et al.,

(Continued)

TABLE 3 Continued

B. Herbivore induced plant volatiles (HIPVs) after *Spodoptera frugiperda* infestation				
Plant species	VOC name	CAS-Nr	ID level	Reference
				2013; De Lange et al., 2016; Pinto-Zevallos et al., 2016; ; De Lange et al., 2020; Yactayo-Chang et al., 2021
Maize	(*E*)-α-Farnesene	502-61-4	1	Turlings et al., 1998a
Maize	(*E*)-β-Caryophyllene	87-44-5	1	Turlings et al., 1998b; Turlings et al., 1998a; Hoballah et al., 2002; Peñaflor et al., 2011; Pinto-Zevallos et al., 2016; De Lange et al., 2016; De Lange et al., 2020
Maize	(*E*)-β-Farnesene	18794-84-8	1,2	Turlings et al., 1993; Turlings et al., 1998b; Turlings et al., 1998a; Turlings et al., 2000; Hoballah et al., 2002; Carroll et al., 2006; Peñaflor et al., 2011; Robert et al., 2013; Pinto-Zevallos et al., 2016; De Lange et al., 2016; De Lange et al., 2020
Maize	(*E*)-β-Ocimene	3779-61-1	1	Hoballah et al., 2002; Carroll et al., 2006; Robert et al., 2013; Pinto-Zevallos et al., 2016; De Lange et al., 2016
Maize	(*Z*)-3-Hexenal	6789-80-6	1,2	Turlings et al., 1998a; Hoballah et al., 2002; Peñaflor et al., 2011; Robert et al., 2013; De Lange et al., 2020
Maize	(*Z*)-3-Hexenyl acetate	3681-71-8	1,2	Turlings et al., 1993; Turlings et al., 1998a; Turlings et al., 2000; Hoballah et al., 2002; Carroll et al., 2006; Peñaflor et al., 2011; Robert et al., 2013; De Lange et al., 2016; Pinto-Zevallos et al., 2016; De Lange et al., 2020
Maize	(*Z*)-β-Ocimene	3338-55-4	1	De Lange et al., 2020
Maize	Anthranilic acid	118-92-3	2	Pinto-Zevallos et al., 2016
Maize	Benzyl acetate	140-11-4	1	Peñaflor et al., 2011; De Lange et al., 2020
Maize	Decanal	112-31-2	2	Pinto-Zevallos et al., 2016
Maize	Geranyl acetate	105-87-3	1,2	Hoballah et al., 2002; Peñaflor et al., 2011; Pinto-Zevallos et al., 2016; De Lange et al., 2020; Yactayo-Chang et al., 2021
Maize	Linalool	78-70-6	1,2	Turlings et al., 1993; Turlings et al., 1998a; Turlings et al., 2000; Hoballah et al., 2002; Carroll et al., 2006; Peñaflor et al., 2011; Robert et al., 2013; De Lange et al., 2016; Pinto-Zevallos et al., 2016; De Lange et al., 2020
Maize	Methyl-anthranilate	85-91-6	1	De Lange et al., 2020
Maize	Nerolidol	7212-44-4	1	Turlings et al., 1993; Hoballah et al., 2002; Carroll et al., 2006; Pinto-Zevallos et al., 2016; De Lange et al., 2020
Maize	Nonanal	124-19-6	2	Pinto-Zevallos et al., 2016

(*Continued*)

TABLE 3 Continued

B. Herbivore induced plant volatiles (HIPVs) after *Spodoptera frugiperda* infestation				
Plant species	**VOC name**	**CAS-Nr**	**ID level**	**Reference**
Maize	Phenethyl acetate	103-45-7	1	Hoballah et al., 2002; Peñaflor et al., 2011; De Lange et al., 2016; De Lange et al., 2020
Maize	Ylangene	14912-44-8	2	Pinto-Zevallos et al., 2016
Maize	α-Humulene	6753-98-6	1,2	Carroll et al., 2006; Pinto-Zevallos et al., 2016
Maize	α-Muurolene	10208-80-7	2	Pinto-Zevallos et al., 2016
Maize	α-Zingiberene	495-60-3	2	Pinto-Zevallos et al., 2016
Maize	β -Bisabolene	495-61-4	1,2	Hoballah et al., 2002; Pinto-Zevallos et al., 2016
Maize	β-Sesquiphellandrene	20307-83-9	1,2	Hoballah et al., 2002; Pinto-Zevallos et al., 2016; De Lange et al., 2020
Maize	β-Myrcene	123-35-3	1,2	Hoballah et al., 2002; Carroll et al., 2006; Peñaflor et al., 2011; Robert et al., 2013; Pinto-Zevallos et al., 2016; De Lange et al., 2020

The ID level reports the VOCs identification levels reported by the literature (1= identified compound, 2= putatively identified compound, based upon physiochemical properties of a chemical class and/or by spectral similarities). The CAS number is a compound-specific unique identification number assigned by the Chemical Abstracts Service (CAS).

3.3 Candidate VOCs for *Spodoptera frugiperda* detection

There are three compounds that adult females of *S. frugiperda* emit (dodecanyl acetate; (*Z*)-7-dodecenyl acetate and (*Z*)-11-dodecenyl acetate) and are found only in this species compared to other species of *Spodoptera*. They have biological relevance for male attraction in the field. Plant-produced VOCs induced by *S. frugiperda* caterpillars are released in considerably larger amounts and easier to detect. As mentioned in the previous section, there are no unique compounds emitted by maize plants under *S. frugiperda* attack in comparison to attacks by other *Spodoptera* species, but ratios differences can be used to determine which species is attacking a plant. The most relevant compounds that are consistently emitted and have an ecological relevance are (*Z*)-3-hexenyl acetate, linalool, indole, (3*E*)-4,8-dimethyl-1,3,7-nonatriene (DMNT), (3*E*,7*E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene (TMTT) and (*E*)-β-farnesene (Table 4).

4 Volatile organic compounds produced and induced by *Helicoverpa armigera*

4.1 The cotton bollworm: distribution, biology and management

The Cotton Bollworm (CBW) *Helicoverpa armigera* Hübner (Lepidoptera: Noctuidae) (Figures 1F, G) is considered as one of the major pests in tropical and warm-temperate regions worldwide (Jones et al., 2019). Global economic losses caused by this species are estimated at over 3 billion US dollars per year (Haile et al., 2021; Riaz et al., 2021). *Helicoverpa armigera* is widely distributed throughout Asia, Oceania, Africa, and southern Europe, and has recently invaded South America (Tay et al., 2013; Jones et al., 2019).

Helicoverpa armigera is a highly polyphagous pest infesting more than 200 host plant species of diverse plant families. Many crops of high economic importance are included in its host range, such as cotton, maize, tomato (Figure 1H), sunflower (Figure 1G), soybean, and several legumes (Cunningham et al., 1999; Cunningham and Zalucki, 2014). The adults of *H. armigera* are excellent flyers and can migrate over long distances up to 2000 km (Behere et al., 2013; Jones et al., 2015). The species has a high

TABLE 4 List of candidate Volatile Organic Compounds (VOCs) for *Spodoptera frugiperda* detection.

VOC name	CAS-Nr	Biological relevance
Dodecanyl acetate	112-66-3	Sexual pheromone
7-Dodecenyl acetate	16677-06-8	Sexual pheromone
11-Dodecenyl acetate	35153-10-7	Sexual pheromone
(*Z*)-3-Hexenyl acetate	3681-71-8	Relevant HIPV
Indole	120-72-9	Relevant HIPV
Linalool	78-70-6	Relevant HIPV
(*E*)-β-Farnesene	18794-84-8	Relevant HIPV
(3*E*)-4,8-Dimethyl-1,3,7-nonatriene	19945-61-0	Relevant HIPV
(3*E*, 7*E*)-4,8,12-Trimethyl-1,3,7,11-tridecatetraene	62235-06-7	Relevant HIPV

The CAS number is a compound-specific unique identification number assigned by the Chemical Abstracts Service (CAS).

TABLE 5 List of Volatile Organic Compounds (VOCs) released by *Helicoverpa armigera* (A), and list of Herbivore Induced Plant Volatiles (HIPVs) released by damaged plants (B) described in the literature.

A. Insect volatiles

Pest developmental stage	VOC name	CAS-Nr	ID level	Reference
Adult, egg, larval frass	Oleic acid	112-80-1	2,1	Guoqing et al., 2001; Liu et al., 2008; Xu et al., 2006
Adult, egg, larval frass	Palmitic acid	57-10-3	2,1	Guoqing et al., 2001; Liu et al., 2008; Xu et al., 2006
Adult	4-hydroxy-4-methyl-2-pentanone	123-42-2	2	Guoqing et al., 2001
Egg	Myristic acid	544-63-8	1	Liu et al., 2008
Egg, larval frass	Stearic acid	57-11-4	1	Liu et al., 2008; Xu et al., 2006
Larval frass	Pentadecanoic acid	1002-84-2	1	Xu et al., 2006
Larval frass	Methyl palmitate	112-39-0	1	Xu et al., 2006
Larval frass	Methyl oleate	112-62-9	1	Xu et al., 2006
Larval frass	Methyl linoleate	112-63-0	1	Xu et al., 2006
Larval frass	Methyl stearate	112-63-8	1	Xu et al., 2006
Larval frass	Linoleic acid	463-40-1	1	Xu et al., 2006

B. Herbivore induced plant volatiles (HIPVs) after *Helicoverpa armigera* infestation

Plant species	VOC name	CAS-Nr	ID level	Reference
Cotton (*Gossypium hirsutum* L.)	3-Hexenyl isovalerate	10032-11-8	1	Huang et al., 2015
Cotton	Limonene	138-86-3	1	Huang et al., 2015
Cotton	β- Elemene	33880-83-0	1	Huang et al., 2015
Cotton	α-Guaiene	3691-12-1	1	Huang et al., 2015
Cotton	β-Ocimene	3779-61-1	1	Huang et al., 2015
Cotton	δ-Cadinene	483-76-1	1	Huang et al., 2015
Cotton	Hexenyl valerate	56922-74-8	1	Huang et al., 2015
Cotton	TMTT	62235-06-7	1	Huang et al., 2015
Cotton	1-Decyne	764-93-2	1	Huang et al., 2015
Cotton, French bean (*Phaseolus vulgaris*), maize (*Zea mays* L.), tobacco (*Nicotiana tabacum* L.), tomato (*Solanum lycopersicum* L.)	(*Z*)-3-Hexenol	928-96-1	1,2	Huang et al., 2015; Gebreziher and Nakamuta, 2016; Yan and Wang, 2006; Yan et al., 2005
Cotton, maize	β-Myrcene	123-35-3	1	Huang et al., 2015; Yan and Wang, 2006
Cotton, maize	Hexyl acetate	142-92-7	1	Huang et al., 2015; Yan and Wang, 2006
Cotton, maize	DMNT	19945-61-0	1	Huang et al., 2015; Yan and Wang, 2006
Cotton, maize	(*E*)-2-Hexenol	928-95-0	1	Huang et al., 2015; Yan and Wang, 2006; Yan et al., 2005
Cotton, maize, tobacco	(*E*)-2-Hexenyl acetate	2497-18-9	1,2	Huang et al., 2015; Yan and Wang, 2006; Yan et al., 2005
Cotton, maize, tobacco, tomato	β-Pinene	18172-67-3	1,2	Huang et al., 2015; Yan and Wang, 2006; Yan et al., 2005; Gebreziher and Nakamuta, 2016

(Continued)

TABLE 5 Continued

B. Herbivore induced plant volatiles (HIPVs) after *Helicoverpa armigera* infestation				
Plant species	VOC name	CAS-Nr	ID level	Reference
Cotton, maize, tobacco, tomato	(*Z*)-3-Hexenyl acetate	3681-71-8	1,2	Huang et al., 2015; Yan and Wang, 2006; Yan et al., 2005; Gebreziher and Nakamuta, 2016
Cotton, maize, tobacco, tomato	(*E*)-2-Hexenal	6728-26-3	1,2	Huang et al., 2015; Yan and Wang, 2006; Yan et al., 2005; Gebreziher and Nakamuta, 2016
Cotton, maize, tomato	Linalool	126-91-0	1,2	Huang et al., 2015; Yan and Wang, 2006; Gebreziher and Nakamuta, 2016
Cotton, tomato	α-Caryophyllene	6753-98-6	1,2	Huang et al., 2015; Gebreziher and Nakamuta, 2016
Cotton, tomato	α-Pinene	7785-70-8	1,2	Huang et al., 2015; Gebreziher and Nakamuta, 2016
Cotton, tomato	β-Caryophyllene	87-44-5	1,2	Huang et al., 2015; Gebreziher and Nakamuta, 2016
French bean	Thujapsene	470-40-6	2	Gebreziher and Nakamuta, 2016
French bean	1-Propanone	71-23-8	1	Gebreziher and Nakamuta, 2016
French bean	Ethanal	75-07-0	2	Gebreziher and Nakamuta, 2016
French bean	2-Butenol	764-01-2	1	Gebreziher and Nakamuta, 2016
French bean, maize	(*E*)-2-Eicosene	121909-29-3	1	Gebreziher and Nakamuta, 2016
French bean, maize	2-Butyl-1-octanol	3913-02-8	1	Gebreziher and Nakamuta, 2016
French bean, maize)	3-Methyl-2-butenol	556-82-1	2	Gebreziher and Nakamuta, 2016
French bean, maize	2-Ethyl-2-hexenal	645-62-5	2	Gebreziher and Nakamuta, 2016
French bean, maize	(*Z*)-2-Hexenol	928-94-9	2	Gebreziher and Nakamuta, 2016
French bean, maize, tomato	2-Ethyl-1-hexanol	104-76-7	2	Gebreziher and Nakamuta, 2016
French bean, maize, tomato	D-Limonene	5989-27-5	1	Gebreziher and Nakamuta, 2016; Yan and Wang, 2006
French bean, maize, tomato	o-Cymene	527-84-4	2	Gebreziher and Nakamuta, 2016
French bean, maize, tomato	α-Terpinene	99-86-5	1	Gebreziher and Nakamuta, 2016
Maize	Phenylethyl acetate	103-45-7	1	Yan and Wang, 2006
Maize	Geranyl acetate	105-87-3	1	Yan and Wang, 2006
Maize	1-Octene	111-66-0	2	Gebreziher and Nakamuta, 2016

(Continued)

TABLE 5 Continued

B. Herbivore induced plant volatiles (HIPVs) after *Helicoverpa armigera* infestation

Plant species	VOC name	CAS-Nr	ID level	Reference
Maize	Indole	120-72-9	1	Yan and Wang, 2006
Maize	(*E*)-α-Bergamotene	13474-59-4	2	Yan and Wang, 2006
Maize	(*E*)-β-Farnesene	18794-84-8	1	Yan and Wang, 2006
Maize	β-Sesquiphellandrene	20307-83-9	2	Yan and Wang, 2006
Maize	5-Methyl-2-(1-methyl ethyl)-1-hexanol	2051-33-4	2	Gebreziher and Nakamuta, 2016
Maize	2-Ethyl-1-decanal	21078-65-9	2	Gebreziher and Nakamuta, 2016
Maize	(*E*)-Nerolidol	40716-66-3	1	Yan and Wang, 2006
Maize	α-Farnesene	502-61-4	2	Gebreziher and Nakamuta, 2016
Maize	Pentadecane	629-62-9	2	Yan and Wang, 2006
Maize	2-Ethylhexyl, 2-ethylhexanoate	7425-14-1	2	Gebreziher and Nakamuta, 2016
Maize, tobacco	γ-Terpinene	99-85-4	1	Yan and Wang, 2006, Yan and Wang, 2006
Tobacco	Hexanol	111-27-3	1	Yan and Wang, 2006
Tobacco	Methyl salicylate	119-36-8	1	Yan and Wang, 2006
	Nonanal	124-19-6	2	Yan and Wang, 2006
Tobacco	(*Z*)-3-Hexenyl butyrate	16491-36-4	2	Yan and Wang, 2006
Tobacco	Nicotine	54-11-5	1	Yan and Wang, 2006
Tobacco	(*Z*)-3-Hexenal	69112-21-6	1	Yan and Wang, 2006
Tomato	3-Carene	13466-78-9	2	Gebreziher and Nakamuta, 2016
Tomato	(*E*)-3-Hexenyl-acetate	3681-82-1	2	Gebreziher and Nakamuta, 2016
Tomato	(+)-4-Carene	5208-49-1	2	Gebreziher and Nakamuta, 2016
Tomato	β-Phellandrene	555-10-2	1	Gebreziher and Nakamuta, 2016
Tomato	Tridecane	629-50-5	2	Gebreziher and Nakamuta, 2016
Tomato	Tetradecane	629-59-4	2	Gebreziher and Nakamuta, 2016
Tomato	α-Phellandrene	99-83-2	2	Gebreziher and Nakamuta, 2016
Tomato	p-Cymene	99-87-6	2	Gebreziher and Nakamuta, 2016
Tomato	(*E*)-2-Eicosene	64615-82-3	1	Gebreziher and Nakamuta, 2016

The ID level reports the VOCs identification levels reported by the literature (1= identified compound, 2= putatively identified compound, based upon physiochemical properties of a chemical class and/or by spectral similarities). The CAS number is a compound-specific unique identification number assigned by the Chemical Abstracts Service (CAS).

fecundity and rapid reproduction rates, resulting in average in 4-6 generations per year and up to 10-11 generations per year in tropical regions (Riaz et al., 2021). The larvae are highly destructive plant feeders and very polyphagous, not only regarding plant species but also concerning plant parts (Figures 1F–H). The species has the ability to adapt its diapause depending on environmental conditions, in order to optimize survival. All these characteristics in their biology – its polyphagy, high mobility and reproduction rates and its facultative diapause - make *H. armigera* a serious pest, quickly invading new areas.

A blind trust of synthetic pesticides as main control measure for *H. armigera* has led to resistance development to all major classes of synthetic insecticides across many regions of the world (Downes et al., 2016; Jones et al., 2019; Riaz et al., 2021). As an alternative pest control measure have genetically modified crops, such as Bt (with a toxin from *Bacillus thuringiensis*) cotton, shown a good control effect of *H. armigera* over a period. But, as for synthetic pesticides, resistant populations have developed also for Bt crops, making well deliberated resistance management strategies necessary (Jin et al., 2015; Downes et al., 2016; Tabashnik and Carrière, 2017). Today, IPM strategies based on forecast, monitoring and decision support systems combined with biological, chemical, and physical control measures must be developed and used for successful control of *H. armigera* (Downes et al., 2016; Jones et al., 2019; Riaz et al., 2021).

4.2 Summary of literature on *Helicoverpa armigera* VOCs

We focus here on studies on *H. armigera*-related VOCs, which have shown that the pest itself (4.2) or plants infested by *H. armigera* (4.3) can release herbivore-specific signals which can be measured by chemical analyzes and behavioral and/or electrophysiological bioassays. The huge number of studies regarding other issues of the chemical ecology of *H. armigera* are not included here.

Research on *H. armigera* VOCs has started in the 1970s with the identification of sex pheromones in *H. armigera*, namely (*Z*)-9-hexadecenal, (*Z*)-11-hexedecenal, hexadecanol, (*Z*)-11-hexadecenol and (*Z*)-9-tetradecenal (Piccardi et al., 1977; Nesbitt et al., 1980; Wu et al., 1997; Zhang et al., 2012). We want to highlight here for our purpose the most promising pheromones, the oviposition marking pheromones (OMPs) or oviposition deterring pheromones (ODPs) (Table 5). ODPs have been identified for *H. armigera* around the turn of the millennium (Guoqing et al., 2001; Xu et al., 2006; Liu et al., 2008). ODPs are deposited by many parasitic and phytophagous insects associated with egg-laying, aiming for modification of the oviposition behavior of conspecifics such that subsequent eggs are not deposited into an already utilized resource. After behavioral observations on *H. armigera* have indicated the existence of oviposition-deterrent compounds, the three compounds 4-hydroxy-4-methyl-2-pentanone, hexadecanoic acid (palmitic acid) and (*Z*)-9-octadecenoic acid (oleic acid) have been identified from the tarsi of female *H. armigera* as oviposition-deterrent compounds (Guoqing et al., 2001). In further studies on ODPs in larval frass of *H. armigera*, a blend of fatty acid and corresponding methyl esters was found in the larval frass. Some compounds were found independent of the diet of the larvae, while others seem to be dependent on the food source. All compounds elicited responses in *H. armigera* moth antennae using electroantennography (EAG) analyzes (Xu et al., 2006). Moreover, it was found that laid eggs resulted in similar EAG responses. Compounds identified from the laid eggs were the 4-oviposition deterring fatty acids myristic, palmitic, stearic, and oleic acid and their corresponding methyl esters (Liu et al., 2008).

TABLE 6 List of candidate Volatile Organic Compounds (VOCs) for *Helicoverpa armigera* detection.

VOC name	CAS-Nr	Biological relevance
Oleic acid	112-80-1	Oviposition deterrent pheromone
Palmitic acid	57-1-01-3	Oviposition deterrent pheromone
β-Myrcene	123-35-3	Herbivore induced plant volatile
β-Pinene	18172-67-3	Herbivore induced plant volatile
D-Limonene	5989-27-5	Herbivore induced plant volatile
(*E*)-Nerolidol	40716-66-3	Herbivore induced plant volatile

The CAS number is a compound-specific unique identification number assigned by the Chemical Abstracts Service (CAS).

4.3 Summary of literature on *Helicoverpa armigera* - induced plant VOCs

Another important type of *H. armigera* related VOCs is herbivore induced plant volatiles (HIPVs) (Table 5). The HIPVs emission of tobacco plants induced by larvae feeding of the sibling species *H. armigera* and *H. assulata* were studied, and the corresponding behavioral response (wind tunnel bioassay) of a main parasitoid of both species, *Campoletis chlorideae* Uchida (Hymenoptera: Ichneumonidae), towards the different HIPV blends were recorded. GC/MS analyzes showed that β-pinene was specifically measured after feeding of *H. armigera* larvae, whereas (*Z*)-3-hexenal was particularly measured after infestation of both species, and hexyl acetate by mechanical damage (Yan et al., 2005). In another study, the HIPVs emission of maize plants induced by feeding of larvae of *H.armigera* and *Pseudaletia separata* Walker (Lepidoptera: Noctuidae) and the behavioral response of *C. chlorideae* in a wind tunnel were investigated. After infestation of *H. armigera* particularly the four terpenoids β-pinene, β-myrcene, D-limonene, and (*E*)-nerolidol were measured. All these compounds were not measured after attack of *P. separata* or mechanical damage (Yan and Wang, 2006). Also the volatile characteristics of cotton plants after larvae infestation of *H. armigera* have been investigated. GC/MS analyzes showed that several green leaf volatiles and terpenoids were measured after *H. armigera* infestation of cotton plants, whereas other compounds were found in both, infested and non-infested plants (Huang et al., 2015). Further studies compared by chemical analyzes the HIPV emission of tomato, French bean, and maize plants after infestation of *H. armigera* larvae, and by Y-tube olfactometer bioassays the behavioral response of the predator *Orius strigicollis* Poppius (Heteroptera: Anthocoridae). In all three plant species, a higher number and larger amounts of VOCs were found on *H. armigera* infested plants than undamaged or mechanically damaged plants (Gebreziher and Nakamuta, 2016). In some of these studies the odor profile of *H. armigera* infested plants have been compared with mechanical damaged plants, as both types of damage, biotic and abiotic, are stresses for the plants and induce specific VOC emission. However, to our knowledge no study compares the volatile profiles from *H. armigera*-infested plants with those of plants stressed by other abiotic factors such as water logging, drought, darkness, or extreme temperatures, or even volatile profiles of plants stressed by both, *H. armigera* infestation and abiotic factors, at the same time.

4.4 Candidate VOCs for *Helicoverpa armigera* detection

As ODPs are species-specific VOCs, detectable also in absence of the adult pest insect and identified for *H. armigera*, these compounds might be potential candidates for detection of *H. armigera*. In all three studies, we found the specific fatty acids myristic, palmitic, stearic, and oleic acid and their corresponding methyl esters have been identified as ODPs of *H. armigera* (Guoqing et al., 2001; Xu et al., 2006; Liu et al., 2008). Particularly, palmitic and oleic acid have been extracted from female moths (tarsi), larval frass and laid eggs of *H. armigera*, which might render them as robust and reliable candidates for detection purpose (Table 6).

With a view to detecting an herbivore-specific volatile blend measured from plants in response to *H. armigera* larvae feeding, we compared the volatile profiles from *H. armigera* infested plants with those from non-infested plants of different plant species found in literature. Compounds reported to be measured after *H. armigera* larval infestation of different plant species, but not or in very small amounts only from non-infested, mechanically damaged or plants infested of another pest species, might be possible candidates for detection of *H. armigera*. The terpenoids β-pinene, β-myrcene, D-limonene, and (*E*)-nerolidol were found to be species-specific for *H. armigera* larval infestation of maize plants (Yan and Wang, 2006) (Table 6). The compound β-myrcene was found in maize and cotton particularly after *H. armigera* larval infestation (Yan and Wang, 2006; Huang et al., 2015). D-limonene was species-specific measured after *H. armigera* larval infestation on maize, French bean and tomato (Gebreziher and Nakamuta, 2016; Yan and Wang, 2006). A compound noticed in four different studies as species-specific volatile measured from a plant in response to *H. armigera* larvae feeding on maize, cotton, tobacco, and tomato is β-pinene (Huang et al., 2015; Yan and Wang, 2006; Yan et al., 2005; Gebreziher and Nakamuta, 2016).

5 Volatile organic compounds produced and induced by *Bursaphelenchus xylophilus*

5.1 The pinewood nematode: distribution, biology and management

The Pinewood Nematode (PWN), *Bursaphelenchus xylophilus* (Steiner & Buhrer 1934) (Rhabditida: Aphelenchoididae), is a migratory plant parasitic nematode (Figure 1I) responsible for pine wilt disease (PWD), a serious forest disease that has devastated vast pine stands in Asia and Europe (Figures 1K, L) causing substantial ecological, economic, and cultural impacts (Back et al., 2024). Originally from North America, where the incidence of *B. xylophilus* is very low due to a co-evolution between the nematode and native pine species (Sutherland, 2008), the nematode was first noted in Japan in the early 20th century Futai, 2008. *Bursaphelenchus xylophilus* spread to Taiwan, China (in 1982), and Korea (in 1988), and was detected in Portugal, within the European Union, in 1999 (Mota et al., 1999). By 2008, mainland Portugal was declared a quarantine zone, and wood export

TABLE 7 List of Herbivore Induced Plant Volatiles (HIPVs) released by *Bursaphelenchus xylophilus* infected plants (B) described in the literature.

B. Herbivore induced plant volatiles (HIPVs) after *Bursaphelenchus xylophilus* infection				
Plant species	VOC name	CAS-Nr	ID level	Reference
Pinus thunbergii	Sativene	6813-05-4	2	Takeuchi et al., 2006
Pinus thunbergii	Carvacrol methyl ether	6379-73-3	2	Takeuchi et al., 2006
Pinus thunbergii	Camphor	76-22-2	2	Takeuchi et al., 2006
Pinus pinaster	Limonene	138-86-3	2	Gaspar et al., 2020
Pinus densiflora and *P. koraiensis*	3-Carene	13466-78-9	2	Hwang et al., 2021
Pinus thunbergii	Borneol	507-70-0	2	Wang et al., 2022

The ID level reports the Volatiles Organic Compounds (VOCs) identification levels reported by the literature (1= identified compound, 2= putatively identified compound, based upon physiochemical properties of a chemical class and/or by spectral similarities). The CAS number is a compound-specific unique identification number assigned by the Chemical Abstracts Service (CAS).

FIGURE 2
Phytophthora structures (on V8-juice agar) and typical disease symptoms (all photos: Thomas Jung). **(A)** Mature nonpapillate sporangium of the soilborne *Phytophthora ×cambivora*. **(B)** Caducous sporangium of the aerial *Phytophthora ramorum* releasing zoospores (arrow). **(C)** Chlamydospore of the soilborne *Phytophthora cinnamomi*. **(D)** Oogonium of *Phytophthora cinnamomi* with mature thick-walled oospore and amphigynous antheridium. Scale bar = 20 µm and applies to **(A–D)**. **(E)** Shoot and leaf blight of a Rhododendron shrub caused by *Phytophthora ramorum*. **(F)** Stem of a mature beech (*Fagus sylvatica*) tree with an aerial bark canker with dark exudations caused by *Phytophthora plurivora*. **(G)** Stembase of a young cork oak (*Quercus suber*) tree with a bark canker with orange-brown exudations caused by *Phytophthora cinnamomi*. **(H)** Woody roots (diameters 0.5-1.0 cm) of a mature sessile oak (*Quercus petraea*) tree with bark cankers (arrows) caused by *Phytophthora ×cambivora*. **(I)** Woody roots (diameters <0.6 cm) of a mature sessile oak tree with severe losses of lateral roots and fine roots caused by *Phytophthora plurivora* and *Phytophthora ×cambivora*. **(J)** Acute mortality of mature cork oak trees due girdling bark cankers at the stembase and main roots caused by *Phytophthora cinnamomi*.

restrictions extended nationwide (Rodrigues, 2008). *Bursaphelenchus xylophilus* was found in Madeira Island in 2010 (Fonseca et al., 2012) and in Spain in 2011 (Abelleira et al., 2011), even attacking different species of *Pinus* trees (Inácio et al., 2015; Zamora et al., 2015).

The European Plant Protection Organization (EPPO) classifies *B. xylophilus* as an A2 type quarantine pest in the EU, given its extreme pathogenicity and the abundance of susceptible pines in Europe (e.g., *Pinus pinaster*, *P. sylvestris* L., and *P. nigra* Arnold) (EPPO, 2023). Although currently limited to Portugal and Spain, future climate conditions in northern Europe might create a highly susceptible environment for *B. xylophilus*, threatening northern pine forests (Hirata et al., 2017; De la Fuente et al., 2018).

The infection mechanism of PWD involves the host pine tree, an insect vector (mainly *Monochamus* sp. beetles) (Figure 1J), *B. xylophilus*, and associated microbiota (Zhao et al., 2014; Vicente et al., 2012). During beetle maturation feeding, *B. xylophilus* enters healthy pines through beetle wounds, causing severe damage by invading resin canals, attacking epithelial cells, and disrupting water and mineral transport (Mamiya, 1983). This leads to pine wilting within three weeks, resulting in tree collapse within 40 to 60 days post-infection, with millions of nematodes infecting the trunk and branches (Kuroda, 2008) (Figures 1K, L). The decaying pine becomes attractive to the adult *Monochamus* beetles and, consequently, a source for new infections spread by the insect-vector (Jones et al., 2008; Futai, 2013).

Control strategies for PWD include breeding resistant pine species (Nose and Shiraishi, 2008; Carrasquinho et al., 2018; Menéndez-Gutiérrez et al., 2018) eradicating infected trees, treating wood (Kamata, 2008; Rodrigues, 2008; Xu, 2008) and controlling beetle populations. Infected wood can be treated chemically or thermally before its use for exportation or industrial purposes. Chemical insecticides prevent beetle spread, though they may harm beneficial organisms and accumulate in ecosystems (Kamata, 2008; Bi et al., 2015). Alternative controls include pheromone traps for controlling the spread of insect-vector populations and biological control using beetle predators or parasites (Nakamura, 2008; Shimazu, 2008; Kim et al., 2016). Trunk injection of nematicides is also effective, despite the toxicity risks associated with chemicals (Kamata, 2008). Integrated management strategies combining various methods are crucial for effective *B. xylophilus* containment.

5.2 Summary of literature on *Bursaphelenchus xylophilus* - related VOCs

Literature on the volatiles emitted by *B. xylophilus* -infected plant material is very scarce and only six volatiles were reportedly influenced by *B. xylophilus* infection, in field and greenhouse grown infected pines (Table 7). Although no induced volatiles were reported, some constitutive pine compounds were reportedly emitted in greater proportions by the affected trees. In a study using 30-year-old *Pinus thunbergii* Parlatore trees, the proportions of sativene, carvacrol methyl ether and camphor were seen to increase, however the number of samples was low (7 infected individuals) and this response was detected on a single tree alone (Takeuchi et al., 2006). For volatiles capture, TENAX-TA absorbent filled glass tubes were used to sample 6 L of air surrounding the stem (ca. 2h at 50 mL/min). In a different study using 2-year-old *P. thunbergii* seedlings, slightly higher proportions of borneol were signaled as a result of *B. xylophilus* inoculation in a susceptible variety (Wang et al., 2022). However, sampling was performed using SPME (65 μm PDMS/DVB) adapted to a headspace vial with 1 cm sections of 500 mg pine needles, for 30 min. For *P. densiflora* Siebold & Zuccarini and *P. koraiensis* Siebold & Zuccarini 5-year-old trees, the emission of the monoterpene hydrocarbon 3-carene was 9.7 and 54.7 times higher than in control trees, when analyzed by HS-SPME/GC-MS, by using plastic wrapped plants and analyzing with DVB/CAR/PDMS fibers (df 50/30 μm) for 1 h, at room temperature (Hwang et al., 2021). For *P. pinaster*, limonene emission was seen to increase in *B. xylophilus* -infected trees, however, this was only detected for two out of four tested trees (Gaspar et al., 2020). Sampling was performed with 1.0 g of sample/100 mL of air, using a 65 μm PDMS/DVB coated fiber with 5 min exposure time at 35°C.

5.3 Candidate VOCs for *Bursaphelenchus xylophilus* detection

The available literature lacks an acceptable sample size or repeatability in results as well as variability in the conditions of sampling to conclude on suitable VOC candidates for detection of *B. xylophilus*.

6 Volatile organic compounds produced and induced by *Phytophthora*

6.1 *Phytophthora ramorum* and other important *Phytophthora* species: distribution, biology, diseases and management

The oomycete genus *Phytophthora* de Bary 1876 (Peronosporales: Peronosporaceae) currently includes eight obligate biotrophic unculturable species and ca 260 hemibiotrophic or necrotrophic culturable species and is widely distributed on all continents except Antarctica. Approximately half of the known species have been spread from their native areas to other continents where they became invasive causing severe diseases on non-coevolved host plants in horticultural, forest and natural ecosystems (Erwin and Ribeiro, 1996; Yang et al., 2017; Jung et al., 2018a, Jung et al., 2022, Jung et al., 2024; Brasier et al., 2022; Chen et al., 2022; Abad et al., 2023). Since the 1960s, the global number of epidemic diseases of forests and natural ecosystems caused by invasive *Phytophthora* species has increased exponentially from 5 to currently 41 (Brasier et al., 2022).

All *Phytophthora* species produce sporangia (Figures 2A, B) which usually release biflagellate zoospores (Figure 2B) or germinate directly. Aerial *Phytophthora* species spread during periods of high humidity with caducous sporangia (Figure 2B) via rain splash, fog and wind whereas soilborne *Phytophthoras* spread during wet periods via zoospores in soil and surface water (Erwin and Ribeiro, 1996; Chen et al., 2022). Many *Phytophthora* species form chlamydospores as vegetative survival structures (Figure 2C). Most *Phytophthora* species are characterized by the production of sexually derived enduring oospores (Figure 2D) (Erwin and Ribeiro, 1996; Chen et al., 2022; Jung et al., 2022, Jung et al., 2024).

Generally, the management of *Phytophthora* diseases includes a wide range of measures including the prevention of pathogen introduction by using non-infested nursery stock, substrates and irrigation water, disinfesting of tools, cleaning of vehicles and boots from adhering soil particles, and phytosanitary controls using both visual inspections and high-throughput molecular detection tests; best-practice management in nurseries; avoiding of soil compaction and building of drainage systems to prevent waterlogging and flooding; application of potassium phosphite to stimulate defense reactions of roots (horticulture and forestry); fungicide applications (horticulture and agriculture); eradication via host removal and destruction; use of nanoparticle technologies; resistance screening programs and the use of resistant host genotypes or rootstocks (horticulture, agriculture and forestry); use of effectors and NLR resistance genes; and the development and use of general models to predict regions that might be most susceptible to epidemics by certain *Phytophthora* species (e.g. *P. cinnamomi* Rands, *P. ramorum* Werres, De Cock & Man in' t Veld) or regional models to predict periods with environmental conditions conducive to disease development (e.g. *P. infestans* (Mont.) de Bary) (Harris, 1991; Erwin and Ribeiro, 1996; Colquhoun and Hardy, 2000; Hardy, 2001; Meentemeyer et al., 2004; Rizzo et al., 2005; Robin et al., 2006; Henderson et al., 2007; Stukely et al., 2007; Frankel, 2008; Garbelotto et al., 2009; Brasier and Webber, 2010; Filipe et al., 2012; Pérez-Sierra and Jung, 2013; Crane and Shearer, 2014; Santos et al., 2017; Peterson et al., 2015; Jung et al., 2016, Jung et al., 2018a; O'Hanlon et al., 2016, O'Hanlon et al., 2018; Lu et al., 2019; Sniezko et al., 2019; González et al., 2020; Solla et al., 2021; Santos et al., 2022; Brandano et al., 2023; Martínez et al., 2023).

TABLE 8 List of Volatile Organic Compounds (VOCs) released by *Phytophthora* sp. (A), and list of pathogen-induced plant volatiles released by *Phytophthora* sp. - infected plants (B) described in the literature.

A. Pathogen volatiles				
Pathogen	VOC name	CAS-Nr	ID level	Reference
P. plurivora; *P. cactorum*	Acetone	67-64-1	1	Loulier et al., 2020
P. plurivora	α-Pinene	80-56-8	1	Loulier et al., 2020
P. plurivora	3-Carene	13466-78-9	1	Loulier et al., 2020
P. plurivora	4-Hydroxybutanoic acid	114959-05-6	2	Loulier et al., 2020
P. plurivora; *P. cactorum*	Hexanol	111-27-3	1	Loulier et al., 2020
P. plurivora	Acetoin	513-86-0	1	Loulier et al., 2020
P. cactorum; P. cinnamomi	Dimethyl disulphide	624-92-0	2,2	Loulier et al., 2020; Qiu et al, 2014a
P. cactorum; *P. ramorum*	3-Octanone[b]	106-68-3	1	Loulier et al., 2020
P. cactorum; *P. ramorum*; *P. cinnamomi; P. citricola; P. polonica*	1-Octen-3-ol[b]	3391-86-4	1,2,2	Loulier et al., 2020; Qiu et al., 2014a; Sherwood et al., 2024
P. cactorum; P. multivora	Heptanol	111-70-6	1,2	Loulier et al., 2020; Sherwood et al., 2024
P. cactorum	2-Pentyl furan	3777-69-3	1	Loulier et al., 2020
P. cactorum	2-Octenol	18409-17-1	1	Loulier et al., 2020
P. cactorum	Octanol[b]	111-87-5	1	Loulier et al., 2020
P. ramorum; *P. cinnamomi*	Ethanol	64-17-5	1	Loulier et al., 2020
P. ramorum	Isoamyl alcohol[b]	123-51-3	1	Loulier et al., 2020
P. ramorum; *P. cinnamomi*	Phenylethanol[b]	60-12-8	1,2	Loulier et al., 2020; Qiu et al., 2014a
P. ramorum	2-Methylbutanol	137-32-6	1	Loulier et al., 2020
P. cinnamomi	2-Ethyl-1-hexanol[b]	104-76-7	1	Loulier et al., 2020
P. cinnamomi; P. ×cambivora; P. citricola; P. multivora; P. plurivora; P. polonica	4-Ethyl guaiacol [b]	2785-89-9	2, 2,2	Loulier et al., 2020; Qiu et al., 2014a; Sherwood et al., 2024
P. cinnamomi	2,4,6-Trimethylheptane	2613-61-8	2	Qiu et al., 2014a
P. cinnamomi	6-Methyl-5-hepten-2-ol	1569-60-4	2	Qiu et al., 2014a

(Continued)

TABLE 8 Continued

A. Pathogen volatiles				
Pathogen	VOC name	CAS-Nr	ID level	Reference
P. cinnamomi	6,10-Dimethyl-5,9-undecadien-2-ol	53837-34-6	2	Qiu et al., 2014a
P. cinnamomi	2-Methoxy-4-vinylphenol	7786-61-0	2	Qiu et al., 2014a
P. cinnamomi	5-Methyl-3-heptanone	541-85-5	2	Qiu et al., 2014a
P. cinnamomi	Dimethyl trisulphide	3658-80-8	2	Qiu et al., 2014a
P. cinnamomi	2-Butanone[b]	78-93-3	2	Qiu et al., 2014a
P. cinnamomi	2-Pentanone[b]	107-87-9	2	Qiu et al., 2014a
P. cinnamomi	Butyrolactone[b]	96-48-0	2	Qiu et al., 2014a
P. cinnamomi	2-Undecanol	1653-30-1	2	Qiu et al., 2014a
P. cinnamomi	cis: (Z)-β-Damascenone	59739-63-8	2	Qiu et al., 2014a
P. cinnamomi; P. plurivora	4-Ethylphenol[b]	123-07-9	2,2	Qiu et al., 2014a; Sherwood et al., 2024
P. multivora	2,3-Butanediol	513-85-9	1	Sherwood et al., 2024
P. ×cambivora; P. cinnamomi; P. gonapodyides; P. polonica	Hexanal	66-25-1	1	Sherwood et al., 2024
P. syringae	2-Furanmethanol	98-00-0	1	Sherwood et al., 2024
P. ×cambivora; P. gonapodyides; P. plurivora	2,4-Heptadienal	4313-03-5	1	Sherwood et al., 2024
P. ×cambivora; P. gonapodyides	3,5-Octadien-2-one	38284-27-4	1	Sherwood et al., 2024
P. multivora; P. plurivora	2-Nonanol	628-99-9	1	Sherwood et al., 2024
P. polonica	3-Nonenol	51494-28-1	1	Sherwood et al., 2024
P. ×cambivora; P. gonapodyides	2,6-Nonadienal	26370-28-5	1	Sherwood et al., 2024
P. ×cambivora; P. gonapodyides; P. multivora; P. polonica	Nonanol	143-08-8	1	Sherwood et al., 2024
P. ×cambivora; P. gonapodyides; P. polonica	2,4-Nonadienal	5910-87-2	1	Sherwood et al., 2024
P. polonica	4-Decenol	57074-37-0	1	Sherwood et al., 2024
P. ×cambivora; P. gonapodyides; P. multivora; P. plurivora; P. polonica	Decanol	112-30-1	1	Sherwood et al., 2024
P. cinnamomi; P. citricola; P. polonica; P. syringae	6-Undecen-2-one	NA	2	Sherwood et al., 2024
P. ×cambivora; P. gonapodyides; P. multivora; P. polonica	(*E,Z*)-2,4-Decadienal	25152-83-4	1	Sherwood et al., 2024
P. ×cambivora; P. gonapodyides; P. polonica	(*E,E*)-2,4-Decadienal	25152-84-5	1	Sherwood et al., 2024
P. ×cambivora; P. cinnamomi; P. gonapodyides; P. multivora; P. plurivora; P. polonica	3-Undecen-2-one	10522-37-9	1	Sherwood et al., 2024
P. cinnamomi	Methyl 2,4,6-trimethyl benzoate	2282-84-0	1	Sherwood et al., 2024
P. ×cambivora; P. gonapodyides; P. plurivora	Decanoic acid	334-48-5	1	Sherwood et al., 2024
P. polonica	2-Undecenal	2463-77-6	1	Sherwood et al., 2024
P. polonica	2,4-Undecadienol	59376-58-8	2	Sherwood et al., 2024
P. multivora	Phenyl-2-hexanone	25870-62-6	2	Sherwood et al., 2024
P. gonapodyides	2,6-Dodecadienal	21662-13-5	1	Sherwood et al., 2024
P. multivora	2-Tridecanol	1653-31-2	1	Sherwood et al., 2024
P. cinnamomi	Aristolochene	26620-71-3	1	Sherwood et al., 2024

(Continued)

TABLE 8 Continued

A. Pathogen volatiles				
Pathogen	VOC name	CAS-Nr	ID level	Reference
P. ×cambivora; P. gonapodyides; P. multivora	Dodecanoic acid	143-07-7	1	Sherwood et al., 2024
P. multivora	Tridecanol	112-70-9	1	Sherwood et al., 2024
P. ×cambivora; P. multivora	Tetradecanol	112-72-1	1	Sherwood et al., 2024
P. multivora	6-Pentadecen-2-one	NA	1	Sherwood et al., 2024
P. cinnamomi; P. gonapodyides; P. multivora; P. polonica	γ-Dodecalactone	2305-05-7	1	Sherwood et al., 2024
P. ×cambivora; P. gonapodyides	δ-Dodecalactone	713-95-1	1	Sherwood et al., 2024
P. multivora	Hexadecanol	36653-82-4	1	Sherwood et al., 2024
B. Pathogen-induced plant volatiles after *Phytophthora* sp. infection				
Plant species	VOC name	CAS-Nr	ID level	Reference
Quercus robur L. (seeds)	Neophytadiene isomer 2		3	Borowik et al., 2021a
Quercus robur (seeds)	Neophytadiene isomer 3		3	Borowik et al., 2021a
Quercus robur (seeds); *Lupinus angustifolius* L. (seedlings)	Isoamyl alcohol	123-51-3	2	De Lacy Costello et al., 2001; Borowik et al., 2021a; Qiu et al., 2014a
Potato (*Solanum tuberosum* L.) (tubers)	Pentanol	71-41-0	2	De Lacy Costello et al., 2001
Potato (tubers)	2-Heptanone	110-43-0	2	De Lacy Costello et al., 2001
Potato (tubers)	Styrene	100-42-5	2	De Lacy Costello et al., 2001
Potato (tubers)	2-Ethyl-1-hexanol	104-76-7	2	De Lacy Costello et al., 2001
Potato (tubers)	(*E*)-2-Octenal	2548-87-0	2	De Lacy Costello et al., 2001
Potato (tubers)	Acetophenone	98-86-2	2	De Lacy Costello et al., 2001
Potato (tubers)	Octanol	111-87-5	2	De Lacy Costello et al., 2001
Potato (tubers)	Methylbenzoate	93-58-3	2	De Lacy Costello et al., 2001
Potato (tubers)	Benzothiazole	95-16-9	2	De Lacy Costello et al., 2001
Potato (tubers)	3-Hydroxy-2,2-dimethyl-1-(1-methylethyl) propyl isobutyrate	18491-15-1	2	De Lacy Costello et al., 2001
Potato (tubers)	Propanoic acid, 2-methyl-, 3-hydroxy-2,4,4-trimethylpentyl ester	74367-34-3	2	De Lacy Costello et al., 2001
Potato (tubers)	Iso-caryophyllene	118-65-0	2	De Lacy Costello et al., 2001
Potato (tubers)	Dodecanol	112-53-8	2	De Lacy Costello et al., 2001
Potato (tubers); Strawberry (fruit)	Nonanal	124-19-6	2,1	De Lacy Costello et al., 2001; Jeleń et al., 2005
Potato (tubers)	Isomenthol	23283-97-8	2	De Lacy Costello et al., 2001
Potato (leaves); Tomato (leaves)	(*E*)-2-Hexenal	6728-26-3	1,1	Laothawornkitkul et al., 2010; Li et al., 2019
Potato (leaves)	5-Ethyl-2(5H)-Furanone	2407-43-4	2	Laothawornkitkul et al., 2010
Strawberry (*Fragaria x ananassa* Duchesne) (fruit)	3-Octanone	106-68-3	1	Jeleń et al., 2005
Strawberry (fruit)	o-Cymene	527-84-4	2	Jeleń et al., 2005
Strawberry (fruit)	Phenylacetaldehyde	122-78-1	2	Jeleń et al., 2005
Strawberry (fruit)	(*Z*)-Linalool oxide	1365-19-1	2	Jeleń et al., 2005
Strawberry (fruit)	Pentyl benzene	538-68-1	2	Jeleń et al., 2005

(Continued)

TABLE 8 Continued

B. Pathogen-induced plant volatiles after *Phytophthora* sp. infection				
Plant species	VOC name	CAS-Nr	ID level	Reference
Strawberry (fruit)	Phenethyl acetate	103-45-7	2	Jeleń et al., 2005
Strawberry (fruit)	2-Undecanone	112-12-9	1	Jeleń et al., 2005
Strawberry (fruit)	Tetradecanoic acid methyl ester	124-10-7	2	Jeleń et al., 2005
Strawberry (fruit); *Lupinus angustifolius* L.(seedlings); Potato (leaves)	Phenylethanol	60-12-8	1,2,1	Jeleń et al., 2005; Qiu et al., 2014a; Laothawornkitkul et al., 2010
Strawberry (fruit); *Lupinus angustifolius* (seedlings)	Benzyl alcohol	100-51-6	2	Jeleń et al., 2005; Qiu et al., 2014a
Strawberry (fruit); *Lupinus angustifolius* (seedlings)	4-Ethyl guaiacol	2785-89-9	1,2	Jeleń et al., 2005; Qiu et al., 2014a
Strawberry (fruit); *Lupinus angustifolius* (seedlings)	4-Ethylphenol	123-07-9	1,2	Jeleń et al., 2005; Qiu et al., 2014a
Strawberry (fruit); *Rhododendron* hybrid (leaf extract)	Camphene	79-92-5	1,1	Jeleń et al., 2005; McCartney et al., 2018
Strawberry (fruit); *Rhododendron* hybrid (leaf extract)	1-Octen-3-ol	3391-86-4	1,1	Jeleń et al., 2005; McCartney et al., 2018
Rhododendron hybrid (branch)	Linalool	78-70-6	1	McCartney et al., 2018
Rhododendron hybrid (branch)	(*Z*)-4-Hexen-1-ol	928-91-6	2	McCartney et al., 2018
Rhododendron hybrid (branch)	(*Z*)-3-Hexenyl pentanoate	35852-46-1	2	McCartney et al., 2018
Rhododendron hybrid (leaf extract)	Pinocarvone	30460-92-5	2	McCartney et al., 2018
Rhododendron hybrid (leaf extract)	Cintronellol	106-22-9	1	McCartney et al., 2018
Rhododendron hybrid (leaf extract)	(*E*)-β-Caryophyllene	87-44-5	1	McCartney et al., 2018
Rhododendron hybrid (leaf extract)	4,4-Dimethyl-3-(3-methylbut-3-enylidene)-2-methylenebicyclo[4.1.0]heptane	79718-83-5	2	McCartney et al., 2018
Rhododendron hybrid (leaf extract)	8,9-Dehydroneoisolongifolene	67517-14-0	2	McCartney et al., 2018
Rhododendron hybrid (leaf extract)	Calarene	17334–55-3	2	McCartney et al., 2018
Rhododendron hybrid (leaf extract)	β-Vatirenene	NA	2	McCartney et al., 2018
Rhododendron hybrid (leaf extract)	Isogermacrene D	317819-80-0	2	McCartney et al., 2018
Rhododendron hybrid (leaf extract)	Alloaromadendrene	25246-27-9	2	McCartney et al., 2018
Rhododendron hybrid (leaf extract)	β-Chamigrene	18431-82-8	2	McCartney et al., 2018
Rhododendron hybrid (leaf extract)	γ-Muurolene	30021-74-0	2	McCartney et al., 2018
Rhododendron hybrid (leaf extract)	(+)-ß-Selinene	17066-67-0	2	McCartney et al., 2018
Rhododendron hybrid (leaf extract)	α-Selinene	473-13-2	2	McCartney et al., 2018
Rhododendron hybrid (leaf extract)	Ledene	21747-46-6	2	McCartney et al., 2018
Rhododendron hybrid (leaf extract)	4,5,9,10-Dehydroisolongifolene	156747-45-4	2	McCartney et al., 2018
Rhododendron hybrid (leaf extract)	Caryophyllene oxide I	1139-30-6	2	McCartney et al., 2018
Rhododendron hybrid (leaf extract)	(+)-Spathulenol II	6750-60-3	2	McCartney et al., 2018
Rhododendron hybrid (leaf extract)	Ledol	577-27-5	2	McCartney et al., 2018
Rhododendron hybrid (leaf extract)	Globulol	51371-47-2	2	McCartney et al., 2018
Rhododendron hybrid (leaf extract)	Ledene oxide	NA	2	McCartney et al., 2018
Rhododendron hybrid (leaf extract)	Juniper camphor	473-04-1	2	McCartney et al., 2018
Rhododendron hybrid (leaf extract)	Agarospirol	1460-73-7	2	McCartney et al., 2018

(Continued)

TABLE 8 Continued

B. Pathogen-induced plant volatiles after *Phytophthora* sp. infection				
Plant species	VOC name	CAS-Nr	ID level	Reference
Rhododendron hybrid (leaf extract)	Sesquiterpene oxide I	NA	3	McCartney et al., 2018
Rhododendron hybrid (leaf extract)	Aristolone	6831-17-0	2	McCartney et al., 2018
Rhododendron hybrid (leaf extract)	Diterpene I	NA	3	McCartney et al., 2018
Rhododendron hybrid (leaf extract)	Diterpene II	NA	3	McCartney et al., 2018
Rhododendron hybrid (leaf extract)	Labd-14-ene	1227-93-6	2	McCartney et al., 2018
Rhododendron hybrid (leaf extract)	Diterpene III	NA	3	McCartney et al., 2018
Rhododendron hybrid (runoff water)	(*Z*)-11-Hexadecenoic acid[a]	2416-20-8	2	McCartney et al., 2018
Rhododendron hybrid (runoff water)	(*Z*)-9-Hexadecenoic acid[a]	373-49-9	2	McCartney et al., 2018
Rhododendron hybrid (runoff water)	Cyclic octaatomic sulfur	10544-50-0	2	McCartney et al., 2018
Rhododendron hybrid (runoff water)	Oleic acid[a]	112-80-1	2	McCartney et al., 2018
Lupinus angustifolius (seedlings)	Ethyl acetate	141-78-6	2	Qiu et al., 2014a
Lupinus angustifolius (seedlings)	2-Butanone	78-93-3	2	Qiu et al., 2014a
Lupinus angustifolius (seedlings)	Ethyl isobutyrate	97-62-1	2	Qiu et al., 2014a
Lupinus angustifolius (seedlings)	2-Pentanone	107-87-9	2	Qiu et al., 2014a
Lupinus angustifolius (seedlings)	Ethyl 2-methylbutyrate	7452-79-1	2	Qiu et al., 2014a
Lupinus angustifolius (seedlings)	Butyrolactone	96-48-0	2	Qiu et al., 2014a
Lupinus angustifolius (seedlings)	Benzyl alcohol	100-51-6	2	Qiu et al., 2014a
Lupinus angustifolius (seedlings)	4-Ethyl-1,2-dimethoxybenzene	5888-51-7	2	Qiu et al., 2014a
Fagus sylvatica (tree)	Anisole	100-66-3	2	Sherwood et al., 2024
Fagus sylvatica (tree)	Isokaurene[a]	511-85-3	2	Sherwood et al., 2024
Populus sp. (hybrid poplar tree)	α-Cubebene	17699-14-8	2	Durkovic et al., 2021
Populus sp. (hybrid poplar tree)	Germacrene D	23986-74-5	2	Durkovic et al., 2021
Potato (tubers)	Benzaldehyde	100-52-7	2	De Lacy Costello et al., 2001
Strawberry (fruit)	α-Muurolene	10208-80-7	2	Jeleń et al., 2005

[a] Compound listed as VOC in the source publication but boiling point higher than 350°C.
[b] Identified in pure culture and infected plant.

The ID level reports the VOCs identification levels reported by the literature (1= identified compound, 2= putatively identified compound, based upon physiochemical properties of a chemical class and/or by spectral similarities, 3= putatively characterized compound classes, based upon characteristic physicochemical properties of a chemical class of compounds, or by spectral similarity to known compounds of a chemical class). The CAS number is a compound-specific unique identification number assigned by the Chemical Abstracts Service (CAS).

Phytophthora ramorum (Figure 2B), an airborne pathogen, originates from the Laurisilva forests of East Asia (Jung et al., 2020, Jung et al., 2021). Since the early 1990s, each two lineages have been introduced to Europe (EU1 and EU2) and the Pacific Northwest (NA1 and NA2) where they became highly invasive causing leaf and shoot blights and bark cankers on a wide range of more than 100 host species, including *Rhododendron* (Figure 2E), *Camelia* and *Viburnum* spp., and the devastating epidemics "Sudden Oak Death" (California and Oregon) and "Sudden Larch Death" (UK and Republic of Ireland) which killed millions of oak, tanoak and larch trees (Werres et al., 2001; Rizzo et al., 2002; Brasier and Webber, 2010; Grünwald et al., 2012; Van Poucke et al.; 2012; Harris and Webber, 2016; Jung et al., 2018a; Cobb et al., 2020). In the EU, all *P. ramorum* lineages not yet introduced (= all lineages except of EU1) are listed as A1 quarantine pests.

The panglobal soilborne pathogen *Phytophthora cinnamomi* (Figures 2C, D) is the most notorious and invasive member of the genus infecting and causing root rot, bark cankers (Figure 2G), dieback and mortality (Figure 2J) of more than 5000 woody plant species worldwide (Erwin and Ribeiro, 1996; Hardham and Blackman, 2018). A recent population genomic study showed that *P. cinnamomi* originates in Southeast Asia and that the global pandemic is driven by two clonal A2 mating type lineages (Shakya et al., 2021). Besides being a major pathogen of many horticultural crops and ornamentals, *P. cinnamomi* causes some of the most devastating epidemics of forest trees and natural ecosystems including decline and dieback of eucalypt forests across Australia; fynbos heathlands in South Africa; Valdivian rainforests and *Araucaria* forests in Chile; oak and chestnut forests in Southern Europe (Figures 2G, J) and the USA (Von Broembsen and Kruger, 1985; Shearer and Tippett, 1989; Brasier et al., 1993; Erwin and Ribeiro, 1996; Shearer et al., 2004; Vettraino et al., 2005; Dos Santos et al., 2011; Jung et al., 2016, Jung et al., 2018a, Jung et al., 2018b; McConnell and Balci, 2014; Sanfuentes et al., 2022).

Phytophthora cactorum (Leb. and Cohn) Schroeter is native to North America and has reached a panglobal distribution (Bourret et al., 2022). It causes both air- and soilborne diseases on a wide range of host plants including many ornamentals; forest trees like *Fagus sylvatica* L. (damping-off, root and collar rot, aerial bleeding cankers) and *Betula pendula* Roth (root and collar rot); horticultural crops like strawberries (collar rot and leather rot of fruits); and fruit trees, in particular apple trees (root, collar rot and fruit rot) (Harris, 1991; Erwin and Ribeiro, 1996; Jung et al., 2016, Jung et al., 2018a, Jung et al., 2019; Hantula et al., 2000; Jung, 2009; Corcobado et al., 2020).

Phytophthora plurivora Jung & Burgess originates from East Asia (Vettraino et al., 2011; Huai et al., 2013; Jung et al., 2017a, Jung et al., 2024). It is a soilborne introduced pathogen in both Europe and North America causing root and collar rot, aerial bleeding bark cankers (Figures 2F, I), and leaf and shoot blight on a wide range of woody host plants in natural ecosystems, nurseries and planting sites across; it is also one of the main drivers of current oak and beech declines across Europe (Jung, 2009; Jung and Burgess, 2009; Orlikowski et al., 2011; Reeser et al., 2011; Hansen et al., 2012; Jung et al., 2016, Jung et al., 2018a, Jung et al., 2019; Bienapfl and Balci, 2014; Brazee et al., 2016; Corcobado et al., 2020; Frankel et al., 2020).

Phytophthora ×cambivora (Petri) Buisman (Figure 2A) is a soilborne pathogen with a cosmopolitan distribution which originates from East Asia (Erwin and Ribeiro, 1996; Jung et al., 2017b; Mullett et al., 2023). It causes root (Figures 2H, I) and collar rot and infrequently aerial bleeding bark cankers on a wide range of woody host plants including many ornamentals, fruit trees and forest trees, and is one of the main drivers of the devastating Ink disease of sweet chestnut (*Castanea sativa*) in Europe and oak and beech declines across Europe (Mircetich and Matheron, 1976; Erwin and Ribeiro, 1996; Jung et al., 2000, Jung et al., 2018a, Jung et al., 2019; Vettraino et al., 2005; Jung, 2009; Corcobado et al., 2020).

6.2 Summary of literature on VOCs produced and induced by *Phytophthora* species

In this summary we focus on studies with *Phytophthora*-infection related VOCs from different *Phytophthora*-inoculated substrates i.e., chemical analyzes of VOCs directly from the pathogens or from the plants infected by *Phytophthora* species. A limited number of studies have identified and described VOCs emitted from substrates infected with *Phytophthora* species (and other oomycetes). For this work we included 12 studies, but only two studies are focused on or include VOCs from quarantine pathogen *P. ramorum*, the target pathogen in this review.

McCartney et al. (2018), used headspace sorptive extraction (HSSE), stir bar sorptive extraction (SBSE) and SPME combined with GC-MS to find specific VOCs and VOC profiles from *P. ramorum*-infected *Rhododendron* hybrid 'Cunningham's White' plants. This is currently the only published study that investigates VOCs from *P. ramorum*-infected plants. For the HSSE method (*in situ* branch enclosure technique), 79 VOCs were detected. Three compounds were statistically different for *P. ramorum*-inoculated *Rhododendron* plants vs controls: linalool, (*Z*)-4-hexenol and (*Z*)-3-hexenyl pentanoate. For the SBSE liquid extraction method (leaf volatiles from a methanol extract), 115 VOCs were detected, and 31 compounds were statistically different for the inoculated *Rhododendron* plants (see Table 8). One compound, (*Z*)-3-hexenyl pentanoate, was produced in higher abundances in healthy plants (control) for both HSSE and SBSE. The SPME method (water runoff from the soil of potted healthy and inoculated plants), four compounds were only present in runoff water from soil infested with *P. ramorum*: (*Z*)-11-hexadecenoic acid, (*Z*)-9-hexadecenoic acid, cyclic octaatomic sulfur, oleic acid. These identified fatty acids have boiling points higher than 350°C and can be difficult to detect in ambient air except under specific experimental conditions. Loulier et al (2020), utilized SPME/GC-MS to investigate VOCs from cultures in potato dextrose agar (PDA) of *P. ramorum*, *P. plurivora*, *P. cinnamomi*, *P. cactorum* and a range of fungi. It was found that ethanol was shared between *P. ramorum* and *P. cinnamomi* (see Table 8). Other VOCs detected (but also present in various species of fungi) were 3-octanone, 1-octen-3-ol, 2-methylbutanol and isoamyl alcohol from *P. ramorum*. *P. ramorum* also emitted 2-phenylethanol. Loulier et al. (2020) further found that *P. ramorum* emitted higher amounts of compounds compared to the other *Phytophthora* species, and this was also confirmed in an analysis using an e-nose instrument developed in the same study. The e-nose could discriminate between VOCs emitted by *P. ramorum*, *Fusarium poae* (Peck) Wollenweber, *Trichoderma asperellum* Samuels, Lieckfeldt & Nirenberg and *Rhizoctonia solani* (Prillieux & Delacroix) Donk. Interestingly, *P. plurivora* emitted two monoterpenes α-pinene and 3-carene. Furthermore, Loulier et al. (2020) found that a major difference between the *Phytophthora* species and the fungi could be the amount of sesquiterpene produced, where the *Phytophthora* tested does not release these compounds/VOCs, but all tested fungal species did (except one). A recent study by Sherwood et al. (2024) used SPME/GC-MS to analyze the volatile organic compounds (VOCs) emitted by eight *Phytophthora* species cultivated on medium: *P. cambivora, P. cinnamomi, P. citricola, P. gonapodyides, P. multivora, P. plurivora, P. polonica*, and *P. syringae*. A total of 58 compounds were identified. However, identification from mass spectral libraries was not possible for some compounds, and these were excluded from Table 8. Surprisingly, there was very little overlap with the VOCs identified in the Loulier et al. (2020), sharing only three VOCs: 1-octen-3-ol, heptanol, and 4-ethyl guaiacol. Additionally, the sesquiterpene aristolochene was identified in *P. cinnamomi*, which contradicts Loulier et al. (2020)'s results. Some

Phytophthora species may lack some genes for terpene biosynthesis (Chen et al., 2016), limiting their ability to produce a diverse range of terpenes compared to fungal organisms.

Qiu et al., 2014a; Qiu et al., 2014b optimized and used SPME to find specific VOCs from *Phytophthora cinnamomi*. After inoculation of different substrates [V8A, PDA, lupin seedlings (*Lupinus angustifolius* L. 'Danja'), soil, and soil + lupin seedlings] with *P. cinnamomi*, this study identified 87 VOCs from infected and non-infected substrate. Four of these, 4-ethyl guaiacol (4-ethyl-2-methoxy phenol), 4-ethylphenol, butyrolactone, and phenylethanol, were significant and specific for *P. cinnamomi*-infections. This study shows that it is possible to detect differences between inoculated and non-inoculated plants and substrates. Borowik et al. (2021a) used SPME and found specific VOCs for *P. plurivora* and *Pythium intermedium* (de Bary) Uzuhashi, Tojo & Kakishima from *in vitro* infected germinated acorns of *Quercus robur* L. In total, four VOCs were detected on the inoculated acorns, which were not found in the control acorns. Three of them, neophytadiene isomer 2, neophytadiene isomer 3 and isoamyl alcohol were significant and specific for acorns infected with *P. plurivora*, whereas methylcarveol were specific for *Pythium intermedium*-infected acorns. Furthermore, Borowik et al. (2021b) also developed a low-cost electronic nose that applies six non-specific Figaro Inc. metal oxide sensors. A machine learning approach with this system was able to distinguish between *P. plurivora* and *Pythium intermedium* grown on Petri dishes with V8-Agar media (Borowik et al., 2021b) and using *in vitro* infected germinated acorns of *Q. robur* (Borowik et al., 2021a). Durkovic et al. (2021) used HS/GC-MS to analyze emissions from field-grown hybrid poplar infected with *P. cactorum* and *P. plurivora*. Their findings showed that the emissions of both sesquiterpenes, α-cubebene and germacrene D, were induced solely by the *Phytophthora* inoculations (both species).

De Lacy Costello et al. (2001) used improvised thermal desorption system (sorbent Tenax TA, Tenax GR and Carbosieve III) for *P. infestans*- and *Fusarium coeruleum* Libert ex Saccardo inoculated potato tubers (*Solanum tuberosum* L. cv. Maris Piper). The four most abundant and significant VOCs were common for both pathogens, but not present in the control: benzothiazole, 2-ethyl-1-hexanol, 3-hydroxy-2,2-dimethyl-1-(1-methylethyl)propyl isobutyrate and propanoic acid, 2-methyl-, 3-hydroxy-2,4,4-trimethylpentyl ester (see Table 8). Laothawornkitkul et al. (2010) detected three VOCs specific for *P. infestans*-infected potato leaves: 5-ethyl-2(5H)-furanone, (*E*)-2-hexenal, and phenylethanol (VOCs were trapped on volatile traps (Tenax sorbent) and then eluted with a solvent). Even though both studies on potato used similar technology the experimental conditions, potato growth stage and variety differed could explain the difference in the VOCs emitted from *P. infestans*-infected potato. Li et al. (2019), developed a smartphone-based VOC fingerprinting platform that could detect *P. infestans* in tomato (*Solanum lycopersicum* L.) both *in vitro* and *in vivo*. They suggest that (*E*)-2-hexenal is a major diagnostic VOC marker for *P. infestans* infection, which aligns with the findings of an earlier study by Laothawornkitkul et al. (2010). However, Xu et al. (2021) later demonstrated that (*E*)-2-hexenal is involved in *Botrytis cinerea* infection in tomato plants.

Jeleń et al., 2005 used SPME/GC-MS to find specific VOCs for *P. cactorum*-infected strawberries (*Fragaria* × *ananassa* (Duchesne ex Weston) Duchesne ex Rozier). Of 160 VOCs, 17 compounds were specific for inoculated strawberries and were absent in non-inoculated strawberries. Of these VOCs, two were found to be causing the characteristic off-odor from *P. cactorum*-infected strawberries (using gas chromatography–olfactometry): 4-ethylphenol and 4-ethyl guaiacol.

Each of these studies found different VOCs and different VOC profiles obtained from the different *Phytophthora* species-infected substrates, indicating there are *Phytophthora* species-specific VOCs and VOC profiles. Hence, enabling the development of e-noses for aiding detection of these pathogens, especially those of quarantine status and high destructive potential. However, of the above referenced papers, only twelve species of oomycetes (*P. cactorum*, *P. cinnamomi*, *P. infestans*, *P. ramorum*, *P. plurivora, P. cambivora, P. citricola, P. gonapodyides, P. multivora, P. polonica, P. syringae* and *Pythium intermedium*) have been investigated so far and they have utilized several different infected substrates and various methods to collect VOCs from the pathogens themselves or the infected plants. The VOC information for *Phytophthora* is very scarce compared to other pests such as the fall armyworm *Spodoptera frugiperda*, the brown marmorated stink bug *Halyomorpha halys* or the cotton Boll worm *Helicoverpa armigera*. It is not yet possible for any *Phytophthora* species to find a VOC profile that is robustly produced in connection with the target organisms i.e., VOCs that are not only produced in one infected plant variety or under one certain temperature/light regime. Three VOCs were consistently identified in at least three independent studies of *Phytophthora*: 1-octen-3-ol, 4-ethylguaiacol, and phenylethanol (see Table 8). However, a limitation of these potential biomarkers is that they are also produced by several other organism.

Finding suitable VOCs for the early detection of *Phytophthora* in woody plants is challenging. The genus *Phytophthora* often lacks genes necessary for the biosynthesis of secondary metabolites which are commonly used for fungal detection. This could be potentially utilized. Research by Loulier et al. (2020) using electronic noses (E-noses) demonstrates that the detection of specific terpenes can potentially distinguish between fungal infections and *Phytophthora* infections. Another challenge is that a significant portion of the pathogen resides within the roots, unlike infections caused by organisms like *P. infestans*. For the latter, a simpler device for VOC collection was successfully developed (Li et al., 2019). To capture sufficient VOCs for future analysis from this root-dwelling pathogen, a more sensitive method of collection and analysis, such as TD-GC-MS, is recommended.

6.3 Candidate VOCs for *Phytophthora ramorum* detection

Since only two studies included VOCs from *P. ramorum*, either *P. ramorum*-infected plants (McCartney et al., 2018) or from the pathogen in culture (Loulier et al., 2020), it is not possible to select any robust candidate VOCs for this pathogen. Therefore, all current

VOCs that do not appear in the controls in these studies are listed as *P. ramorum* candidate VOCs in Table 8. More VOC profiling of *P. ramorum* and other *Phytophthora* species and *Phytophthora*-infected plants are urgently needed to find functioning candidate VOCs for these pathogens.

7 Discussion

Exploiting VOCs released by the pests and infested plants has shown to be a promising approach to assess the presence of quarantine organisms (MacDougall et al., 2022). Our review, however, highlights how crucial it is to have clear target signature VOCs for prompt and accurate pest detection. Volatiles specific to the organism (in case of insect, the pheromones) and herbivore-induced plant volatiles clearly appear as reliable VOCs for pest detection and identification. In the three insects we considered, at least one candidate compound was found among aggregation, defense, alarm, sexual and oviposition deterrent pheromones. No specific volatile has yet been identified for the nematode *Bursaphelenchus xylophilus* and for the oomycete *Phytophtora ramorum*.

Among the five organisms we analyzed, the insect pheromones appeared to be the most reliable candidates. Although the specificity of insect pheromones is geared toward precise communication within a species, the generalization and quantities of HIPVs released by plants serves a broader ecological context, influencing a wide array of interactions within an ecosystem (Shivaramu et al., 2017). In the case of insect pheromones, the specificity is often a result of coevolution between the emitter and the receiver within the same species. The accuracy of the signal is crucial for reproductive success. On the other hand, the generalization of HIPVs in plants is likely to be a strategy to maximize the benefits of indirect defense against herbivores and to establish complex ecological relationships with various organisms in the environment. For a precise detection through VOCs to be effective and applicable, pest-specific signals independent of the plant species should be desirable, pheromones satisfy this requirement more than HIPVs. Pheromones present, however, limitations. Since pheromones primary function is to deliver precise information within the species only at specific time periods, they are not constantly emitted. For instance, *H. halys* does not release defensive odors if not disturbed (Nixon et al., 2018), and the aggregation pheromone is emitted by males only (Weber et al., 2017). In *Spodoptera frugiperda* only adult virgin females emit the sexual pheromone. Therefore, eggs and immature insect stages would not be identified based on the pheromones that we currently know about. In contrast, the oviposition deterrent pheromones in *Helicoverpa armigera* are not only produced by females after oviposition, but also by eggs and larval frass (Guoqing et al., 2001; Xu et al., 2006; Liu et al., 2008), making them a more reliable VOCs for pest identification. It is highly desirable that similar compounds would be found for other insect species.

The HIPVs described in this review may have limitations as candidates in the case of *H. halys* and *S. frugiperda*. In *H. halys*, the HIPVs are different depending on plant species, and no apparent common VOC was released following *H. halys* damage. In the case of maize plants infested with different species of the genus *Spodoptera*, the HIPV blends lack unique molecules that could identify the attacking species. However, there are consistent difference in ratios that could provide such information. Further research is needed to determine consistencies and specificities in host plant responses to determine reliable combinations of compounds as candidates of pest identification.

A more favorable situation emerged in the HIPVs of *H. armigera*. Four terpenoids were found to be specific to CBW infestation of maize plants, among which β-myrcene was found in cotton too, and D-limonene also in French bean and tomato. β-Pinene was common in maize, cotton, tobacco, and tomato. Specificity and consistency allowed to select these HIPVs as candidates for the CBW detection, also showing that the use of HIPVs as identification cues is possible.

The use of HIPVs as marker signals should be considered carefully, because of the complexity that emerges from real-life conditions. Pest surveillance usually applies to international trade, and plant might face long and stressful journeys. Abiotic stress factors, such as drought, temperature extremes, and nutrient deficiencies, can vary widely in intensity and duration. The plant volatilome responses to such stressors must be considered when targeting for specific VOCs. In an extensive review, Loreto and Schnitzler (2010) reported how abiotic stresses enhance biogenic VOC emission rates and patterns, and how these stressors can alter the constitutive VOCs, causing them to either increase or decrease in emission, or they can cause the synthesis of new VOCs and suppression of others. The capacity of discerning HIPVs from abiotic stress-related plant VOCs becomes crucial. More data are needed to get a full picture of the diversity of plant responses under different stress combinations.

In case of the nematode *Bursaphelenchus xylophilus*, the scarce literature available did not provide any robust data to allow the selection of candidate VOCs. The few compounds mentioned are common terpenoids that lack consistency between the pine species and are thus unreliable. A considerable effort is required to expand the information available on the *B. xylophilus*-induced plant volatiles. Similarly, the number of studies on *Phytophthora ramorum* did not provide enough evidence to confidently select signature VOCs. Only one research paper (Loulier et al., 2020) analyzed the volatiles released by a pure *P. ramorum* culture, and another one (McCartney et al., 2018) from infected hybrid *Rhododendron* plants. As for the nematode, the need to expand the literature on the subject is essential.

8 Conclusions

This review collected and analyzed the available literature concerning pest VOCs and pest-induced VOCs from five selected pests/pathogens relevant to the international pest surveillance programs. The aim was to select the pest signature volatiles that can be employed in specific volatile detection. The picture that appears shows that insects pheromones are reliable indicators of the pest presence, albeit with limitations. The use of induced plant VOCs is a viable solution but requires in depth exploration that takes into account the complexity of the plant response to abiotic and biotic factors. As the development of volatiles-based approaches are advancing, their use is increasingly seen as a viable solution for early pest detection. It is imperative to increase the number of studies and the quality of information available on the most crucial pest species. The research in this direction should be methodical, precise and rigorous, aiming at offering a broad database of volatiles signatures.

Author contributions

RF: Conceptualization, Writing – original draft, Writing – review & editing. MP: Writing – original draft, Writing – review & editing. GT: Writing – original draft, Writing – review & editing. CA: Writing – original draft, Writing – review & editing. MI: Writing – original draft, Writing – review & editing. TT: Writing – review & editing. JF: Writing – original draft, Writing – review & editing. TJ: Writing – original draft, Writing – review & editing. DB: Writing – review & editing. AP: Writing – review & editing. SA: Writing – review & editing. LC: Conceptualization, Writing – original draft, Writing – review & editing. MB: Writing – review & editing.

Funding

The author(s) declare financial support was received for the research, authorship, and/or publication of this article. This research was funded by the project PurPest, grant number 101060634 supported under HORIZON-CL6-2021-FARM2FORK-01-04-Tackling outbreaks of plant pests, funded under the HORIZON Research and Innovation Action (RIA) from the European Research Executive Agency (REA)-Green Europe REA.B.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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