Scientific and technological developments in mating disruption of scale insects

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With 1 figure and 2 tables

Abstract: Mating disruption (MD) is a species-specific and environmentally friendly pest management tactic based on the release of synthetic sex pheromones aiming to interrupt the mate-finding communication and prevent mating in the target pest. The present work aims to provide an overview of the current scientific and technical knowledge on mating disruption of scale pests (Hemiptera: Coccoidea). Biparental scales are suitable targets for mating disruption (technically, MD is not suitable for parthenogenetic scales), as the females have a limited spreading ability, and adult males are short lived and have a narrow window of time for mate searching. In this perspective, delayed mating also plays an important role by reducing female attractiveness and population growth potential. The mechanisms involved in MD of scales are most likely assigned to 'competitive disruption' rather than 'noncompetitive' mechanisms, although no specific studies addressed this issue. Mating disruption has been commercially developed and increasingly applied against the vine mealybug *Planococcus ficus* (Signoret) (Hemiptera: Pseudococcidae) and the California red scale *Aonidiella aurantii* (Maskell) (Hemiptera: Diaspididae) to a lesser extent. Critical factors affecting MD effectiveness are the pest density and effective disruption late in the season. Mating disruption applied to scale pests is effective in small plots and compatible with biological control and integrated management programs. In conclusion, MD has a high potential for management of scale pests, providing that key factors such as technological advances in pheromone synthesis and pheromone formulations, elucidation of disruption mechanisms, and simplification of the registration process are addressed.

Keywords: Pheromones, behavioural manipulation methods, IPM, Coccoidea, mealybugs, armoured scales

1 Introduction

Mating disruption (MD) is a behavioural-modifying tactic of pest management, based on the application of synthetic sex pheromones formulated for release in the air to prevent mating in a target insect pest (Suckling 2000). It is considered an environment-friendly plant protection approach, as sex pheromones are species-specific, non-toxic and active in very small amounts, as compared with other pest management chemicals. In fact, although many pheromone compounds have been registered and applied worldwide,

there is no evidence of negative effects on human health, non-target organisms or the environment (Witzgall et al. 2010).

While MD was initially proposed as a new approach in late 1960s (Gaston et al. 1967), its commercial application was only possible in the end of 1970s, after industrial-scale synthesis had become available (Doane & Brooks 1981; Cardé & Minks 1995; Witzgall et al. 2010). Since the 1990s, practical implementation of MD has registered an almost exponential growth (Witzgall et al. 2010), though it is still far from reaching its full potential (Miller & Gut 2015).

MD has been mainly applied to control lepidopteran pests in various agroecosystems, including vineyards, fruit orchards, cotton and forests, across more than 750,000 ha (Witzgall et al. 2010; Miller & Gut 2015). Only recently, MD has been integrated in pest management of other insect taxa, such as scale insects (Hemiptera, Sternorrhyncha, Coccomorpha) (Walton et al. 2006; Vacas et al. 2009). Nevertheless, despite the scientific and technical knowledge that has been accumulated, almost no reviews were published on MD of non-lepidopteran pests, including scale insects (e.g., Tabata 2020). The scientific, technological and practical developments in MD of scale insects are reviewed here, aiming at summarizing the current knowledge and stimulating future studies and practical implementation of MD, for a sustainable management of this economically important group of plant insect pests.

2   Economic importance of scale insects

Scale insects or coccoids (hereafter designated as scales) are small, cryptic, piercing-sucking hemipterans, mostly feeding on phloem sap, comprising more than 8,300 species, distributed among 55 families and 1,214 genera (Garcia Morales et al. 2016). Scales include serious pests of various agricultural, forest, and ornamental plants (Kosztarab 1996; Franco et al. 2009; Garcia Morales et al. 2016; Mansour et al. 2017a). The majority of economically important species belong to the two largest families, i.e., armoured scales (Diaspididae, 32% of scale species) and mealybugs (Pseudococcidae, 24% of scale species).

Direct damage is inflicted by feeding activity, as plant sap ingestion and injection of toxic saliva components may result in leaf and fruit discoloration, defoliation, flower and fruit drop, reduction of fruit growth rate, distortion of leaves, new shoots and fruits, and reduction of plant vigour, leading to plant death in extreme cases (Kosztarab 1996; Franco et al. 2009). Indirect damage is the result of honeydew excretion and development of sooty mould (except for Diaspididae), which may reduce photosynthesis and plant growth. Honeydew often attracts ants, which may disrupt the activity of natural enemies and facilitate the spread of scales on the crop (Franco et al. 2009; Quesada et al. 2018). Some scales, mainly mealybugs, are also vectors of plant viruses (Nault 1997; Perilla-Henao & Casteel 2016). For example, several mealybug species, including the vine mealybug (hereafter notated as VMB) *Planococcus ficus* (Signoret) and soft scales (Coccidae) have been recognised as vectors of Grapevine leafroll-associated viruses (GLRaV) (Tsai et al. 2008; Mahfoudhi et al. 2009). GLRaV is the most economically important viral disease of grapevines in many producing regions in the world, with an estimated loss of about $25,000 – $40,000 per hectare, if no control measures are applied (Atallah et al. 2012).

Pest status of a scale is often associated with invasive species. Outside their native range, the populations of invasive scales usually profit from the absence of their natural enemies and, without natural control, often originate outbreaks and economic damage. Some biological traits may favour the invasiveness of scales. Their small size and cryptic behaviour make them difficult to detect in quarantine inspections. Also, parthenogenetic reproduction in some species and high fecundity (e.g., some scales may oviposit up to 8,000 eggs) facilitate the establishment of scales in new territories based on just a few females (Pellizzari & Germain 2010). For example, from the 256 scale species considered as pests in the USA, about 75% are non-native, representing 25% of the total number of scale species known in the country (Miller et al. 2005). In Europe, alien species represent near 30% of scale fauna (Pellizzari & Germain 2010) and the EPPO A1 list of pests recommended for regulation as quarantine pests include four scale species, i.e., *Ripersiella hibisci* (Kawai & Takagi) (Pseudococcidae), *Margarodes prieskaensis* (Jakubski), *M. vitis* (Philippi) and *M. vredendalensis* De Klerk (Margarodidae) (EPPO 2020). *Ripersiella hibisci* and *Margarodes* spp. are considered a serious phytosanitary risk to potted plants and vineyards in the EPPO region, respectively.

The main pathway of introduction of alien scales is the horticultural and ornamental trade. It is expected that the growth of global trade will contribute to an increase in the number of new introductions. The observed trend in Europe of the mean number of new alien scales per year corroborates this prediction: 0.7 new alien species per year, in the period 1950-1974; 1.2 in 1975-1999; and 1.3 in 2000-2007 (Pellizzari & Germain 2010). Among these, new alien scales can have a high economic impact. For example, the South African mealybug *Delottococcus aberiae* (De Lotto) was detected in 2009 in Eastern Spain, causing serious damage to citrus crops (Beltrà et al. 2015). Since then, it has been expanding its geographical distribution in the country. Recently, the Farmers Association of Valencia (AVA-ASAJA) estimated that the direct losses from *D. aberiae* in 2020 were about 113 million € (PHYTOMA 2020).

3   Identification and analysis of scale sex pheromones

3.1   Scale sex pheromones identified

Most scales reproduce sexually. The females produce sex pheromone to attract the conspecific males. Specifically, the pheromone chemical structure of 32 scale species belonging to the families Diaspididae, Matsucoccidae, Margarodidae, and Pseudococcidae has been reported to date (see Table 1 for references). This number has been increasing enormously since the 2000s, with 68% of these structures reported in the last 20 years (Fig. 1). The highest number of reported chemi-

Table 1. List of identified scale sex pheromones.

Family/species	Pheromone compound	Reference	Type	Molecular formula
Diaspididae				
Acutaspis albopicta (Cockerell)	[(1S,3S)-2,2-dimethyl-3-(prop-1-en-2-yl) cyclobutyl)]methyl (R)-2-methylbutanoate	Millar et al. (2012)	Ester-sesquiterpenic cyclobutane	C15H26O2
Aonidiella aurantii (Maskell)	3-methyl-6-isopropenyl-9-decen-1-yl acetate	Roelofs et al. (1977)	Sesquiterpenol ester	C16H28O2
	(Z)-3-methyl-6-isopropenyl-3, 9-decadien-l-yl acetate			C16H26O2
Aonidiella citrina (Coquillett)	(E)-3,9-dimethyl-6-isopropyl-5,8-decadien-l-yl acetate	Gieselmann et al. (1979a)	Sesquiterpenol ester	C17H30O2
Aspidiotus nerii Bouché	(1R,2S)-cis-2-isopropenyl1-(4'-methyl-4'-penten-1'-yl)cyclobutaneethanol acetate	Einhorn et al. (1998)	Cyclobutane sesquiterpenol ester	C17H28O2
Aulacaspis murrayae Takahashi	(5R,6E)-5-isopropyl-8-methyl-6,8-nonadien-2-one	Ho et al. (2014)	Nor-sesquiterpene ketone	C13H22O
Pseudaulacaspis pentagona (Targioni Tozzetti)	(R,Z)-3,9-dimethyl-6- isopropenyl-3,9-decadien-l-ol propionate	Heath et al. (1979)	Sesquiterpenol ester	C18H30O2
Comstockaspis perniciosa (Comstock)	(Z)-3,7-dimethyl-2,7-octadien-l-yl propanoate	Gieselmann et al. (1979b)	Esters of geraniol and nerol	C13H22O2
	3-methylene-7- methyl-7-octen-l-yl propanoate			C13H22O2
	(E)-3,7-dimethyl-2,7-octadien-l-yl propanoate	Anderson et al. (1981)		C13H22O2
Margarodidae				
Margarodes prieskaensis (Jakubski)	(2R,4R,6R,8R)-2,4,6,8-tetramethylundecan-1-ol	Burger et al. (2017)	Tetramethyl primary alcohol	C15H32O
Matsucoccidae				
Matsucoccus feytaudi Ducasse	(E,E)-8,10-(3S,7R)-3,7,9-trimethyldodecadien-6-one	Einhorn et al. (1990)	Unsaturated aliphatic ketones	C15H26O
	(8Z, 10E)-3,7,9-trimethyl-8, 10-dodecadien-6-one			C15H26O
Matsucoccus josephi Bodenheimer & Harpaz	(2E,4E,8E)-4,6dimethyl-2,4, 8-decatrien-7-one	Dunkelblum et al. (1993)		C12H18O
	(2E,4Z,8E)-4,6-dimethyl-2,4,8-decatrien-7-one			C12H18O
Matsucoccus matsumurae (Kuwana) (= *Matsucoccus resinosae* (Kuwana), *Matsucoccus thunbergianae* Miller & Park)	(2E, 4E)-4,6,10,12-tetramethyl-2,4-tridecadien-7-one	Lanier et al. (1989)		C17H30O
Pseudococcidae				
Crisicoccus matsumotoi (Siraiwa)	3-methyl-3-butenyl-5-methylhexanoate	Tabata et al. (2012)	Hemiterpenol ester	C12H22O2
Delottococcus aberiae (De Lotto)	(4,5,5-trimethyl-3-methylenecyclopent-1-en-1-yl)methyl acetate	Vacas et al. (2019)	β-necrodol ester	C12H18O2
Dysmicoccus brevipes (Cockerell)	(-)-(anti-1,2-dimethyl-3-methylenecyclopentyl)acetaldehyde	Tabata et al. (2017)	Cyclopentane/ aldehyde	C10H16O

Table 1. continued.

| Family/species	Pheromone compound	Reference	Type	Molecular formula
Dysmicoccus grassii (Leonardi)	(R)-5-Methyl-2-(prop-1-en-2-yl)-hex-4-enyl acetate	de Alfonso et al. (2012)	Lavandulol ester	C13H22O2
	(R)-5-Methyl-2-(prop-1-en-2-yl)-hex-4-enyl propionate			C12H20O2
Dysmicoccus neobrevipes Beardsley	(+)-(E)-2-isopropyl-5-methylhexa-3,5-dienyl acetate	Tabata & Ichiki (2015)	Acyclic ester	C12H20O2
Ferrisia virgata (Cockerell)	(Z)-((1S,3R)-2,2-dimethyl-3-(2-methylprop-1-enyl)cyclopropyl) 2-methylbut-2-enoate	Tabata & Ichiki (2017)	Chrysanthemol ester	C14H22O2
Maconellicoccus hirsutus (Green)	(R)-2,2-dimethyl-3-(1-methylethylidene) cyclobutyl]methyl (S)-2-methylbutanoate	Zhang et al. (2004)	Cyclobutane/ maconelliol ester	C15H26O2
	(R)-2- isopropenyl-5-methyl-4-hexenyl (S)-2-methylbutanoate		Lavandulol ester	C15H26O2
Nipaecoccus viridis (Newstead)	2,2,3,4-tetramethyl-3-cyclopentenyl-methyl isobutyrate	Levi-Zada et al. (2019)	γ-necrodol ester	C14H24O2
Phenacoccus madeirensis Green	trans-(1R,3R)-chrysanthemyl (R)-2-methylbutanoate	Ho et al. (2009)	Chrysanthemol ester	C15H26O2
	(R)-2- isopropenyl-5-methyl-4-hexenyl (R)-2-methylbutanoate		Lavandulol ester	C15H26O2
Phenacoccus solenopsis Tinsley	(2,2-dimethyl-3-isopropylidenecyclobutyl) methyl 3-methyl-2-butenoate	Tabata et al. (2016)	Maconelliol ester	C15H24O2
Planococcus citri (Risso)	(1-R- cis)-(+)-2,2-dimethyl-3-(1-methylethenyl)cyclobutanemethanol acetate	Bierl-Leonhardt et al. (1981)	Cyclobutane/ester	C12H20O2
Planococcus ficus (Signoret)	(S)-5-methyl-2-(prop-1-en-2-yl)-hex-4-enyl 3-methyl-2-butenoate	Hinkens et al. (2001)	Lavandulol ester	C15H24O2
Planococcus kraunhiae (Kuwana)	2-isopropyliden-5- methyl-4-hexen-1-yl butyrate	Sugie et al. (2008)	Lavandulol ester	C14H24O2
Planococcus minor (Maskell)	(E)2-isopropyl-5-methyl-2,4-hexadienyl acetate	Ho et al. (2007)	Lavandulol ester	C12H20O2
Pseudococcus baliteus Lit	2-((S)-1,2,2-trimethyl-3-cyclopentenyl)-2-oxoethyl (S)-2-methylbutyrate	Tabata et al. (2020)	Ester of α-hydroxyketone	C15H24O3
Pseudococcus calceolariae (Maskell)	(1R,2R)-[2,2-dimethyl-3-(2-methylprop-1-enyl)cyclopropyl]methyl (R)-2-acetoxy-3-methylbutanoate	El-Sayed et al. (2010)	Chrysanthemol ester	C17H28O4
Pseudococcus comstocki (Kuwana)	2,6-dimethyl-3-acetoxy-1,5-heptadiene	Negishi et al. (1980)	Lavandulol ester/ norterpenol	C11H18O2
Pseudococcus cryptus Hempel	(1R,3R)-3-isopropenyl-2,2-dimethylcyclobutylmethyl 3-methyl-3-butenoate	Arai et al. (2003)	Cyclobutane/ester	C15H24O2
Pseudococcus longispinus (Targioni Tozzetti)	2-(1,5,5-trimethylcyclopent-2-en-1-yl) ethyl acetate	Millar et al. (2009)	Ester of 1,2,2-trimethylcyclopen-tane	C12H20O2
Pseudococcus maritimus (Ehrhorn)	(R,R)-trans-(3,4,5,5-tetramethylcyclopent-2-en-1-yl)methyl 2-methylpropanoate	Figadere et al. (2007)	α-necrodol ester	C14H24O2
Pseudococcus viburni (Signoret)	(1R,2R,3S)-(2,3,4,4-tetramethylcyclopentyl)methyl acetate	Millar et al. (2005b)	Ester of 2,3,4,4-tetramethylcyclopen-tane	C12H22O2
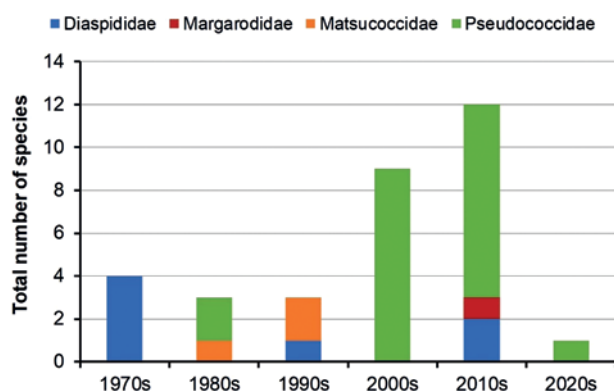
Fig. 1. Evolution of the total number of sex pheromones described for scale species reported by families, from seventies to date.

cal structures belongs to mealybugs (65.6%), followed by armoured scales (21.9%). The recent increase in the pace of pheromone identification is possibly the result of a combination of different factors, including: the growing number of new alien pest scales; the demand for sustainable pest management solutions in response to the increasing social and political pressures for reducing the use of pesticides; and the technological advances on the identification and synthesis of insect pheromones.

3.2 Major patterns in scale sex pheromone structures

Compared with moth sex pheromones, which usually consist of straight-chain 10-18 carbon acetates, aldehydes, and alcohols with 0-3 double bonds (Millar 2000), scale pheromones are mainly terpenoid derivatives with unique skeletons (Zou & Millar 2015). Many of the scale pheromones identified to date are different carboxylic esters of monoterpene, hemiterpene or sesquiterpene alcohols but with a common structural feature, the two units of the alcohol moieties are linked with irregular non-head-to-tail connections, whereas monoterpenes are generally composed of two isoprene units coupled by a regular 1−4' head-to-tail connection (Breitmaier 2006). The resulting skeletons are mainly related to lavandulol(5-methyl-2-isopropenyl-4-hexenol), maconelliol[(2,2-dimethyl-3-isopropylidencyclobutyl)methanol], chrysanthemol[(2,2-dimethyl-3-isobutenylcyclopropyl) methanol], cyclopentylmethanol and necrodane(1,2,2,3,4-pentamethylcyclopentane) derivatives. Interestingly, some patterns are typical from a specific family (Table 1). Acyclic esters of sesquiterpenols are more abundant among the pheromones of the armoured scales, whereas necrodols and esters of lavandulol and chrysanthemol are exclusively found in mealybugs. In contrast, the pheromones of *Matsucoccus* spp. are unsaturated aliphatic ketones and *M. prieskaensis*

possesses a tetramethyl primary alcohol. All armoured-scale and mealybug species whose sex pheromone was identified display a wide range of host plants and their pheromone structures indicate that they come from the terpenoid biosynthetic pathway. On the other hand, *Matsucoccus* spp. develop exclusively on a few closely related pine species and the pattern of their pheromone structures suggests the polyketide biosynthetic pathway (Zou & Millar 2015). The site of production and release of sex pheromones in scales is apparently more variable than in lepidopterans. In the case of moths, it is widely documented that the pheromone production occurs in glands located near the tip of the abdomen through modifications of fatty acid biosynthesis pathways (Jurenka 2003). However, it may differ among scales. In armoured scales, pheromones are produced in glands located in the pygidium and released through the rectum and anus (Moreno et al. 1972; Gullan & Kosztarab 1997). In the case of mealybugs, Williams (1985) suggested that the pheromone source could be the translucent pores on the hind legs of adult females, and more recently this hypothesis was tested experimentally and confirmed by Waterworth et al. (2012).

Despite the mentioned structural similarities among species in the same family of scales, it is likely that the diversification of scale pheromones is not related to the phylogeny. By building a maximum-likelihood phylogenetic tree, Tabata et al. (2017) found that structural similarities of pheromones among mealybug taxa are discordant with their phylogenetic relationships. These authors described the pheromone of *Dysmicoccus brevipes* (Cockerell) as an aldehyde with a cyclopentane but the pheromone of the most closely related species, *D. neobrevipes* Beardsley, is very different. It is an acyclic acetate, more similar to that of *Planococcus minor* (Maskell). Likewise, cyclobutane structures are found in four different genera of mealybugs (*Planococcus, Pseudococcus, Phenacoccus, Maconellicoccus*) and two of armoured scales (*Acutaspis* and *Aspidiotus*). This discordance between phylogeny and chemical structures probably points out that selection has worked on these families of insects to generate chemical signals that can be clearly discriminated from those of closely related taxa for reproductive isolation (Tabata et al. 2017), which can be especially relevant for coccoids, highly sedentary insects that cannot easily change their host.

The only known case of shared structures between scale insect species is (R)-lavandulyl 2-methylbutanoate, one of the pheromone components of the mealybugs *Maconellicoccus hirsutus* (Green) and *Phenacoccus madeirensis* Green, consisting of the same enantiomer of lavandulol, but esterified with different 2-methylbutanoic acid enantiomers (S and R, respectively) (Ho et al. 2009). Zhang et al. (2006) found that the compound in the sex pheromone of *P. madeirensis*, (R) (R)-2-methylbutanoate, was inhibitory for the attraction of *M. hirsutus* to (R)-lavandulyl (S)-2-methylbutanoate. Hence, there is no cross-attraction, suggesting a unique chirality recognition system t-lavandulyl that assures the reproductive isolation of the species.

Many moth pheromones are blends of several compounds that can be shared between species and the species-specific signals are generally produced by mixing these constituents in different ratios, and there are few examples of moths using unique pheromone components, such as the epoxides produced by some geometrid and lymantriid moth species (Millar 2000). However, all sex pheromones reported to date for scales are species-specific chemicals that create singular communication channels, free of any possible interference with the pheromone channel (Millar et al. 2005a). A single compound generally provides a strong activity. In fact, only seven out of the 32 species reported have pheromone blends of two or three compounds. For example, the first sex pheromone described for a scale species was the binary blend of CRS, composed by two different esters of sesquiterpenols (Roelofs et al. 1977). Other species with binary compound blends as sex pheromones are the pink hibiscus mealybug *M. hirsutus*, with esters of lavandulol and maconelliol (Zhang et al. 2004), *P. madeirensis*, with esters of lavandulol and chrysanthemol (Ho et al. 2009), and *Dysmicoccus grassi* (Leonardi), with two esters of lavandulol (de Alfonso et al. 2012). In other species employing binary blends, such as *Matsucoccus josephi* Bodenheimer & Harpaz (Dunkelblum et al. 1993) and *M. feytaudi* (Einhorn et al. 1990), sex pheromones are mixtures of two geometric isomers. The rarest case is the pheromone blend reported for *Comstockaspis perniciosa* (Comstock), which was finally described as a mixture of three compounds: 3-methylene-7-methyl-7-octen-l-yl propanoate and the E/Z geometric isomers of 3,7-dimethyl-2,7-octadien-l-yl propanoate (Gieselmann et al. 1979b; Anderson et al. 1981). Interestingly, for those species producing blends, each compound has independent attractant activity and their combination does not usually have significant additive or synergistic effects (Roelofs et al. 1977; Anderson et al. 1981; Ho et al. 2009). The only exception known is the two-component blend of *M. hirsutus*, with both components needed to attract males to the pheromone source (Zhang et al. 2004).

As Mori reviewed in 2007, bioactivity of pheromones depends on their chirality and usually a single enantiomer is the responsible for the activity. However, this is not the only case and there is a wide diversity in the recognition of chirality by insects, which was mainly classified by Mori (2007) as follows: 1) the opposite enantiomer does not inhibit the activity of the active stereoisomer; 2) the opposite enantiomer inhibits the response to the active enantiomer; 3) the corresponding diastereomer inhibits the response to the active enantiomer; 4) the opposite enantiomer or diastereomer are also active; 5) the natural pheromone is a mixture of enantiomers or diastereomers and all of them are separately active; 6) different enantiomers or diastereomers are employed by different species; 7) both enantiomers are necessary for activity; 8) one enantiomer is more active than the other but their mixture is synergistic. Most scale sex pheromones can be classified in groups (1) and (4). Unnatural stereoisomers

in general have no biological activity or are slightly active (Einhorn et al. 1990; Zhang et al. 2004; Millar et al. 2012; Tabata et al. 2017a; Tabata & Ichiki 2017) and their presence in the mixture does not negatively affect the biological activity of the pheromone. Thus, in many cases it is not necessary to remove the opposite enantiomer generated during pheromone synthesis to be employed in pest management programs and racemates are perfectly active (Hinkens et al. 2001; Zada et al. 2003; El-Sayed et al. 2010; Vacas et al. 2019), which is economically favourable for their implementation. Possible inhibitory effects were reported in a rather few cases: the (S)-isomer of solanone might be responsible for the weak activity of the racemic solanone in the field for *Aulacaspis murrayae* Takahashi (Ho et al. 2014). Similarly, when mixing the unnatural Z-isomer with the *P. minor* pheromone (E-isomer), the effect was inhibitory and the mixture was unattractive, which suggests that stereospecific synthesis of the E-isomer will be required for practical use of this pheromone (Ho et al. 2007).

3.3   Techniques for isolation and identification of scale sex pheromones

The classical methods employed since the 1970s for the isolation and identification of sex pheromones consist mainly of volatile collection and chromatographic techniques. For this purpose, an abundant supply of insects is needed because virgin females of scale species release smaller amounts of pheromone, i.e., 0.2-10 ng/day (Levi-Zada et al. 2014; Tabata & Ichiki 2015; 2016; Vacas et al. 2019) and 75 ng/day as the maximum reported (Tabata et al. 2012), than female moths, which release 0.3-25 ng/h (Lacey & Sanders 1992; Anfora et al. 2005). This implies that tens of thousands (Zada et al. 2003) and even hundreds of millions (Roelofs et al. 1977) of female-day equivalents (quantity of pheromone collected from one female each day) have to be sampled to obtain enough crude quantity that allows isolation of the target compound and the employment of spectroscopic techniques for its identification. To obtain cohorts of virgin females, males have to be eliminated from the population by manually removing their prepupae or pupae, before adult emergence, or treating the rearing substrates with discriminating doses of an insect growth regulator, such as pyriproxifen (Zhang et al. 2004), to prevent males from undergoing full metamorphosis.

Once obtained, cohorts of virgin females are aerated, usually together with the rearing substrate (e.g., pumpkin, squash, germinated broad beans, potato sprouts, citrus fruits, or saplings), by passing a purified or clean air stream through a chamber containing the individuals, for the collection of the volatiles they release on adsorbent materials. These are mainly activated charcoal or different resins, such as Porapak Q, Tenax GC or HayeSep Q. Then, the collected substances are extracted with solvent from the adsorbents and the crude extract is first submitted to fractionation by column chromatography (successively eluting with differ-

ent solvent mixtures), preparative HPLC or preparative GC. The composition of each fraction is studied and candidate compounds are located, guided by biological activity (attraction of males) of each fraction or by comparing the volatile profiles of the extracts from cohorts of virgin females with those of the controls, which can be extracted from cohorts of mated females, immature stages or uninfested rearing substrates.

When the target compound is isolated by HPLC or GC from the crude extract or the corresponding fraction, the elucidation of the pheromone structure is then based on spectroscopic data (MS – mass spectrometry or NMR – nuclear magnetic resonance) and chemical microreactions (e.g., hydrogenation, hydrolysis, esterification, ozonolysis) that allow determining, for example, functional groups, number of unsaturations, and position of double bonds. The confirmatory synthesis of the candidate structure supplies the final proof, when matching synthetic and natural chromatographic and spectroscopic data, coupled with the behavioural assays.

Other techniques of volatile collections, rather than the classical use of adsorbent resins, offer advantages regarding sensitivity. Solid-phase microextraction (SPME) is a sample preparation technique that integrates sampling and concentration, avoiding the use of solvents (Arthur & Pawliszin 1990) and allowing the direct introduction of the sample into the GC injection port. SPME/GC was first employed for the study of airborne pheromones of coleopterans (Malosse et al. 1995), but it is nowadays a widespread technique. More recently, the automated sequential SPME/GC-MS analysis (SSGA), which consists of a programmable GC-MS autosampler equipped with a SPME syringe, has been employed to study pheromones in Lepidoptera (Levi-Zada et al. 2011) and later in mealybugs (Levi-Zada et al. 2014; 2019).

4   Are scales suitable targets for mating disruption?

Only obligate amphimictic insects are potential targets for MD, as facultative or obligate parthenogenesis would deeply reduce the effectiveness of this control tactic. Several species of Margarodidae, Coccidae, Pseudococcidae, and Diaspididae are parthenogenetic (Nur 1971; Miller & Kosztarab 1979; Gullan and Kosztarab 1997), and some species have both sexual and parthenogenetic lineages, including *Aspidiotus nerii* Bouché and *D. brevipes* (Andersen et al. 2014; Tabata et al. 2016). Furthermore, hermaphroditism has been reported in *Icerya* spp. (Margarodidae). However, most scales reproduce sexually, including many species of high economic importance, such as the mealybugs *Planococcus citri* (Risso), *P. ficus, Pseudococcus viburni* (Signoret), *P. calceolariae* (Maskell), and *P. longispinus* (Targioni Tozzetti) (James 1937; Huang et al. 2013; Waterworth et al. 2011; Silva et al. 2013).

Biparental scales have peculiar biological traits that are expected to make them particularly susceptible to MD (Millar et al. 2005a). First, biparental scales are sexually dimorphic. Adult males are delicate, short-lived (few days at most), neometabolic, winged insects, with no functional mouthparts. In contrast, females are wingless and neotenic, and may live for several months, if unmated or when in dormancy (Gullan & Kosztarab 1997; Franco et al. 2009). Scale males seem to display a daily cycle of flight activity. Three different flight patterns have been identified so far: 1) morning flight onsets with sunrise; 2) near sunset; or 3) both in early morning and late afternoon (Rice & Moreno 1970; Moreno et al. 1974; Franco et al. 2009). Recent studies using automated sequential SPME GC−MS analysis (SSGA) showed that the emission of sex pheromone by females of *P. citri, P. ficus,* and *Nipaecoccus viridis* (Newstead) follows a circadian rhythm (Levi-Zada et al. 2014; 2019), in parallel with the daily flight pattern of the males. Thus, mate location flight is limited to a few hours per day and male scales have a narrow window of opportunity to search for females and to mate during their short life, estimated as less than 12 hours in *P. citri*, although males may mate outside this period, if they succeeded in finding receptive females (Silva et al. 2009; 2013; Mendel et al. 2012). This represents an advantage for MD, as a short-time alteration of mate search would deeply impact the reproductive success of scales. As male scales do not feed and thus are not able to replenish their limited energy budget, the existence of a trade-off between flight activity, mating and longevity is expected, as flight is energy-demanding and thoracic flight muscles are expensive to maintain (Denno et al. 1989; Legaspi & Legaspi 1998; Mendel et al. 2012). For example, a trade-off between the number of copulations and longevity was recently demonstrated in *Phenacoccus solenopsis* Tinsley (Tong et al. 2019). Therefore, it is expected that under MD conditions, when exposed to synthetic conspecific pheromone, males may waste their short window of opportunity for mating, by rapidly spending their energy reserves and strongly reducing their chance of mate location and mating performance. Millar et al. (2005a) suggested that the pheromone in scale MD will rapidly exhaust the males, removing them from the system, in a similar manner as an insecticide, but without its negative side effects. Furthermore, knowledge on the existence of a circadian rhythm of female pheromone emission and male flight may allow to improve MD, by programming the daily timing of pheromone release (for example in aerosol spray cans, see 7.1.1), and synchronizing pheromone application with female calling and male flight period, thus reducing the amount of pheromone (dose) needed for scale MD.

Secondly, as male scales are very sensitive to conspecific sex pheromone, it is expected that the necessary amount of pheromone for obtaining an effective control of scale populations in MD will be relatively small (Millar et al. 2005a). As mentioned before (see 3.3), the amount of phero-

mone released by females is much smaller in scales than in lepidopterans.

Thirdly, the prevalence of migration of mated females is considered the most critical trait to estimate pest susceptibility to pheromone-mediated MD (Cardé & Minks 1995). For example, in the case of lepidopteran pests, the possibility of immigration of fertilised females from habitats surrounding MD plots is considered a major constraint of the method (Ioriatti et al. 2008; Ioriatti & Lucchi 2016; Benelli et al. 2019). In such a case, the effectiveness of MD is dependent on its application in relatively large areas, to reduce the perimeter/area ratio of the treated crop, and consequently the likelihood of female immigration, oviposition and damage. However, in the case of scales this is not an issue, as the adult females are sessile and wingless (Millar et al. 2005a). In fact, MD has been shown to be effective in small plots (> 0.5 ha) for both the VMB (Sharon et al. 2016; Mansour et al. 2017b; Cocco et al. 2018) and the CRS (Vacas et al. 2009; 2010).

Other biological traits that may influence the effectiveness of MD in scales will be treated in the section 5. It is known that the success of MD as a pest management tactic is highly dependent on the biological characteristics of the target pest (Gut et al. 2004).

5   Biological traits of scales that may influence the effectiveness of mating disruption

The wingless, and sometimes legless, scale females have limited spreading ability. The dispersal is mostly performed by first-instar nymphs (crawlers), the most mobile stage, displaying morphological and behavioural adaptations for walking and aerial dispersal (Washburn & Washburn 1984). Through wind dispersal, scale crawlers may settle in new host plants up to a few hundred meters from the source (Willard 1974). On the other hand, dispersal by walking is extremely slow and mostly occurs within adjacent plants, as crawlers tend to settle as soon as they find a suitable feeding substrate (Grasswitz & James 2008). The short-range dispersal of nymphs and wingless adult females determines that scale pests usually show an aggregated spatial distribution (Meats & Wheeler 2011; Pérez-Rodríguez et al. 2017; Cocco et al. 2018). Differences in the degree of aggregation depend on species-specific dispersal behaviour, such as thigmotaxis and phototaxis, morphological traits of host plants, and natural enemy-pest interactions (Nestel et al. 1995). Aggregated distribution is a potential constraint for effective MD control of scales, as the odds of short-distance fortuitous male-female encounters are expected to increase in dense colonies.

Scale males show a positive pheromone dose-response up to a certain pheromone concentration (Branco et al. 2006). Therefore, scale aggregation may promote polygyny (i.e., multiple copulations in males), as it is expected that males will be more attracted by large colonies of virgin females,

collectively generating a stronger pheromone signal than single calling females. By locating female colonies, males will increase their chance of multiple mating, minimizing the energy cost of mate searching. This behavioural strategy is particularly beneficial for short-lived insects, such as scale males. A higher number of male copulations and a reduced mating duration and intervals have been observed under laboratory conditions at higher female densities (Silva et al. 2013; Tong et al. 2019).

The population age structure of scales may play a role in MD success. For example, in Sardinia (Italy), the overwintering population of VMB is mainly represented by mated females, which start ovipositing in March-April, before the first flight of males (Lentini et al. 2008). Therefore, MD dispensers, which are usually applied in late April-early May before adult male appearance, are ineffective against the first generation and do not prevent the development of the progeny from overwintering mated females. In this perspective, it is of outmost importance the season-long effectiveness of MD dispensers, as a significant reduction of matings in autumn would significantly reduce the proportion of overwintering mated females.

Sexual communication in biparental scales is mediated by female sex pheromones. The possibility of intraspecific variation in sex pheromone signals has been reported in the VMB. The sex pheromone of the VMB was identified in Californian populations as a single-component pheromone, i.e., (S)-lavandulyl senecioate (Hinkens et al. 2001). Soon afterward, this and a second component, i.e., (S)-lavandulyl isovalerate, were detected in Israeli populations of the mealybug (Zada et al. 2003). Kol-Maimon et al. (2010) showed that VMB males might respond differently to the two-pheromone components, indicating the existence of different male pherotypes. Based on the three possible behavioural responses (attraction, indifference, repulsion) of mealybug males to each of the two components, nine different pherotypes were defined, including fertile male pherotypes indifferent to both pheromone compounds. Kol-Maimon et al. (2010) compared the pherotypes of VMB populations from eastern (Israel) and western (Portugal) Mediterranean and found that the variability of male response was much higher in eastern (9 pherotypes) than in western (5 pherotypes) populations, where no males were attracted to the isovalerate component. This apparent different pherotype composition in Mediterranean populations, indicating a different genetic makeup, is in accordance with the results of the most recent phylogeographic study on the VMB (Daane et al. 2018). The latter study suggested the existence of two major population groups: 1) a European group, originating in Europe, Tunisia and Turkey, which likely spread in Argentina and South Africa; and 2) a Middle East group, from Israel and Egypt, which was introduced in North America and Mexico. Different degrees of responses of CRS males to wild and laboratory-reared virgin females have been also reported (Tashiro et al. 1969).

The existence of male pherotypes in scales may bear practical implications for MD. For example, the effectiveness of the actual MD formulations for the VMB, based on (S)-lavandulyl senecioate, in populations with pherotypes attracted to (S)-lavandulyl isovalerate (e.g., some Israeli populations) may be compromised, as the mating activity of part of males in the mealybug population will not be affected by the pheromone treatment. Furthermore, it is expected that, in such populations, the successive application of MD during several years, will create a selection pressure favouring isovalerate pherotypes, which may alter the genetic structure of local VMB populations and result in resistance to MD.

Scales may exhibit different levels of polyandry (i.e., multiple mating in females) and polygyny. Overall, scale males show high mating capacity under laboratory conditions, when exposed to *ad libitum* virgin females, as they are able to mate multiple times, with relatively short mating intervals between consecutive copulations (James 1937; Tashiro & Moffitt 1968; Mendel et al. 1990; Waterworth et al. 2011; Ricciardi et al. 2019; Silva et al. 2019; Tong et al. 2019). Polygyny, concurrently with scale clumped distribution, may hinder the effectiveness of MD, as a single male may fertilize several females (Silva et al. 2013; 2019; Tong et al. 2019). However, laboratory studies probably overestimated male fecundity. In the field, male performance is expected to be much lower, especially in low population densities, due to the limited energy reserve of males, their short lifespan and the restricted daily flight activity period (Silva et al. 2019). In addition, in mealybug males, the number of copulations decrease over time, likely because of depletion of energy reserves or sperm (Waterworth et al. 2011; Ricciardi et al. 2019).

The possibility of female multiple mating (polyandry) in mealybugs has been recently observed in laboratory conditions (Waterworth et al. 2011; Silva et al. 2013) and confirmed by genotype analysis of *P. citri* eggs produced by single females mated with two males (Seabra et al. 2013). Nevertheless, no data are yet available on the frequency of polyandry in field conditions. *Pseudococcus longispinus* females mated up to 8 times in a single day and subsequent copulations occurred up to 23 days after the first event. However, receptivity may be restricted to a shorter period in other species, such as *P. citri* (Waterworth et al. 2011; Silva et al. 2019). After mating, females of VMB and *P. citri* cease pheromone emission within 48 hours, and CRS females become unattractive within 24 hours (Tashiro & Moffitt 1968; Levi-Zada et al. 2014). The existence of polyandry in scales may have implications in the effectiveness of MD. Effective MD is expected to have more impact on polyandrous than in monandrous females, as in the absence of multiple mating, none of the benefits of polyandry will occur (Silva et al. 2019). Mated females may compete with virgin females thus reducing the male reproductive success (Waterworth et al. 2011). However, this possibility is unlikely under MD conditions, as virgin females are more frequent and more attractive to males than mated ones (Silva et al. 2019). Data collected by Cocco et al. (2014) in MD plots support this hypothesis.

6 Mechanisms explaining the effectiveness of mating disruption in scales

The effectiveness of MD is dependent on both direct and indirect factors. Direct factors are related to the mechanisms involved in the disruption of pheromone-mediated communication between male and female insects (Miller & Gut 2015). Indirect factors include other mechanisms, "when mating disruption does not disrupt mating", such as delayed mating (Mori & Evenden 2013).

Different MD mechanisms have been postulated (Bartell 1982; Cardé & Minks 1995; Miller et al. 2006a), which can be divided in two main categories: competitive and noncompetitive (Miller et al. 2006a). Competitive disruption includes competitive attraction (false-trail-following, confusion), induced allopatry, and induced arrestment, whereas noncompetitive disruption involves other mechanisms, such as suppressed calling/mating, camouflage, sensory imbalance, induced allochrony, and desensitisation (habituation) (Miller & Gut 2015). More than one disruption mechanism may be involved, depending on the type of MD formulation and insect species (Mori & Evenden 2014; Miller & Gut 2015). However, relatively few studies investigated the mechanisms responsible for MD in particular cases (e.g., Flint & Merkle 1983; Lapointe et al. 2009; Rodriguez-Saona et al. 2010; Mori & Evenden 2014). The meta-analysis carried out by Miller et al. (2006b), based on moth sex-pheromone literature, indicated that competitive disruption is the dominant mechanism.

Under MD conditions, other mechanisms unrelated to the disruption of mating may be also involved, such as delayed mating, which may reduce female fitness and thus contribute to MD effectiveness. For example, Mori & Evenden (2013) performed a meta-analysis on the effect of delayed mating in female moth fitness and found a significant decrease in fecundity, fertility, and pre-oviposition period and an increase in female longevity.

To the best of our knowledge, no specific studies were carried out to clarify the type of mechanisms responsible for scale MD. Nevertheless, available data suggest that the involved mechanisms are most likely part of competitive disruption. Suckling et al. (2018) found no experimental evidence of habituation in males of *P. calceolariae,* as no significant differences were observed in male response to sex pheromone lures (100 μg) between males pre-exposed to the sex pheromone (1 mg) for 24 h and control males pre-exposed to clean air. On the other hand, in a flight-tunnel simulating MD conditions (16 pheromone lures distributed in 4 × 4 array, with a virgin female in the centre), males of the same mealybug species showed to be attracted to the

lures (Ricciardi et al. 2019). This behaviour was associated with a significant decrease in female detection, compared to the control (16 rubber septa without pheromone), thus suggesting competitive disruption. Also, maximum CRS captures were obtained in traps baited with pheromone dispensers releasing ca. 300 µg/day (Vacas et al. 2017), whereas the calculated minimal release rate for successful MD treatments is 250 µg/day (Vacas et al. 2010).

As competitive disruption is a "numbers game", its outcome in what concerns pest control is dependent on the ratio between the number of pheromone release points (e.g., dispensers) and the number of virgin females, i.e., it is pest-density-dependent, in contrast with noncompetitive disruption mechanisms, which are pest-density-independent (Miller & Gut 2015). This prediction is in accordance with field results on MD of scales. In fact, Sharon et al. (2016) observed that the effectiveness of MD, in the management of VMB populations, decreased at high pest densities. Therefore, these results also support the hypothesis of competitive disruption.

The fact that no complete shutdown effect (zero captures) has been reported by different authors (e.g., Cocco et al. 2018; Daane et al. 2020; Silva et al. 2020) in male captures registered in pheromone traps installed in MD plots for the VMB is also indirect evidence supporting the hypothesis of competitive disruption mechanisms in scales.

Furthermore, in disruption by competition, it is expected that the additional disruption effect resulting from adding more pheromone dispensers in a certain crop area, to be protected by MD, will diminish with the increasing number of dispensers (Miller & Gut 2015). Experimental results on scale MD also support this prediction. In a two-years experiment on MD of the VMB, Lucchi et al. (2019) found no dose effect on the pheromone application rate, as no significant differences were found in grape damage among 300, 400, and 500 dispensers/ha (i.e., 54, 72, and 90 g/ha of VMB racemic pheromone, respectively). Vacas et al. (2010) compared the application of 420 and 840 dispensers/ha, for MD of CRS, keeping the total release rate in 113 mg/ha/day, and observed no significant differences in fruit damage.

Delayed mating has been reported to occur in scale insect populations under MD. In MD conditions for the VMB, Cocco et al. (2018) observed 18.8-66.2% reduction in the percentage of ovipositing females, a mating delay of 5.5-12.5 days, a significant increase of the pre-oviposition period (up to 12.5 days), and in female longevity, a significant decrease in fertility, and no effect on fecundity. Lentini et al. (2018) studied in laboratory conditions the effect of mating delay on the reproductive performance and population growth rates of the VMB. They concluded that only a mating delay longer than 7 days would lead to a reduction in the population growth rates. In the case of CRS, Vacas et al. (2012) found a significant lower number of gravid females in MD plots, in comparison with control, as well as a delay in the development of CRS instars.

As in MD conditions unmated females live longer, the increase in female longevity is expected also to affect the relative attractiveness of the aging females due to a reduction in the emission rate of the sex pheromone. In fact, Levi-Zada et al. (2014) showed that the females of both *P. citri* and VMB have an age-dependent pattern of sex pheromone emission, with a maximum release rate registered for middle-age females. For example, at 25±1 °C and 13L:11D photoperiod, pheromone emission in *P. citri* started at 4-6 days-old females, reached the maximum at 9-12 days-old females (2 ng/h), and decreased for older females. In the case of VMB, the emission of pheromone also started at 4-6 days-old females and decreased for females older than 20 days. The maximum amount of sex pheromone was released by 10-20 days-old females (1-2 ng/2h). Females of both mealybug species ceased pheromone release after mating (Levi-Zada et al. 2014). According to these data, and for the same conditions, a reduced attractiveness would be expected for unmated females older than 20 days. However, in the case of the VMB, females of 1-28 days old were equally attractive to males in the field (Lentini et al. 2018).

Under MD conditions, semiochemical-mediated interactions between scales and their natural enemies may also contribute to its global effectiveness as a pest management tactic. Sex pheromones and volatile cues of scales elicit kairomonal responses in several parasitoids and predators and are exploited for host/prey selection (Branco et al. 2007; Ishaaya & Horowitz 2009; Pekas et al. 2015; Urbina et al. 2018). For example, the encyrtid *Anagyrus vladimiri* Triapitsyn (= *A.* sp. near *pseudococci*) uses the sex pheromone of the VMB as a chemical cue for host location (Franco et al. 2008; 2011). This kairomonal response of the parasitoid may contribute to enhance biological control of the VMB in MD conditions. In fact, in most of the cases, the level of parasitism of the VMB has been reported to be higher in MD plots compared to control (Walton et al. 2006; Cocco et al. 2014; Shapira et al. 2018). However, the higher parasitism level observed in MD plots may be also related with the higher longevity of VMB females, which are thus expected to be exposed to parasitisation for a longer period. This is apparently the explanation for the increased parasitism of CRS by *Aphytis melinus* DeBach, observed under MD conditions. The presence of the pheromone in MD treated plots was reported to delay the development of CRS allowing a higher parasitism rate compared with untreated plots and a significant higher total predation and parasitism in MD treated plots (Vacas et al. 2012; Vanaclocha et al. 2012). Although the hypothesis that the CRS sex pheromone could attract *A. melinus* was raised by Sternlicht (1973), later Morgan & Hare (1998) found no evidence of a kairomonal response of the parasitoid to the host sex pheromone, in olfactometer experiments. More recently, in field experiments, Pekas et al. (2015) also revealed no attractant effect of CRS pheromone for both *Aphytis lepidosaphes* Compere and *A. melinus*, although a positive response was observed for *A. chrysomphali* Mercet.

7   Development and application of mating disruption formulations in pest management of scales

Here we summarize the accumulated knowledge and recent developments on the implementation of MD for the control of two major scale pests, VMB and CRS, for which this pheromone-based management tactic is already practiced with commercial formulations.

7.1   The vine mealybug

The VMB is the most economically important mealybug species infesting grapevine (*Vitis vinifera* L.) worldwide (Walton & Pringle 2004; Franco et al. 2009; Daane et al. 2012; Reineke & Thiéry 2016; Mansour et al. 2018). The isolation, identification and synthesis of the sex pheromone of the VMB (Hinkens et al. 2001; Millar et al. 2002) allowed its application for pest management purposes. Since then, different MD formulations have been developed, tested and applied for the control of its populations in many grape-growing areas in Europe, North Africa, Middle East, and North and South America (Walton et al. 2006; Miano et al. 2011; Cocco et al. 2014; 2018; Sharon et al. 2016; Mansour et al. 2017b; Lucchi et al. 2019).

7.1.1   Formulations

Over the last two decades, four formulations of MD have been tested and whenever appropriate, implemented as a control tactic against VMB, in different grape-producing areas in Europe, North Africa, Middle East, or America. These formulations exploiting different materials and technologies include (Table 2): 1) sprayable microencapsulated formulation (Checkmate®VMB-F); 2) membrane dispensers (Checkmate®VMB-XL); 3) aerosol spray cans (Puffer®); and 4) rope (reservoir) dispensers (Isonet®PF). A double rope dispenser (Isonet®LPF) is also under evaluation for the combined MD of VMB and the European grapevine moth *Lobesia botrana* (Den. & Schiff.) (Baba et al. 2019; Ricciardi et al. 2021).

7.1.2   Dose effectiveness

The first MD test against VMB was carried out in California table grapes using a sprayable microencapsulated formulation, containing 16.3 and 10.8% of active ingredient (a.i.) by weight of racemic lavandulyl senecioate, in 2003 and 2004, respectively (Walton et al. 2006). Three to four applications of 10.7 g a.i./ha were carried out, between April and August, corresponding to a total of 32.1 g a.i./ha and 53.5 g a.i./ha per season, respectively (Table 2). In addition, a delayed dormant (February) application of chlorpyrifos or an in-season (June) application of buprofezin were carried out in the experiments of 2003 and 2004, respectively. A reduction in trap catches of adult males, mealybug density (only in 2003) and crop damage was obtained, but the formulation showed

a relatively short (3 to 5 weeks) effective lifetime. More recently, Suterra developed a new microencapsulated formulation (Checkmate®VMB-F), which was tested by applying 4-5 monthly pheromone treatments, between late May and early September, at 12.4 g a.i./ha per treatment, corresponding to a total of 49.4-61.8 g a.i./ha per season (Haviland 2017a; 2017b). The possibility of being applied by conventional sprayers, along with insecticides or fungicides (except those containing oil-based products, emulsifiable concentrates or including organosilicone surfactants) and the inexistence of pre-harvest intervals, residues, or international maximum residue limits for exported fruits, constitutes the major advantages of microencapsulated formulations. In addition, the cost of each treatment (Checkmate®VMB-F) corresponds to about 20% of the cost of membrane dispensers (Checkmate®VMB-XL). That is, in the maximal number of five applications per season it has a similar cost to that of membrane dispenser system. As a rule, microencapsulated formulations are not permitted in organic farming. However, some exceptions for its use in organic table grape fields in California have been granted by some organic-certifying organizations in 2019 and 2020 (KCDA 2020).

Membrane dispensers (Checkmate® VMB-XL) loaded with 150 mg of the racemic sex pheromone have been tested against VMB populations in different grapevine regions and using different number of dispensers (Table 2). In California (USA), Langone et al. (2014) applied ca. 400 dispensers per ha (62-93 g a.i./ha), in combination with a delayed dormant application (before pheromone dispenser set up) of chlorpyrifos and a post-harvest treatment of spirotetramat. A total of 620-625 dispensers per ha was tested in Sardinia (Italy) (62.5-93.8 g a.i./ha; Cocco et al. 2014; 2018), Israel (93.8 g a.i./ha; Sharon et al. 2016), and Central-South Tunisia (93 g a.i./ha; Mansour et al. 2017b). In the case of Sardinia, MD was combined with a treatment of chlorpyrifos or lambda-cyhalothrin, and in Tunisia, with imidacloprid. In all experiments, MD significantly reduced male captures in pheromone traps and mealybug densities on grapevines. Field lifetime of pheromone membrane dispensers was estimated to be 130-150 days in Sardinia, with a mean pheromone release rate of 484 mg/ha/day (Cocco et al. 2014; 2018), and 120 days in warmer Central-South Tunisia (Mansour et al. 2017b).

The aerosol spray cans (Puffer®) controlled by programmable chips were also tested against VMB populations, in California vineyards at a rate of ca. 4.9 spray cans per ha, in combination with a delayed dormant application of chlorpyrifos and a post-harvest application of spirotetramat. Spray devices were timed to release 1.3 g a.i./day throughout the entire growing season. In addition, membrane dispensers were installed in the treated plot perimeter, emitting about one-eighth as much pheromone as the aerosol spray cans. Pheromone treated plots showed a reduction in male trap captures and grapevine damage, in comparison with control plots (Langone 2013; Langone et al. 2014).

Table 2. Worldwide application of mating disruption in the control of the vine mealybug (VMB) and California red scale (CRS): formulations and grape-growing areas.

Scale species	Type of formulation	Trade name	Country or region	References
VMB	Sprayable microencapsulated formulation	Checkmate®VMB-F (Suterra LLC)	California (USA)	Daane et al. (2006; 2020); Walton et al. (2006); Haviland (2017a; 2017b)
	Membrane (reservoir) dispensers	Checkmate®VMB-XL (Suterra LLC)	California (USA), Israel, Italy,Tunisia	Cocco et al. (2014; 2018); Langone et al. (2014); Sharon et al. (2016); Mansour et al. (2017a); Daane et al. (2020)
	Aerosol spray cans	Puffer® (Suterra LLC)	California (USA)	Langone et al. (2014)
	Rope dispensers	Isonet®PF (Shin-Etsu Chemical Co. Ltd)	California (USA), Italy	Cocco et al. (2018); Lucchi et al. (2019); Daane et al. (2020)
CRS	Mesoporous dispensers	Scalebur® (EPA SL); Dardo® (Syngenta Agro SA); Masslure®AoAu (Massó)	Spain, Portugal	Vacas et al. (2009; 2010)
	Membrane dispensers	CheckMate®CRS Dispenser (Suterra LCC)	California (USA), Uruguay	Casado et al. (2018)

More recently, pheromone rope dispensers (Isonet® PF) have been tested against VMB in Italian vineyards. Field trials conducted at a dose of 90 g a.i./ha (500 dispensers × 180 mg a.i./ha) resulted in a noteworthy delayed mating and decrease in the number of matings, as the number of ovipositing females was significantly reduced (Cocco et al. 2018). Furthermore, this formulation, applied over consecutive years, significantly reduced VMB density and showed a field lifetime of about 200 days and a release rate of 385 mg/ha/day (Cocco et al. 2018). Similar results were observed in a three-year study in Portugal, with the same dosage (Silva et al. 2020). Lucchi et al. (2019) compared the efficacy of different pheromone dosages, i.e., 300, 400 or 500 rope dispensers per ha (180 mg of racemic lavandulyl senecioate per dispenser, i.e., 54, 72, and 90 g a.i./ha, respectively), in northern and southern Italian vineyards. They observed that all pheromone treatments significantly decreased VMB density on grape bunches, and found no significant differences among dosages. These results suggest that the minimal effective dose for this MD formulation (Isonet®PF) is 300 dispensers per ha.

Recently, based on experiments carried out in California, between 2004 and 2007, Daane et al. (2020) provided further information on the effectiveness of different MD formulations, including sprayable formulation, membrane dispensers and rope dispensers. They concluded that sprayable formulation was slightly more effective than dispensers, for the same pheromone dose.

The new double rope dispenser (Isonet®LPF) was evaluated in 2017 and 2018 by testing 400, 500 and 600 units/ha at three study sites located in Southern (Sicily), Central (Tuscany) and Northern (Veneto) Italy (Ricciardi et al. 2021). Trials were performed by monitoring *L. botrana* and VMB populations in wine and table grape vineyards managed with MD and no-treated control vineyards. MD results showed a significant reduction of the number of infested inflorescences, as well as of the number of *L. botrana* nests and VMB individuals per inflorescence compared with untreated controls. No significant differences were found between the three dosages of Isonet® LPF dispensers. Performing MD against both insect species using a single dispenser reduced the labour costs, the amount of plastic tools used in the field, as well as the insecticide applications.

7.1.3   Timing of mating disruption application

No specific studies have been carried out to determine the optimal application timing of MD. However, most studies on MD of VMB testing membrane and rope dispensers report a field deployment before the first seasonal flight of males (Cocco et al. 2014; 2018; Sharon et al. 2016; Mansour et al. 2017b), which depends on climatic conditions. For example, it usually occurs in March, April, and mid-May in Israel, Central-South Tunisia, and Sardinia (Italy), respectively. Setting up the pheromone treatment before first male flight is in accordance with best practices applied for lepidopteran pests (Ioriatti et al. 2008). In this perspective, it is of outmost importance to consider the season-long effective lifespan of MD dispensers, which as mentioned before was estimated as 120-150 days, in membrane dispensers, and about 200 days, in rope dispensers (Cocco et al. 2014; 2018; Mansour et al. 2017b). In the case of microencapsulated formulations, the effective lifetime is only about 3-5 weeks, which impose up to 5 treatments per year, to cover the whole season (Haviland 2017a; 2017b). Above all, an effective disruption of male-female communication and a consequent reduction of mating activity in autumn are expected to markedly reduce the proportion of overwintering mated females, and thus the size of VMB population escaping MD in the following spring. In

fact, membrane dispensers reduced the percentage of ovipositing females in October to 40-50%, whereas rope dispensers were more effective late in the season by reducing the percentage of matings to 0-10% (Cocco et al. 2018). The reduction of overwintering mated females by MD applied for consecutive years led to an increased effectiveness of this control method resulting in a reduction of VMB density (Sharon et al. 2016; Cocco et al. 2018). The cumulative effectiveness of MD in reducing the population density of VMB is in accordance with findings on lepidopteran pests (Stockel et al. 1994; Varner et al. 2001).

In hot-climate areas, the build-up of VMB populations starts as early as February and up to nine generations per year have been estimated (Sharon et al. 2017). Under such conditions, a single release of pheromone dispensers is not sufficient to disrupt mealybug male activity for the whole season. The application of membrane dispensers twice a year, i.e. February and August, induced a year-round effective MD and a significant reduction of VMB population in the following year (Sharon et al. 2017).

The results of a four-year study carried out in California (Daane et al. 2020) suggested that season-long or late-season coverage of MD is probably more important than the applied pheromone dose, for the control of the VMB.

7.1.4 Compatibility of mating disruption with biological and chemical control

MD is considered a very selective pest management tactic, with no expected negative impact on non-target organisms, as it is based on the use of sex pheromones, which are species-specific semiochemicals. However, in case of parasitoids or predators showing kairomonal responses to the sex pheromone of their host/prey, we may expect some negative side effects. For example, it was expected that the host location process of the parasitoid *A. vladimiri,* which displays a high kairomonal response to VMB sex pheromone, might be disrupted by VMB MD (Franco et al. 2008; 2011). Nevertheless, the experimental data available on MD of the VMB do not support this hypothesis. In fact, experiments showed no significant differences, in the level of parasitisation of VMB by *A. vladimiri,* between MD and control vineyards (Walton et al. 2006), or even an increase of parasitism level in pheromone-treated plots (Daane et al. 2006; Cocco et al. 2014), suggesting that MD does not disrupt parasitism or may even enhance it. More recently, Shapira et al. (2018) tested whether the use of MD to control the VMB and *L. botrana* affects hymenopteran parasitoids and spiders in wine-producing vineyards in Israel. The results showed that MD did not influence the abundance, diversity and community composition of most parasitoids and spiders. The sampled hymenopterans were mainly parasitoids of leafhoppers, whiteflies, leafmining dipterans, and thrips. In the case of the VMB parasitoid *A. vladimiri,* the number of female wasps captured in traps baited with the pheromone of the VMB was significantly lower in MD than in control vineyards.

However, the parasitism of the VMB was only detected in MD vineyards. This apparent contradictory result is most probably explained by a competitive effect between pheromone traps used to monitor *A. vladimiri* and other pheromone sources associated with MD dispensers, in a similar way to that occurring with mealybug males, due to the kairomonal attraction of the parasitoid to the VMB pheromone. Overall, available data clearly indicate that MD is compatible and may even enhance biological control of the VMB and other grapevine pests.

As in moth pest species (Cardé & Minks 1995), the effectiveness of MD in the control of VMB populations is density-dependent, as its efficacy decreases at high pest densities (Sharon et al. 2016). Therefore, at moderate-high VMB densities MD should be combined with chemical or biological control tactics, following an IPM approach (Mansour et al. 2017b; 2018; Lucchi & Benelli 2018). In fact, MD of the VMB has been often associated with insecticide applications in IPM programs. All the available formulations increased the effectiveness of insecticides commonly used in VMB control, namely chlorpyrifos, buprofezin, imidacloprid, and spirotetramat (Walton et al. 2006; Cocco et al. 2014; 2018; Langone et al. 2014; Haviland 2017a; Mansour et al. 2017b, 2018). Nonetheless, MD was effective in reducing the mealybug density also as a stand-alone control tactic (Sharon et al. 2016; Lucchi et al. 2019).

7.2 California red scale

Once the pheromone of CRS was identified, it was used for the monitoring of the scale. The first trials of MD were conducted in the early 1980s, using rubber septa pheromone dispensers (Barzakay et al. 1986; Hefetz et al. 1988). These dispensers were loaded with low amounts of pheromone (below 6 mg) and needed replacement every 2 months. Although the treatment reached male capture reduction in monitoring traps, the efficacy in terms of pest damage reduction was not proved. Later, in the early 2000s, a new formulation with 0.4 mg/dispensers was registered by the United States EPA and commercialised under the name Red Scale Down™. These dispensers installed at a density of 250 units per ha, and replaced every 3 months, showed low to moderate efficacy in orchards with low infestation levels (Sousa et al. 2008). Twenty years after the first tests, MD studies were started over in Spain employing mesoporous dispensers and using pheromone loads over 50 mg per dispenser (Vacas et al. 2009).

7.2.1 Formulations

There are currently two main formulations commercially available for MD of CRS (Table 2): mesoporous and membrane dispensers. Both types of formulations are passive dispensers (usually applied at a rate of 300-600 units per ha), in which the pheromone is continuously released, regardless of the time of day or the pest flight activity.

Mesoporous dispensers were developed by Vacas et al. (2009), consisting of cylindrical tablets of clay material on which the pheromone is retained, not only by physical methods, but also by the chemical interaction of the emitter matrix with the pheromone (Domínguez-Ruiz et al. 2008). These dispensers have been available in the market with several trademarks, such as Scalebur® (EPA SL), Dardo® (Syngenta Agro SA) and, more recently, Masslure®AoAu (Massó) (Table 2). They exhibit good performance during long periods and are less temperature-dependent compared with rubber septa or polymeric dispensers (Domínguez-Ruiz et al. 2008). It should be taken into account that a temperature-dependent dispenser wastes a high amount of pheromone in the warmer hours of the day when the flight activity of CRS males is very low (Gieselmann 1990). The main disadvantage of these mesoporous dispensers is the affinity that some corvid birds, especially magpies, have for the pheromone tablets. In areas where these birds are abundant, the dispensers are pecked and thrown to the ground, with the consequent loss of pheromone sources and efficacy of the treatment.

Membrane dispensers are based in a plastic recipient containing the pheromone, with a semipermeable membrane that regulates its emission. They are commercially available as CheckMate®CRS Dispenser (Suterra LCC) (Table 2). This kind of dispenser is more sensitive to high range temperature variations, although their average pheromone release rate is substantially constant under the typical temperatures of Mediterranean climates where citrus crops are cultivated.

7.2.2   Dose effectiveness

Several studies have been carried out to calculate the quantity of pheromone required for an effective MD of CRS, but the information about dispensers' release rate was not always complete. First field trials conducted by Hefetz et al. (1988) demonstrated that a reduction of male captures was achieved by placing 400 rubber septa per ha, with a total load of 30 mg of pheromone per tree, for the whole season. However, no data on the quantity of pheromone released were given. In studies carried out with rubber septa emitters, the amount of residual pheromone after 2-3 months varied between 36% (McQuate et al. 2019) and 72% (Smit et al. 1997). Even in a longer period of 6 months, rubber septa loaded with pheromones could contain up to 71% of initial load (Zhang et al. 2013). Taking the most unfavourable scenario, we could ensure that the pheromone emitters described by Hefetz et al (1988) would contain at least one third of their initial charge at the end of their useful life. Calculating a total pheromone dose of 12 g/ha/season and considering one third of residual pheromone not emitted, we can assume that 8 g/ha/season (6 months) were effectively released, with a mean rate of 44 mg/ha/day to reach the MD showed in this work. However, no fruit damage assessments were performed and the effect of MD was only evaluated regarding male capture reduction in pheromone traps placed in the treated vs. control area.

A second work demonstrated that a pheromone release rate over 105 mg/ha/day was the most suitable to reach effective MD (Vacas et al. 2009). Results showed that release rates of 16.8 mg/ha/day did not originate male catch reduction in monitoring traps, whereas release rates of 42 mg/ha/day achieved moderate male catch reduction, but the level of MD in the last case was not enough to reduce fruit damage in the pheromone-treated areas. Another study conducted in commercial orchards demonstrated that release rates of 113 mg/ha/day were more effective than oil treatments, achieving 70% fruit damage reduction in the MD treated plots, during the first year of treatment (Vacas et al. 2010).

In the trials described above, the number of dispensers per tree was one, with a plant density of 400-450 trees per ha. Hefetz et al. (1988) suggested that using four dispensers per tree, with a quarter of the pheromone load, and maintaining the total dose of pheromone, could lead to a higher reduction in male catches. Vacas et al. (2010), in MD trials with a pheromone release rate of 113 mg/ha/day, registered no significant differences in fruit damage between 420 and 840 dispensers per ha. Therefore, a single dispenser per tree is sufficient for effective MD, with dispenser densities over 400/ha and ensuring a pheromone release rate over 113 mg/ha/day.

7.2.3   Timing of mating disruption application

The date of dispenser deployment is always a key point for the success of MD. A general rule in case of moth pests is setting up the dispensers before the first generation male flight, to prevent early potential mating and the build-up of the population. However, this rule has not been demonstrated in other insects, including scales. In CRS, this may not be the best strategy. CRS can complete three to five generations per year (Grout et al. 1989). In the Mediterranean region, three generations usually occur and a possible fourth generation could take place in some areas and warmer autumns. First male flight takes place in spring and CRS populations in the first generation usually show low densities, whereas the third and occasional fourth generations are abundant and directly responsible for fruit infestation, in most cases. Vacas et al. (2015) conducted a two-year study to adjust the timing of dispenser application and assess the importance of controlling the first generation of CRS. Results demonstrated that the control of the first CRS generation is not essential for achieving a good efficacy, and applying the pheromone just before the second male flight can generate at least the same efficacy. Furthermore, considering that there is a period of 30-40 days without male activity, between the first and the second CRS male flights, dispenser deployment before the first flight will originate a wasting of about 2 months of pheromone emission, when compared with the application before the second male flight. Therefore, according to the results obtained by Vacas et al. (2015), between the two timing options for MD of CRS, i.e., disrupting the first generation or completely disrupting the third or even the fourth generation, the last one seems to be the optimal management tactic.

Another point to consider is the cumulative effect of MD. One of the main advantages of MD is the reduction of pest populations year after year (Cardé & Minsk 1995). This cumulative effect can only be achieved if MD is acting during the main part of the pest population growth. For this reason, when the cost of the pheromone or the lifespan of the dispensers do not allow keeping them active in the field during the whole year, the deployment of pheromone dispensers should be timed to cover the generations that are most responsible for population growth, that is the third and fourth generations, in the case of CRS.

7.2.4 Plot shape and size requirements for mating disruption

The minimum size of the treated plots and the distance to untreated areas are also important factors for MD success. Although the migration of fertile females from outside the pheromone-treated plots is not an issue in CRS, as the females are sessile, the airborne pheromone concentration is lower in the edge of the treated plots, and thus males may be able to find receptive females and mate. In field trials conducted by Vacas et al. (2009), a buffer area of 15 m around the treated plot was delimited to obtain the best performance of CRS MD. However, in the case of plots treated with MD at the lowest pheromone doses, a higher fruit damage was observed in the buffer area. For this edge effect, MD treatment is not recommended in plots of less than 0.5 ha and it is necessary to avoid narrow and elongated shapes that do not allow fulfilling the requirements of the edges.

7.2.5 Compatibility of mating disruption with biological and chemical control

It is important to know whether and how MD treatment can influence mortality caused by parasitoids (mainly *A. melinus*) and predators (e.g., *Rhyzobius lophanthae* (Blaisdell)) of CRS. As mentioned earlier, the hypothesis raised by Sternlicht (1973) that CRS sex pheromone could attract *Aphytis* species was confirmed for *A. chrysomphali*, an endemic parasitoid of the Mediterranean area (Pekas et al. 2015). In contrast, no attractant effect was detected for the main *Aphytis* species, *A. melinus* and *A. lepidosaphes*. In the same way, Morgan & Hare (1998) and Vacas et al. (2012) demonstrated that the presence of CRS pheromone in the environment does not affect *A. melinus* mating behaviour or its capacity to parasitize or feed on CRS. Moreover, the presence of the pheromone in MD plots was reported to delay the development of CRS, allowing a higher parasitism rate compared with untreated plots and a significant higher total predation and parasitism in MD plots (Vacas et al. 2012, Vanaclocha et al. 2012)

Another important point to highlight is the high compatibility of MD with chemical control. In fact, several studies demonstrated that MD efficacy is always higher with low to medium pest pressure due to the accidental encounters between males and females that occur when the popula-

tions are very high in competitive mating disruption, as it has been described in section 6 (Sharon et al. 2016). In such high populations, Vacas et al. (2010) showed that a chemical treatment (e.g., mineral oil) in the first CRS generation, combined with MD in the second and third generations engendered better results than chemical or MD treatments alone.

8 Actual worldwide use of mating disruption against scales

Mating disruption is currently applied worldwide in about 184,500 ha against VMB (129,500 ha) and CRS (55,000 ha). Suterra formulations for the VMB (CheckMate®VMB-XL, CheckMate®VMB-F) are used in ca. 120,000 ha, mostly (more than 100,000 ha) in California, but also in Argentina, Uruguay, South Africa, Spain, and Italy, among other countries. In California, the most used product is the microencapsulated formulation CheckMate®VMB-F. CheckMate®VMB-XL has been available since 2010 and was the first registered product worldwide in California (Suterra LLC, pers. comm. 2020). In Europe, MD of VMB using Shin-Etsu formulation Isonet®PF is employed in 9,500 ha, namely in Italy (6,000 ha), Spain (3,000 ha), and Greece (500 ha) (Shin-Etsu Chemical Co. Ltd, pers. comm. 2020).

In relation to CRS, Suterra formulations are applied in ca. 50,000 ha worldwide. Most of that area is covered by CheckMate®CRS, especially in the USA. In California, where it has been registered since April 2016, this product has been used in more than 40,000 ha. It is available or under registration process in the main citrus-producing countries of Latin America and South Africa and is expected to be also available soon in some Southern European countries. Suterra produces another passive dispenser that is commercialised only in Spain, as well as an aerosol formulation that is seldom used in California (Suterra LLC, pers. comm. 2020). In Spain, MD is applied against CRS in ca. 5,000 ha, using different trademark formulations, such as Dardo (Syngenta), Scalebur (EPA SL) and Masslure (Massó). MD formulations for CRS have been registered in Europe since December 2016 (EPA SL, pers. comm. 2020).

9 Future prospects

New developments were registered recently for *Planococcus kraunhiae* (Kuwana), *P. calceolariae, P. solenopsis*, and *C. perniciosa* (Tabata et al. 2015; Ricciardi et al. 2019; Kinsho & Fujii 2020; Tabata 2020; Waqas et al. 2020), However, the exploitation of MD as a sustainable approach for the management of VMB and CRS, the abovementioned species or other major, biparental scale pests depends on future developments on technological, scientific and legal aspects, such as economic synthesis of pheromones, availability of efficient formulations, clarification of MD mechanisms, and

suitable registration procedures. That is, all aspects that may improve MD effectiveness facilitate its practical application and reduce the costs.

The cost of synthetic pheromones is often regarded as the key limiting factor for MD. In the case of scales, several species have pheromones that are structurally complex and difficult to synthesize at the industrial level, which may compromise practical application of MD (Rodriguez-Saona et al. 2009; Tabata 2020). Therefore, technological advances simplifying the methods used for the synthesis of scale pheromones, such as the invention of a new synthetic method for the lavandulol-related pheromones, e.g., VMB and *P. krauniae* (Tabata 2020), can be of critical importance. The level of purity in synthetic pheromones may also influence production cost, as increasing purity requires more rigorous distillation processes (Hinkens et al. 2001). Daane et al. (2020) recently obtained similar efficacy in field trials using 99% and 95% chemically pure racemic lavandulyl senecioate in MD against the VMB.

The development of more efficient formulations, less temperature-dependent and with a longer effective lifespan, should be further explored. For example, the release rate of pheromone from dispensers can be adjusted through membrane permeability (Daane et al. 2020). Multispecies formulations, such as Isonet® LPF (Ricciardi et al. 2021), are another approach, which may contribute to reducing application costs of MD. Suckling et al. (2016) reported an average return on investment of six to one in the use of a multispecies formulation (ISOMATE® 4-Play™) for MD of the codling moth *Cydia pomonella* (L.) and several leafrollers in New Zealand. The use of aerosol spray cans for MD in scales deserves further investigation, as this type of formulation has advantages over passive formulations, including lower application cost, and the possibility of synchronizing the pheromone release with the period of circadian activity of the target pest (Benelli et al. 2019; Daane et al. 2020). As mentioned earlier, male flight activity and female emission of pheromone in scales are limited to a few hours per day.

Further studies are also needed for optimising the pheromone dose (e.g., dependent on the number of dispensers per ha and pheromone load of each dispenser; or the number of applications per season and the application rate, in the case of flowable formulations), and better defining the seasonal coverage of MD in scales (i.e., identification of critical periods, optimisation of coverage strategy; Daane et al. 2020).

The elucidation of MD mechanisms in scales, besides the scientific interest per se, has important practical implications. For example, in competitive disruption, which is pest-density-dependent, the suppression of pest reproduction is not expected in high population densities, whereas in non-competitive disruption mating will be strongly suppressed even in high pest pressure. Further related examples are discussed by Miller & Gut (2015).

Finally, further developments in legal aspects related with MD formulations are still needed to facilitate their reg-istration and use, as part of the global trend aiming to reduce our dependence on pesticides (Lechenet et al. 2017; Brühl & Zaller 2019; Möhring et al. 2020). Regulatory requirements for pheromones should take into consideration the expected low risk for human health and environment of these semiochemicals, due to their specific properties, namely the specificity, the use in low doses close to natural concentrations, and the rapid dissipation and/or degradation (European Commission 2016). In the USA, pheromones are considered biopesticides, which generally require much less data to register than a conventional pesticide. In fact, new biopesticides are often registered in less than a year, compared with an average of more than three years for conventional pesticides (EPA 2020). However, in Europe, pheromones are classified as Plant Protection Products and fall under Regulation 1107/2009, which has been mainly designed for classical synthetic pesticides and does not completely consider the specific nature of pheromones, although the registration process of Straight Chain Lepidopteran Pheromones has been simplified (European Commission 2014). Nevertheless, this is not the case for other groups, including scale pheromones. For example, the registration process for the approval of the VMB pheromone for MD in Europe started four years ago and is still in progress (EFSA 2020).

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