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Additional Information

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3 Short title: Developments in mating disruption of scales

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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 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, 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

72   implementation of MD, for a sustainable management of this economically important group

73   of plant insect pests.

2   Economic importance of scale insects

75   Scale insects or coccoids (hereafter designated as scales) are small, cryptic, piercing-

76   sucking hemipterans, mostly feeding on phloem sap, comprising more than 8,300 species,

77   distributed among 55 families and 1,214 genera (Garcia Morales et al. 2016). Scales

78   include serious pests of various agricultural, forest, and ornamental plants (Kosztarab 1996;

79   Franco et al. 2009; Garcia Morales et al. 2016; Mansour et al. 2017a). The majority of

80   economically important species belong to the two largest families, i.e., armoured scales

81   (Diaspididae, 32% of scale species) and mealybugs (Pseudococcidae, 24% of scale

82   species). The California red scale (CRS) *Aonidiella aurantii* (Maskell) (Diaspididae), the

83   maritime pine bast scale *Matsucoccus feytaudi* Ducasse (Matsucoccidae), and the

84   Bougainvillea mealybug *Phenacoccus peruvianus* Granara de Willink (Pseudococcidae) are

85   examples of important pest scales of *Citrus* spp., *Pinus pinaster* Aiton*, Bougainvillea* spp.

86   and other ornamental plants, respectively (Mendel et al. 2003; Franco et al. 2006; Beltrà et

87   al. 2010).

88   Direct damage is inflicted by feeding activity, as plant sap ingestion and injection of toxic

89   saliva components may result in leaf and fruit discoloration, defoliation, flower and fruit

90   drop, reduction of fruit growth rate, distortion of leaves, new shoots and fruits, and

91   reduction of plant vigour, leading to plant death in extreme cases (Kosztarab 1996; Franco

92   et al. 2009). Indirect damage is the result of honeydew excretion and development of sooty

93   mould (except for Diaspididae), which may reduce photosynthesis and plant growth.

94   Honeydew often attracts ants, which may disrupt the activity of natural enemies and

95   facilitate the spread of scales on the crop (Franco et al. 2009; Quesada et al. 2018). Some

96   scales, mainly mealybugs, are also vectors of plant viruses (Nault 1997; Perilla-Henao &

97   Casteel 2016). For example, several mealybug species, including the vine mealybug

98   (hereafter notated as VMB) *Planococcus ficus* (Signoret) and soft scales (Coccidae) have

99   been recognised as vectors of Grapevine leafroll-associated viruses (GLRaV) (Tsai et al.

100   2008; Mahfoudhi et al. 2009). GLRaV is the most economically important viral disease of

101   grapevines in many producing regions in the world, with an estimated loss of about

102   $25,000 - $40,000 per hectare, if no control measures are applied (Atallah et al. 2012).

103   Pest status of a scale is often associated with invasive species. Outside their native range,

104   the populations of invasive scales usually profit from the absence of their natural enemies

105   and, without natural control, often originate outbreaks and economic damage. Some

106   biological traits may favour the invasiveness of scales. Their small size and cryptic

107   behaviour make them difficult to detect in quarantine inspections. Also, parthenogenetic

108   reproduction in some species and high fecundity (e.g., some scales may oviposit up to

109   8,000 eggs) facilitate the establishment of scales in new territories based on just a few

110   females (Pellizzari & Germain 2010). For example, from the 256 scale species considered

111   as pests in the USA, about 75% are non-native, representing 25% of the total number of

112   scale species known in the country (Miller et al. 2005). In Europe, alien species represent

113   near 30% of scale fauna (Pellizzari & Germain 2010) and the EPPO A1 list of pests

114   recommended for regulation as quarantine pests include four scale species, i.e., *Ripersiella*

115   *hibisci* (Kawai & Takagi) (Pseudococcidae), *Margarodes prieskaensis* (Jakubski)*, M. vitis*

116   (Philippi) and *M. vredendalensis* De Klerk (Margarodidae) (EPPO 2020). *Ripersiella*

117   *hibisci* and *Margarodes* spp. are considered a serious phytosanitary risk to potted plants

118   and vineyards in the EPPO region, respectively.

119   The main pathway of introduction of alien scales is the horticultural and ornamental trade.

120   It is expected that the growth of global trade will contribute to an increase in the number of

121   new introductions. The observed trend in Europe of the mean number of new alien scales

122   per year corroborates this prediction: 0.7 new alien species per year, in the period 1950-

123   1974; 1.2 in 1975-1999; and 1.3 in 2000-2007 (Pellizzari & Germain 2010). Among these,

124   new alien scales can have a high economic impact. For example, the South African

125   mealybug *Delottococcus aberiae* (De Lotto) was detected in 2009 in Eastern Spain, causing

126   serious damage to citrus crops (Beltrà et al. 2015). Since then, it has been expanding its

127   geographical distribution in the country. Recently, the Farmers Association of Valencia

128   (AVA-ASAJA) estimated that the direct losses from *D. aberiae* in 2020 will be reaching

129   113 million € (PHYTOMA 2020).

130   **3   Identification and analysis of scale sex pheromones**

131   **3.1 Scale sex pheromones identified**

132   Most scales reproduce sexually. The females produce sex pheromone to attract the

133   conspecific males. Specifically, the pheromone chemical structure of 32 scale species

134   belonging to the families Diaspididae, Matsucoccidae, Margarodidae, and Pseudococcidae

135   has been reported to date (see Tab. 1 for references). This number has been increasing

136   enormously since the 2000s, with 68% of these structures reported in the last 20 years (Fig.

137   1). The highest number of reported chemical structures belongs to mealybugs (65.6%),

138   followed by armoured scales (21.9%). The recent increase in the pace of pheromone

139   identification is possibly the result of a combination of different factors, including: the

140   growing number of new alien pest scales; the demand for sustainable pest management

141   solutions in response to the increasing social and political pressures for reducing the use of

142   pesticides; and the technological advances on the identification and synthesis of insect

143   pheromones.

144

145   **3.2 Major patterns in scale sex pheromone structures**

146   Compared with moth sex pheromones, which usually consist of straight-chain 10–18

147   carbon acetates, aldehydes, and alcohols with 0–3 double bonds (Millar 2000), scale

148   pheromones are mainly terpenoid derivatives with unique skeletons (Zou & Millar 2015).

149   Many of the scale pheromones identified to date are different carboxylic esters of

150   monoterpene, hemiterpene or sesquiterpene alcohols but with a common structural feature,

151   the two units of the alcohol moieties are linked with irregular non-head-to-tail connections,

152   whereas monoterpenes are generally composed of two isoprene units coupled by a regular

153   1−4' head-to-tail connection (Breitmaier 2006). The resulting skeletons are mainly related

154   to lavandulol(5-methyl-2-isopropenyl-4-hexenol), maconelliol[(2,2-dimethyl-3-

155   isopropylidencyclobutyl)methanol], chrysanthemol[(2,2-dimethyl-3-

156   isobutenylcyclopropyl)methanol], cyclopentylmethanol and necrodane(1,2,2,3,4-

157   pentamethylcyclopentane) derivatives. Interestingly, some patterns are typical from a

158   specific family (Tab. 1). Acyclic esters of sesquiterpenols are more abundant among the

159   pheromones of the armoured scales, whereas necrodols and esters of lavandulol and

160   chrysanthemol are exclusively found in mealybugs. In contrast, the pheromones of

161   *Matsucoccus* spp. are unsaturated aliphatic ketones and *M. prieskaensis* possesses a

162   tetramethyl primary alcohol. All armoured-scale and mealybug species whose sex

163   pheromone was identified display a wide range of host plants and their pheromone

164   structures indicate that they come from the terpenoid biosynthetic pathway. On the other

165   hand, *Matsucoccus* spp. develop exclusively on a few closely related pine species and the

166   pattern of their pheromone structures suggests the polyketide biosynthetic pathway (Zou &

167   Millar 2015). The site of production and release of sex pheromones in scales is apparently

168   more variable than in lepidopterans. In the case of moths, it is widely documented that the

169   pheromone production occurs in glands located near the tip of the abdomen through

170   modifications of fatty acid biosynthesis pathways (Jurenka 2003). However, it may differ

171   among scales. In armoured scales, pheromones are produced in glands located in the

172   pygidium and released through the rectum and anus (Moreno et al. 1972; Gullan &

173   Kosztarab 1997). In the case of mealybugs, Williams (1985) suggested that the pheromone

174   source could be the translucent pores on the hind legs of adult females, and more recently

175   this hypothesis was tested experimentally and confirmed by Waterworth et al. (2012).

176   Despite the mentioned structural similarities among species in the same family of scales, it

177   is likely that the diversification of scale pheromones is not related to the phylogeny. By

178   building a maximum-likelihood phylogenetic tree, Tabata et al. (2017) found that structural

179   similarities of pheromones among mealybug taxa are discordant with their phylogenetic

180   relationships. These authors described the pheromone of *Dysmicoccus brevipes* (Cockerell)

181   as an aldehyde with a cyclopentane but the pheromone of the most closely related species,

182   *D. neobrevipes* Beardsley, is very different. It is an acyclic acetate, more similar to that of

183   *Planococcus minor* (Maskell). Likewise, cyclobutane structures are found in four different

184   genera of mealybugs (*Planococcus*, *Pseudococcus*, *Phenacoccus*, *Maconellicoccus*) and

185   two of armoured scales (*Acutaspis* and *Aspidiotus*). This discordance between phylogeny

186   and chemical structures probably points out that selection has worked on these families of

187   insects to generate chemical signals that can be clearly discriminated from those of closely

188   related taxa for reproductive isolation (Tabata et al. 2017), which can be especially relevant

189   for coccoids, highly sedentary insects that cannot easily change their host.

190   The only known case of shared structures between scale insect species is (R)-lavandulyl 2-

191   methylbutanoate, one of the pheromone components of the mealybugs *Maconellicoccus*

192   *hirsutus* (Green) and *Phenacoccus madeirensis* Green, consisting of the same enantiomer of

193   lavandulol, but esterified with different 2-methylbutanoic acid enantiomers (S and R,

194   respectively) (Ho et al. 2009). Zhang et al. (2006) found that the compound in the sex

195   pheromone of *P. madeirensis*, (R) (R)-2-methylbutanoate, was inhibitory for the attraction

196   of *M. hirsutus* to (R)-lavandulyl (S)-2-methylbutanoate. Hence, there is no cross-attraction,

197   suggesting a unique chirality recognition system t-lavandulyl that assures the reproductive

198   isolation of the species.

199   Many moth pheromones are blends of several compounds that can be shared between

200   species and the species-specific signals are generally produced by mixing these constituents

201   in different ratios, and there are few examples of moths using unique pheromone

202   components, such as the epoxides produced by some geometrid and lymantriid moth

203   species (Millar 2000). However, all sex pheromones reported to date for scales are species-

204   specific chemicals that create singular communication channels, free of any possible

205   interference with the pheromone channel (Millar et al. 2005a). A single compound

206   generally provides a strong activity. In fact, only seven out of the 32 species reported have

207   pheromone blends of two or three compounds. For example, the first sex pheromone

208   described for a scale species was the binary blend of CRS, composed by two different

209   esters of sesquiterpenols (Roelofs et al. 1977). Other species with binary compound blends

210   as sex pheromones are the pink hibiscus mealybug *M. hirsutus*, with esters of lavandulol

211   and maconelliol (Zhang et al. 2004), *P. madeirensis,* with esters of lavandulol and

212   chrysanthemol (Ho et al. 2009), and *Dysmicoccus grassi* (Leonardi), with two esters of

213   lavandulol (de Alfonso et al. 2012). In other species employing binary blends, such as

214   *Matsucoccus josephi* Bodenheimer & Harpaz (Dunkelblum et al. 1993) and *M. feytaudi*

215   (Einhorn et al. 1990), sex pheromones are mixtures of two geometric isomers. The rarest

216   case is the pheromone blend reported for *Comstockaspis perniciosa* (Comstock), which was

217   finally described as a mixture of three compounds: 3-methylene-7- methyl-7-octen-l-yl

218   propanoate and the E/Z geometric isomers of 3,7-dimethyl-2,7-octadien-l-yl propanoate

219   (Gieselmann et al. 1979b; Anderson et al. 1981). Interestingly, for those species producing

220   blends, each compound has independent attractant activity and their combination does not

221 usually have significant additive or synergistic effects (Roelofs et al. 1977; Anderson et al.

222 1981; Ho et al. 2009). The only exception known is the two-component blend of *M.*

223 *hirsutus*, with both components needed to attract males to the pheromone source (Zhang et

224 al. 2004).

225 As Mori reviewed in 2007, bioactivity of pheromones depends on their chirality and

226 usually a single enantiomer is the responsible for the activity. However, this is not the only

227 case and there is a wide diversity in the recognition of chirality by insects, which was

228 mainly classified by Mori (2007) as follows: 1) the opposite enantiomer does not inhibit the

229 activity of the active stereoisomer; 2) the opposite enantiomer inhibits the response to the

230 active enantiomer; 3) the corresponding diastereomer inhibits the response to the active

231 enantiomer; 4) the opposite enantiomer or diastereomer are also active; 5) the natural

232 pheromone is a mixture of enantiomers or diastereomers and all of them are separately

233 active; 6) different enantiomers or diastereomers are employed by different species; 7) both

234 enantiomers are necessary for activity; 8) one enantiomer is more active than the other but

235 their mixture is synergistic. Most scale sex pheromones can be classified in groups (1) and

236 (4). Unnatural stereoisomers in general have no biological activity or are slightly active

237 (Einhorn et al. 1990; Zhang et al. 2004; Millar et al. 2012; Tabata et al. 2017a; Tabata &

238 Ichiki 2017) and their presence in the mixture does not negatively affect the biological

239 activity of the pheromone. Thus, in many cases it is not necessary to remove the opposite

240 enantiomer generated during pheromone synthesis to be employed in pest management

241 programs and racemates are perfectly active (Hinkens et al. 2001; Zada et al. 2003; El-

242 Sayed et al. 2010; Vacas et al. 2019), which is economically favourable for their

243 implementation. Possible inhibitory effects were reported in a rather few cases: the (S)-

244 isomer of solanone might be responsible for the weak activity of the racemic solanone in

245 the field for *Aulacaspis murrayae* Takahashi (Ho et al. 2014). Similarly, when mixing the

246   unnatural Z-isomer with the *P. minor* pheromone (E-isomer), the effect was inhibitory and

247   the mixture was unattractive, which suggests that stereospecific synthesis of the E-isomer

248   will be required for practical use of this pheromone (Ho et al. 2007).

249

250   **3.3 Techniques for isolation and identification of scale sex pheromones**

251   The classical methods employed since the 1970s for the isolation and identification of sex

252   pheromones consist mainly of volatile collection and chromatographic techniques. For this

253   purpose, an abundant supply of insects is needed because virgin females of scale species

254   release smaller amounts of pheromone, i.e., 0.2-10 ng/day (Levi-Zada et al. 2014; Tabata &

255   Ichiki 2015; 2016; Vacas et al. 2019) and 75 ng/day as the maximum reported (Tabata et al.

256   2012), than female moths, which release 0.3-25 ng/h (Lacey & Sanders 1992; Anfora et al.

257   2005). This implies that tens of thousands (Zada et al. 2003) and even hundreds of millions

258   (Roelofs et al. 1977) of female-day equivalents (quantity of pheromone collected from one

259   female each day) have to be sampled to obtain enough crude quantity that allows isolation

260   of the target compound and the employment of spectroscopic techniques for its

261   identification. To obtain cohorts of virgin females, males have to be eliminated from the

262   population by manually removing their prepupae or pupae, before adult emergence, or

263   treating the rearing substrates with discriminating doses of an insect growth regulator, such

264   as pyriproxifen (Zhang et al. 2004), to prevent males from undergoing full metamorphosis.

265   Once obtained, cohorts of virgin females are aerated, usually together with the rearing

266   substrate (e.g., pumpkin, squash, germinated broad beans, potato sprouts, citrus fruits, or

267   saplings), by passing a purified or clean air stream through a chamber containing the

268   individuals, for the collection of the volatiles they release on adsorbent materials. These are

269   mainly activated charcoal or different resins, such as Porapak Q, Tenax GC or HayeSep Q.

270   Then, the collected substances are extracted with solvent from the adsorbents and the crude

271   extract is first submitted to fractionation by column chromatography (successively eluting

272   with different solvent mixtures), preparative HPLC or preparative GC. The composition of

273   each fraction is studied and candidate compounds are located, guided by biological activity

274   (attraction of males) of each fraction or by comparing the volatile profiles of the extracts

275   from cohorts of virgin females with those of the controls, which can be extracted from

276   cohorts of mated females, immature stages or uninfested rearing substrates.

277   When the target compound is isolated by HPLC or GC from the crude extract or the

278   corresponding fraction, the elucidation of the pheromone structure is then based on

279   spectroscopic data (MS - mass spectrometry or NMR - nuclear magnetic resonance) and

280   chemical microreactions (e.g., hydrogenation, hydrolysis, esterification, ozonolysis) that

281   allow determining, for example, functional groups, number of unsaturations, and position

282   of double bonds. The confirmatory synthesis of the candidate structure supplies the final

283   proof, when matching synthetic and natural chromatographic and spectroscopic data,

284   coupled with the behavioural assays.

285   Other techniques of volatile collections, rather than the classical use of adsorbent resins,

286   offer advantages regarding sensitivity. Solid-phase microextraction (SPME) is a sample

287   preparation technique that integrates sampling and concentration, avoiding the use of

288   solvents (Arthur & Pawliszin 1990) and allowing the direct introduction of the sample into

289   the GC injection port. SPME/GC was first employed for the study of airborne pheromones

290   of coleopterans (Malosse et al. 1995), but it is nowadays a widespread technique. More

291   recently, the automated sequential SPME/GC-MS analysis (SSGA), which consists of a

292   programmable GC-MS autosampler equipped with a SPME syringe, has been employed to

293   study pheromones in Lepidoptera (Levi-Zada et al. 2011) and later in mealybugs (Levi-

294   Zada et al. 2014; 2019).

295

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 and 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

321 females and to mate during their short life, estimated as less than 12 hours in *P. citri*,

322 although males may mate outside this period, if they succeeded in finding receptive females

323 (Silva et al. 2009; 2013; Mendel et al. 2012). This represents an advantage for MD, as a

324 short-time alteration of mate search would deeply impact the reproductive success of

325 scales. As male scales do not feed and thus are not able to replenish their limited energy

326 budget, the existence of a trade-off between flight activity, mating and longevity is

327 expected, as flight is energy-demanding and thoracic flight muscles expensive to maintain

328 (Denno et al. 1989; Legaspi & Legaspi 1998; Mendel et al. 2012). For example, a trade-off

329 between the number of copulations and longevity was recently demonstrated in

330 *Phenacoccus solenopsis* Tinsley (Tong et al. 2019). Therefore, it is expected that under MD

331 conditions, when exposed to synthetic conspecific pheromone, males may waste their short

332 window of opportunity for mating, by rapidly spending their energy reserves and strongly

333 reducing their chance of mate location and mating performance. Millar et al. (2005)

334 suggested that the pheromone in scale MD will rapidly exhaust the males, removing them

335 from the system, in a similar manner as an insecticide, but without its negative side effects.

336 Furthermore, knowledge on the existence of a circadian rhythm of female pheromone

337 emission and male flight may allow to improve MD, by programming the daily timing of

338 pheromone release (for example in aerosol spray cans, see 7.1.1), and synchronizing

339 pheromone application with female calling and male flight period, thus reducing the

340 amount of pheromone (dose) needed for scale MD.

341 Secondly, as male scales are very sensitive to conspecific sex pheromone, it is expected that

342 the necessary amount of pheromone for obtaining an effective control of scale populations

343 in MD will be relatively small (Millar et al. 2005a). As mentioned before (see 3.3), the

344 amount of pheromone released by females is much smaller in scales than in lepidopterans.

345   Thirdly, the prevalence of migration of mated females is considered the most critical trait to

346   estimate pest susceptibility to pheromone-mediated MD (Cardé & Minks 1995). For

347   example, in the case of lepidopteran pests, the possibility of immigration of fertilised

348   females from habitats surrounding MD plots is considered a major constraint of the method

349   (Ioriatti et al. 2008; Ioriatti & Lucchi 2016; Benelli et al. 2019). In such a case, the

350   effectiveness of MD is dependent on its application in relatively large areas, to reduce the

351   perimeter/area ratio of the treated crop, and consequently the likelihood of female

352   immigration, oviposition and damage. However, in the case of scales this is not an issue, as

353   the adult females are sessile and wingless (Millar et al. 2005a). In fact, MD has been shown

354   to be effective in small plots (> 0.5 ha) for both the VMB (Sharon et al. 2016; Mansour et

355   al. 2017b; Cocco et al. 2018) and the CRS (Vacas et al. 2009; 2010).

356   Other biological traits that may influence the effectiveness of MD in scales will be treated

357   in the section 5. It is known that the success of MD as a pest management tactic is highly

358   dependent on the biological characteristics of the target pest (Gut et al. 2004).

359   **5   Biological traits of scales that may influence the effectiveness of mating disruption**

360   The wingless, and sometimes legless, scale females have limited spreading ability. The

361   dispersal is mostly performed by first-instar nymphs (crawlers), the most mobile stage,

362   displaying morphological and behavioural adaptations for walking and aerial dispersal

363   (Washburn & Washburn 1984). Through wind dispersal, scale crawlers may settle in new

364   host plants up to a few hundred meters from the source (Willard 1974). On the other hand,

365   dispersal by walking is extremely slow and mostly occurs within adjacent plants, as

366   crawlers tend to settle as soon as they find a suitable feeding substrate (Grasswitz & James

367   2008). The short-range dispersal of nymphs and wingless adult females determines that

368   scale pests usually show an aggregated spatial distribution (Meats & Wheeler 2011; Pérez-

369   Rodríguez et al. 2017; Cocco et al. 2018). Differences in the degree of aggregation depend

370 on species-specific dispersal behaviour, such as thigmotaxis and phototaxis, morphological

371 traits of host plants, and natural enemy-pest interactions (Nestel et al. 1995). Aggregated

372 distribution is a potential constraint for effective MD control of scales, as the odds of short-

373 distance fortuitous male-female encounters are expected to increase in dense colonies.

374 Scale males show a positive pheromone dose-response up to a certain pheromone

375 concentration (Branco et al. 2006). Therefore, scale aggregation may promote polygyny

376 (i.e., multiple copulations in males), as it is expected that males will be more attracted by

377 large colonies of virgin females, collectively generating a stronger pheromone signal than

378 single calling females. By locating female colonies, males will increase their chance of

379 multiple mating, minimizing the energy cost of mate searching. This behavioural strategy is

380 particularly beneficial for short-lived insects, such as scale males. A higher number of male

381 copulations and a reduced mating duration and intervals have been observed under

382 laboratory conditions at higher female densities (Silva et al. 2013; Tong et al. 2019).

383 The population age structure of scales may play a role in MD success. For example, in

384 Sardinia (Italy), the overwintering population of VMB is mainly represented by mated

385 females, which start ovipositing in March-April, before the first flight of males (Lentini et

386 al. 2008). Therefore, MD dispensers, which are usually applied in late April-early May

387 before adult male appearance, are ineffective against the first generation and do not prevent

388 the development of the progeny from overwintering mated females. In this perspective, it is

389 of outmost importance the season-long effectiveness of MD dispensers, as a significant

390 reduction of matings in autumn would significantly reduce the proportion of overwintering

391 mated females.

392 Sexual communication in biparental scales is mediated by female sex pheromones. The

393 possibility of intraspecific variation in sex pheromone signals has been reported in the

394 VMB. The sex pheromone of the VMB was identified in Californian populations as a

395   single-component pheromone, i.e., (S)-lavandulyl senecioate (Hinkens et al. 2001). Soon

396   afterward, this and a second component, i.e., (S)-lavandulyl isovalerate, were detected in

397   Israeli populations of the mealybug (Zada et al. 2003). Kol-Maimon et al. (2010) showed

398   that VMB males might respond differently to the two-pheromone components, indicating

399   the existence of different male pherotypes. Based on the three possible behavioural

400   responses (attraction, indifference, repulsion) of mealybug males to each of the two

401   components, nine different pherotypes were defined, including fertile male pherotypes

402   indifferent to both pheromone compounds. Kol-Maimon et al. (2010) compared the

403   pherotypes of VMB populations from eastern (Israel) and western (Portugal) Mediterranean

404   and found that the variability of male response was much higher in eastern (9 pherotypes)

405   than in western (5 pherotypes) populations, where no males were attracted to the isovalerate

406   component. This apparent different pherotype composition in Mediterranean populations,

407   indicating a different genetic makeup, is in accordance with the results of the most recent

408   phylogeographic study on the VMB (Daane et al. 2018). The latter study suggested the

409   existence of two major population groups: 1) a European group, originating in Europe,

410   Tunisia and Turkey, which likely spread in Argentina and South Africa; and 2) a Middle

411   East group, from Israel and Egypt, which was introduced in North America and Mexico.

412   Different degrees of responses of CRS males to wild and laboratory-reared virgin females

413   have been also reported (Tashiro et al. 1969).

414   The existence of male pherotypes in scales may bear practical implications for MD. For

415   example, the effectiveness of the actual MD formulations for the VMB, based on (S)-

416   lavandulyl senecioate, in populations with pherotypes attracted to (S)-lavandulyl isovalerate

417   (e.g., some Israeli populations) may be compromised, as the mating activity of part of

418   males in the mealybug population will not be affected by the pheromone treatment.

419   Furthermore, it is expected that, in such populations, the successive application of MD

420   during several years, will create a selection pressure favouring isovalerate pherotypes,

421   which may alter the genetic structure of local VMB populations and result in resistance to

422   MD.

423   Scales may exhibit different levels of polyandry (i.e., multiple mating in females) and

424   polygyny. Overall, scale males show high mating capacity under laboratory conditions,

425   when exposed to *ad libitum* virgin females, as they are able to mate multiple times, with

426   relatively short mating intervals between consecutive copulations (James 1937; Tashiro &

427   Moffitt 1968; Mendel et al. 1990; Waterworth et al. 2011; Ricciardi et al. 2019; Silva et al.

428   2019; Tong et al. 2019). Polygyny, concurrently with scale clumped distribution, may

429   hinder the effectiveness of MD, as a single male may fertilize several females (Silva et al.

430   2013; 2019; Tong et al. 2019). However, laboratory studies probably overestimated male

431   fecundity. In the field, male performance is expected to be much lower, especially in low

432   population densities, due to the limited energy reserve of males, their short lifespan and the

433   restricted daily flight activity period (Silva et al. 2019). In addition, in mealybug males, the

434   number of copulations decrease over time, likely because of depletion of energy reserves or

435   sperm (Waterworth et al. 2011; Ricciardi et al. 2019).

436   The possibility of female multiple mating (polyandry) in mealybugs has been recently

437   observed in laboratory conditions (Waterworth et al. 2011; Silva et al. 2013) and confirmed

438   by genotype analysis of *P. citri* eggs produced by single females mated with two males

439   (Seabra et al. 2013). Nevertheless, no data are yet available on the frequency of polyandry

440   in field conditions. *Pseudococcus longispinus* females mated up to 8 times in a single day

441   and subsequent copulations occurred up to 23 days after the first event. However,

442   receptivity may be restricted to a shorter period in other species, such as *P. citri*

443   (Waterworth et al. 2011; Silva et al. 2019). After mating, females of VMB and *P. citri*

444   cease pheromone emission within 48 hours, and CRS females become unattractive within

445 24 hours (Tashiro & Moffitt 1968; Levi-Zada et al. 2014). The existence of polyandry in

446 scales may have implications in the effectiveness of MD. Effective MD is expected to have

447 more impact on polyandrous than in monandrous females, as in the absence of multiple

448 mating, none of the benefits of polyandry will occur (Silva et al. 2019). Mated females may

449 compete with virgin females thus reducing the male reproductive success (Waterworth et

450 al. 2011). However, this possibility is unlikely under MD conditions, as virgin females are

451 more frequent and more attractive to males than mated ones (Silva et al. 2019). Data

452 collected by Cocco et al. (2014) in MD plots support this hypothesis.

453 **6   Mechanisms explaining the effectiveness of mating disruption in scales**

454 The effectiveness of MD is dependent on both direct and indirect factors. Direct factors are

455 related to the mechanisms involved in the disruption of pheromone-mediated

456 communication between male and female insects (Miller & Gut 2015). Indirect factors

457 include other mechanisms, "when mating disruption does not disrupt mating", such as

458 delayed mating (Mori & Evenden 2013).

459 Different MD mechanisms have been postulated (Bartell 1982; Cardé & Minks 1995;

460 Miller et al. 2006a), which can be divided in two main categories: competitive and

461 noncompetitive (Miller et al. 2006a). Competitive disruption includes competitive

462 attraction (false-trail-following, confusion), induced allopatry, and induced arrestment,

463 whereas noncompetitive disruption involves other mechanisms, such as suppressed

464 calling/mating, camouflage, sensory imbalance, induced allochrony, and desensitisation

465 (habituation) (Miller & Gut 2015). More than one disruption mechanism may be involved,

466 depending on the type of MD formulation and insect species (Mori & Evenden 2014;

467 Miller & Gut 2015). However, relatively few studies investigated the mechanisms

468 responsible for MD in particular cases (e.g., Flint & Merkle 1983; Lapointe et al. 2009;

469 Rodriguez-Saona et al. 2010; Mori & Evenden 2014). The meta-analysis carried out by

470   Miller et al. (2006b), based on moth sex-pheromone literature, indicated that competitive

471   disruption is the dominant mechanism.

472   Under MD conditions, other mechanisms unrelated to the disruption of mating may be also

473   involved, such as delayed mating, which may reduce female fitness and thus contribute to

474   MD effectiveness. For example, Mori & Evenden (2013) performed a meta-analysis on the

475   effect of delayed mating in female moth fitness and found a significant decrease in

476   fecundity, fertility, and pre-oviposition period and an increase in female longevity.

477   To the best of our knowledge, no specific studies were carried out to clarify the type of

478   mechanisms responsible for scale MD. Nevertheless, available data suggest that the

479   involved mechanisms are most likely part of competitive disruption. Suckling et al. (2018)

480   found no experimental evidence of habituation in males of *P. calceolariae,* as no significant

481   differences were observed in male response to sex pheromone lures (100 µg) between

482   males pre-exposed to the sex pheromone (1 mg) for 24 h and control males pre-exposed to

483   clean air. On the other hand, in a flight-tunnel simulating MD conditions (16 pheromone

484   lures distributed in 4 x 4 array, with a virgin female in the centre), males of the same

485   mealybug species showed to be attracted to the lures (Ricciardi et al. 2019). This behaviour

486   was associated with a significant decrease in female detection, compared to the control (16

487   rubber septa without pheromone), thus suggesting competitive disruption. Also, maximum

488   CRS captures were obtained in traps baited with pheromone dispensers releasing ca. 300

489   µg/day (Vacas et al. 2017), whereas the calculated minimal release rate for successful MD

490   treatments is 250 µg/day (Vacas et al. 2010).

491   As competitive disruption is a "numbers game", its outcome in what concerns pest control

492   is dependent on the ratio between the number of pheromone release points (e.g., dispensers)

493   and the number of virgin females, i.e., it is pest-density-dependent, in contrast with

494   noncompetitive disruption mechanisms, which are pest-density-independent (Miller & Gut

495   2015). This prediction is in accordance with field results on MD of scales. In fact, Sharon et

496   al. (2016) observed that the effectiveness of MD, in the management of VMB populations,

497   decreased at high pest densities. Therefore, these results also support the hypothesis of

498   competitive disruption.

499   The fact that no complete shutdown effect (zero captures) has been reported by different

500   authors (e.g., Cocco et al. 2018; Daane et al. 2020; Silva et al. 2020) in male captures

501   registered in pheromone traps installed in MD plots for the VMB is also indirect evidence

502   supporting the hypothesis of competitive disruption mechanisms in scales.

503   Furthermore, in disruption by competition, it is expected that the additional disruption

504   effect resulting from adding more pheromone dispensers in a certain crop area, to be

505   protected by MD, will diminish with the increasing number of dispensers (Miller & Gut

506   2015). Experimental results on scale MD also support this prediction. In a two-years

507   experiment on MD of the VMB, Lucchi et al. (2019) found no dose effect on the

508   pheromone application rate, as no significant differences were found in grape damage

509   among 300, 400, and 500 dispensers/ha (i.e., 54, 72, and 90 g/ha of VMB racemic

510   pheromone, respectively). Vacas et al. (2010) compared the application of 420 and 840

511   dispensers/ha, for MD of CRS, keeping the total release rate in 113 mg/ha/day, and

512   observed no significant differences in fruit damage.

513   Delayed mating has been reported to occur in scale insect populations under MD. In MD

514   conditions for the VMB, Cocco et al. (2018) observed 18.8–66.2% reduction in the

515   percentage of ovipositing females, a mating delay of 5.5–12.5 days, a significant increase

516   of the pre-oviposition period (up to 12.5 days), and in female longevity, a significant

517   decrease in fertility, and no effect on fecundity. Lentini et al. (2018) studied in laboratory

518   conditions the effect of mating delay on the reproductive performance and population

519   growth rates of the VMB. They concluded that only a mating delay longer than 7 days

520   would lead to a reduction in the population growth rates. In the case of CRS, Vacas et al.

521   (2012) found a significant lower number of gravid females in MD plots, in comparison with

522   control, as well as a delay in the development of CRS instars.

523   As in MD conditions unmated females live longer, the increase in female longevity is

524   expected also to affect the relative attractiveness of older females due to a reduction in the

525   emission rate of the sex pheromone. In fact, Levi-Zada et al. (2014) showed that the

526   females of both *P. citri* and VMB have an age-dependent pattern of sex pheromone

527   emission, with a maximum release rate registered for middle-age females. For example, at

528   25±1 °C and 13L:11D photoperiod, pheromone emission in *P. citri* started at 4-6 days-old

529   females, reached the maximum at 9-12 days-old females (2 ng/h), and decreased for older

530   females. In the case of VMB, the emission of pheromone also started at 4-6 days-old

531   females and decreased for females older than 20 days. The maximum amount of sex

532   pheromone was released by 10-20 days-old females (1-2 ng/2h). Females of both mealybug

533   species ceased pheromone release after mating (Levi-Zada et al. 2014). According to these

534   data, and for the same conditions, a reduced attractiveness would be expected for unmated

535   females older than 20 days, in the case of the VMB, although females of 1-28 days old

536   were equally attractive to males in the field (Lentini et al. 2018).

537   Under MD conditions, semiochemical-mediated interactions between scales and their

538   natural enemies may also contribute to its global effectiveness as a pest management tactic.

539   Sex pheromones and volatile cues of scales elicit kairomonal responses in several

540   parasitoids and predators and are exploited for host/prey selection (Branco et al. 2007;

541   Ishaaya & Horowitz 2009; Pekas et al. 2015; Urbina et al. 2018). For example, the encyrtid

542   *Anagyrus vladimiri* Triapitsyn (= *A.* sp. near *pseudococci*) uses the sex pheromone of the

543   VMB as a chemical cue for host location (Franco et al. 2008; 2011). This kairomonal

544   response of the parasitoid may contribute to enhance biological control of the VMB in MD

545   conditions. In fact, in most of the cases, the level of parasitism of the VMB has been

546   reported to be higher in MD plots compared to control (Walton et al. 2006; Cocco et al.

547   2014; Shapira et al. 2018). However, the higher parasitism level observed in MD plots may

548   be also related with the higher longevity of VMB females, which are thus expected to be

549   exposed to parasitisation for a longer period. This is apparently the explanation for the

550   increased parasitism of CRS by *Aphytis melinus* DeBach, observed under MD conditions.

551   The presence of the pheromone in MD treated plots was reported to delay the development

552   of CRS allowing a higher parasitism rate compared with untreated plots and a significant

553   higher total predation and parasitism in MD treated plots (Vacas et al. 2012; Vanaclocha et

554   al. 2012). Although the hypothesis that the CRS sex pheromone could attract *A. melinus*

555   was raised by Sternlicht (1973), later Morgan & Hare (1998) found no evidence of a

556   kairomonal response of the parasitoid to the host sex pheromone, in olfactometer

557   experiments. More recently, in field experiments, Pekas et al. (2015) also revealed no

558   attractant effect of CRS pheromone for both *Aphytis lepidosaphes* Compere and *A. melinus*,

559   although a positive response was observed for *A. chrysomphali* Mercet.

560   **7   Development and application of mating disruption formulations in pest**

561   **management of scales**

562   Here we summarize the accumulated knowledge and recent developments on the

563   implementation of MD for the control of two major scale pests, VMB and CRS, for which

564   this pheromone-based management tactic is already practiced with commercial

565   formulations.

566   **7.1. The vine mealybug**

567   The VMB is the most economically important mealybug species infesting grapevine (*Vitis*

568   *vinifera* L.) worldwide (Walton & Pringle 2004; Franco et al. 2009; Daane et al. 2012;

569   Reineke & Thiéry 2016; Mansour et al. 2018). The isolation, identification and synthesis of

570   the sex pheromone of the VMB (Hinkens et al. 2001; Millar et al. 2002) allowed its

571   application for pest management purposes. Since then, different MD formulations have

572   been developed, tested and applied for the control of its populations in many grape-growing

573   areas in Europe, North Africa, Middle East, and North and South America (Walton et al.

574   2006; Miano et al. 2011; Cocco et al. 2014; 2018; Sharon et al. 2016; Mansour et al. 2017b;

575   Lucchi et al. 2019).

576

577   **7.1.1. Formulations**

578   Over the last two decades, four formulations of MD have been tested and whenever

579   appropriate, implemented as a control tactic against VMB, in different grape-producing

580   areas in Europe, North Africa, Middle East, or America. These formulations exploiting

581   different materials and technologies include (Tab. 2): 1) sprayable microencapsulated

582   formulation (Checkmate®VMB-F); 2) membrane dispensers (Checkmate®VMB-XL); 3)

583   aerosol spray cans (Puffer®); and 4) rope (reservoir) dispensers (Isonet®PF). A double

584   rope dispenser (Isonet®LPF) is also under evaluation for the combined MD of VMB and

585   the European grapevine moth *Lobesia botrana* (Den. & Schiff.) (Baba et al. 2019; Ricciardi

586   et al. submitted).

587   **7.1.2. Dose effectiveness**

588   The first MD test against VMB was carried out in California table grapes using a sprayable

589   microencapsulated formulation, containing 16.3 and 10.8% of active ingredient (a.i.) by

590   weight of racemic lavandulyl senecioate, in 2003 and 2004, respectively (Walton et al.

591   2006). Three to four applications of 10.7 g a.i./ha were carried out, between April and

592   August, corresponding to a total of 32.1 g a.i./ha and 53.5 g a.i./ha per season, respectively

593   (Tab. 2). In addition, a delayed dormant (February) application of chlorpyrifos or an in-

594   season (June) application of buprofezin were carried out in the experiments of 2003 and

595   2004, respectively. A reduction in trap catches of adult males, mealybug density (only in

596   2003) and crop damage was obtained, but the formulation showed a relatively short (3 to 5

597   weeks) effective lifetime. More recently, Suterra developed a new microencapsulated

598   formulation (Checkmate®VMB-F), which was tested by applying 4-5 monthly pheromone

599   treatments, between late May and early September, at 12.4 g a.i./ha per treatment,

600   corresponding to a total of 49.4-61.8 g a.i./ha per season (Haviland 2017a; 2017b). The

601   possibility of being applied by conventional sprayers, along with insecticides or fungicides

602   (except those containing oil-based products, emulsifiable concentrates or including

603   organosilicone surfactants) and the inexistence of pre-harvest intervals, residues, or

604   international maximum residue limits for exported fruits, constitutes the major advantages

605   of microencapsulated formulations. In addition, the cost of each treatment

606   (Checkmate®VMB-F) corresponds to about 20% of the cost of membrane dispensers

607   (Checkmate®VMB-XL). That is, in the maximal number of five applications per season it

608   has a similar cost to that of membrane dispenser system. As a rule, microencapsulated

609   formulations are not permitted in organic farming. However, some exceptions for its use in

610   organic table grape fields in California have been granted by some organic-certifying

611   organizations in 2019 and 2020 (KCDA 2020).

612   Membrane dispensers (Checkmate® VMB-XL) loaded with 150 mg of the racemic sex

613   pheromone have been tested against VMB populations in different grapevine regions and

614   using different number of dispensers (Tab. 2). In California (USA), Langone et al. (2014)

615   applied ca. 400 dispensers per ha (62-93 g a.i./ha), in combination with a delayed dormant

616   application (before pheromone dispenser set up) of chlorpyrifos and a post-harvest

617   treatment of spirotetramat. A total of 620-625 dispensers per ha was tested in Sardinia

618   (Italy) (62.5-93.8 g a.i./ha; Cocco et al. 2014; 2018), Israel (93.8 g a.i./ha; Sharon et al.

619   2016), and Central-South Tunisia (93 g a.i./ha; Mansour et al. 2017b). In the case of

620   Sardinia, MD was combined with a treatment of chlorpyrifos or lambda-cyhalothrin, and in

621   Tunisia, with imidacloprid. In all experiments, MD significantly reduced male captures in

622   pheromone traps and mealybug densities on grapevines. Field lifetime of pheromone

623   membrane dispensers was estimated to be 130-150 days in Sardinia, with a mean

624   pheromone release rate of 484 mg/ha/day (Cocco et al. 2014; 2018), and 120 days in

625   warmer Central-South Tunisia (Mansour et al. 2017b).

626   The aerosol spray cans (Puffer®) controlled by programmable chips were also tested

627   against VMB populations, in California vineyards at a rate of ca. 4.9 spray cans per ha, in

628   combination with a delayed dormant application of chlorpyrifos and a post-harvest

629   application of spirotetramat. Spray devices were timed to release 1.3 g a.i./day throughout

630   the entire growing season. In addition, membrane dispensers were installed in the treated

631   plot perimeter, emitting about one-eighth as much pheromone as the aerosol spray cans.

632   Pheromone treated plots showed a reduction in male trap captures and grapevine damage,

633   in comparison with control plots (Langone 2013; Langone et al. 2014).

634   More recently, pheromone rope dispensers (Isonet® PF) have been tested against VMB in

635   Italian vineyards. Field trials conducted at a dose of 90 g a.i./ha (500 dispensers x 180 mg

636   a.i./ha) resulted in a noteworthy delayed mating and decrease in the number of matings, as

637   the number of ovipositing females was significantly reduced (Cocco et al. 2018).

638   Furthermore, this formulation, applied over consecutive years, significantly reduced VMB

639   density and showed a field lifetime of about 200 days and a release rate of 385 mg/ha/day

640   (Cocco et al. 2018). Similar results were observed in a three-year study in Portugal, with

641   the same dosage (Silva et al. 2020). Lucchi et al. (2019) compared the efficacy of different

642   pheromone dosages, i.e., 300, 400 or 500 rope dispensers per ha (180 mg of racemic

643   lavandulyl senecioate per dispenser, i.e., 54, 72, and 90 g a.i./ha, respectively), in northern

644   and southern Italian vineyards. They observed that all pheromone treatments significantly

645 decreased VMB density on grape bunches, and found no significant differences among

646 dosages. These results suggest that the minimal effective dose for this MD formulation

647 (Isonet®PF) is 300 dispensers per ha.

648 Recently, based on experiments carried out in California, between 2004 and 2007, Daane et

649 al. (2020) provided further information on the effectiveness of different MD formulations,

650 including sprayable formulation, membrane dispensers and rope dispensers. They

651 concluded that sprayable formulation was slightly more effective than dispensers, for the

652 same pheromone dose.

653 The new double rope dispenser (Isonet®LPF) was evaluated in 2017 and 2018 by testing

654 400, 500 and 600 units/ha at three study sites located in Southern (Sicily), Central

655 (Tuscany) and Northern (Veneto) Italy (Ricciardi et al. submitted). Trials were performed

656 by monitoring *L. botrana* and VMB populations in wine and table grape vineyards

657 managed with MD and no-treated control vineyards. MD results showed a significant

658 reduction of the number of infested inflorescences, as well as of the number of *L. botrana*

659 nests and VMB individuals per inflorescence compared with untreated controls. No

660 significant differences were found between the three dosages of Isonet® LPF dispensers.

661 Performing MD against both insect species using a single dispenser reduced the labour

662 costs, the amount of plastic tools used in the field, as well as the insecticide treatments.

663 **7.1.3. Timing of mating disruption application**

664 No specific studies have been carried out to determine the optimal application timing of

665 MD. However, most studies on MD of VMB testing membrane and rope dispensers report

666 a field deployment before the first seasonal flight of males (Cocco et al. 2014; 2018; Sharon

667 et al. 2016; Mansour et al. 2017b), which depends on climatic conditions. For example, it

668 usually occurs in March, April, and mid-May in Israel, Central-South Tunisia, and Sardinia

669 (Italy), respectively. Setting up the pheromone treatment before first male flight is in

670   accordance with best practices applied for lepidopteran pests (Ioriatti et al. 2008). In this

671   perspective, it is of outmost importance to consider the season-long effective lifespan of

672   MD dispensers, which as mentioned before was estimated as 120-150 days, in membrane

673   dispensers, and about 200 days, in rope dispensers (Cocco et al. 2014; 2018; Mansour et al.

674   2017b). In the case of microencapsulated formulations, the effective lifetime is only about

675   3-5 weeks, which impose up to 5 treatments per year, to cover the whole season (Haviland

676   2017a; 2017b). Above all, an effective disruption of male-female communication and a

677   consequent reduction of mating activity in autumn are expected to markedly reduce the

678   proportion of overwintering mated females, and thus the size of VMB population escaping

679   MD in the following spring. In fact, membrane dispensers reduced the percentage of

680   ovipositing females in October to 40-50%, whereas rope dispensers were more effective

681   late in the season by reducing the percentage of matings to 0-10% (Cocco et al. 2018). The

682   reduction of overwintering mated females by MD applied for consecutive years led to an

683   increased effectiveness of this control method resulting in a reduction of VMB density

684   (Sharon et al. 2016; Cocco et al. 2018). The cumulative effectiveness of MD in reducing

685   the population density of VMB is in accordance with findings on lepidopteran pests

686   (Stockel et al. 1994; Varner et al. 2001).

687   In hot-climate areas, the build-up of VMB populations starts as early as February and up to

688   nine generations per year have been estimated (Sharon et al. 2017). Under such conditions,

689   a single release of pheromone dispensers is not sufficient to disrupt mealybug male activity

690   for the whole season. The application of membrane dispensers twice a year, i.e. February

691   and August, induced a year-round effective MD and a significant reduction of VMB

692   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

718   monitor *A. vladimiri* and other pheromone sources associated with MD dispensers, in a

719   similar way to that occurring with mealybug males, due to the kairomonal attraction of the

720   parasitoid to the VMB pheromone. Overall, available data clearly indicate that MD is

721   compatible and may even enhance biological control of the VMB and other grapevine

722   pests.

723   As in moth pest species (Cardé & Minks 1995), the effectiveness of MD in the control of

724   VMB populations is density-dependent, as its efficacy decreases at high pest densities

725   (Sharon et al. 2016). Therefore, at moderate-high VMB densities MD should be combined

726   with chemical or biological control tactics, following an IPM approach (Mansour et al.

727   2017b; 2018; Lucchi & Benelli 2018). In fact, MD of the VMB has been often associated

728   with insecticide applications in IPM programs. All the available formulations increased the

729   effectiveness of insecticides commonly used in VMB control, namely chlorpyrifos,

730   buprofezin, imidacloprid, and spirotetramat (Walton et al. 2006; Cocco et al. 2014; 2018;

731   Langone et al. 2014; Haviland 2017a; Mansour et al. 2017b, 2018). Nonetheless, MD was

732   effective in reducing the mealybug density also as a stand-alone control tactic (Sharon et al.

733   2016; Lucchi et al. 2019).

734   **7.2.   California red scale**

735   Once the pheromone of CRS was identified, it was used for the monitoring of the scale. The

736   first trials of MD were conducted in the early 1980s, using rubber septa pheromone

737   dispensers (Barzakay et al. 1986; Hefetz et al. 1988). These dispensers were loaded with

738   low amounts of pheromone (below 6 mg) and needed replacement every 2 months.

739   Although the treatment reached male capture reduction in monitoring traps, the efficacy in

740   terms of pest damage reduction was not proved. Later, in the early 2000s, a new

741   formulation with 0.4 mg/dispensers was registered by the United States EPA and

742   commercialised under the name Red Scale Down[TM]. These dispensers installed at a density

743 of 250 units per ha, and replaced every 3 months, showed low to moderate efficacy in

744 orchards with low infestation levels (Sousa et al. 2008). Twenty years after the first tests,

745 MD studies were started over in Spain employing mesoporous dispensers and using

746 pheromone loads over 50 mg per dispenser (Vacas et al. 2009).

747 **7.2.1. Formulations**

748 There are currently two main formulations commercially available for MD of CRS (Tab.

749 2): mesoporous and membrane dispensers. Both types of formulations are passive

750 dispensers (usually applied at a rate of 300-600 units per ha), in which the pheromone is

751 continuously released, regardless of the time of day or the pest flight activity.

752 Mesoporous dispensers were developed by Vacas et al. (2009), consisting of cylindrical

753 tablets of clay material on which the pheromone is retained, not only by physical methods,

754 but also by the chemical interaction of the emitter matrix with the pheromone (Domínguez-

755 Ruiz et al. 2008). These dispensers have been available in the market with several

756 trademarks, such as Scalebur® (EPA SL), Dardo® (Syngenta Agro SA) and, more recently,

757 Masslure®AoAu (Massó) (Tab. 2). They exhibit good performance during long periods and

758 are less temperature-dependent compared with rubber septa or polymeric dispensers

759 (Domínguez-Ruiz et al. 2008). It should be taken into account that a temperature-dependent

760 dispenser wastes a high amount of pheromone in the warmer hours of the day when the

761 flight activity of CRS males is very low (Gieselmann 1990). The main disadvantage of

762 these mesoporous dispensers is the affinity that some corvid birds, especially magpies, have

763 for the pheromone tablets. In areas where these birds are abundant, the dispensers are

764 pecked and thrown to the ground, with the consequent loss of pheromone sources and

765 efficacy of the treatment.

766 Membrane dispensers are based in a plastic recipient containing the pheromone, with a

767 semipermeable membrane that regulates its emission. They are commercially available as

768 CheckMate®CRS Dispenser (Suterra LCC) (Tab. 2). This kind of dispenser is more

769 sensitive to high range temperature variations, although their average pheromone release

770 rate is substantially constant under the typical temperatures of Mediterranean climates

771 where citrus crops are cultivated.

7.2.2. Dose effectiveness

773 Several studies have been carried out to calculate the quantity of pheromone required for an

774 effective MD of CRS, but the information about dispensers' release rate was not always

775 complete. First field trials conducted by Hefetz et al. (1988) demonstrated that a reduction

776 of male captures was achieved by placing 400 rubber septa per ha, with a total load of 30

777 mg of pheromone per tree, for the whole season. However, no data on the quantity of

778 pheromone released were given. In studies carried out with rubber septa emitters, the

779 amount of residual pheromone after 2-3 months varied between 36% (McQuate et al. 2019)

780 and 72% (Smit et al. 1997). Even in a longer period of 6 months, rubber septa loaded with

781 pheromones could contain up to 71% of initial load (Zhang et al. 2013). Taking the most

782 unfavourable scenario, we could ensure that the pheromone emitters described by Hefetz et

783 al (1988) would contain at least one third of their initial charge at the end of their useful

784 life. Calculating a total pheromone dose of 12 g/ha/season and considering one third of

785 residual pheromone not emitted, we can assume that 8 g/ha/season (6 months) were

786 effectively released, with a mean rate of 44 mg/ha/day to reach the MD showed in this

787 work. However, no fruit damage assessments were performed and the effect of MD was

788 only evaluated regarding male capture reduction in pheromone traps placed in the treated

789 vs. control area.

790 A second work demonstrated that a pheromone release rate over 105 mg/ha/day was the

791 most suitable to reach effective MD (Vacas et al. 2009). Results showed that release rates

792 of 16.8 mg/ha/day did not originate male catch reduction in monitoring traps, whereas

793 release rates of 42 mg/ha/day achieved moderate male catch reduction, but the level of MD

794 in the last case was not enough to reduce fruit damage in the pheromone-treated areas.

795 Another study conducted in commercial orchards demonstrated that release rates of 113

796 mg/ha/day were more effective than oil treatments, achieving 70% fruit damage reduction

797 in the MD treated plots, during the first year of treatment (Vacas et al. 2010).

798 In the trials described above, the number of dispensers per tree was one, with a plant

799 density of 400-450 trees per ha. Hefetz et al. (1988) suggested that using four dispensers

800 per tree, with a quarter of the pheromone load, and maintaining the total dose of

801 pheromone, could lead to a higher reduction in male catches. Vacas et al. (2010), in MD

802 trials with a pheromone release rate of 113 mg/ha/day, registered no significant differences

803 in fruit damage between 420 and 840 dispensers per ha. Therefore, a single dispenser per

804 tree is sufficient for effective MD, with dispenser densities over 400/ha and ensuring a

805 pheromone release rate over 113 mg/ha/day.

806 **7.2.3. Timing of mating disruption application**

807 The date of dispenser deployment is always a key point for the success of MD. A general

808 rule in case of moth pests is setting up the dispensers before the first generation male flight,

809 to prevent early potential mating and the build-up of the population. However, this rule has

810 not been demonstrated in other insects, including scales. In CRS, this may not be the best

811 strategy. CRS can complete three to five generations per year (Grout et al. 1989). In the

812 Mediterranean region, three generations usually occur and a possible fourth generation

813 could take place in some areas and warmer autumns. First male flight takes place in spring

814 and CRS populations in the first generation usually show low densities, whereas the third

815 and occasional fourth generations are abundant and directly responsible for fruit infestation,

816 in most cases. Vacas et al. (2015) conducted a two-year study to adjust the timing of

817 dispenser application and assess the importance of controlling the first generation of CRS.

818 Results demonstrated that the control of the first CRS generation is not essential for

819 achieving a good efficacy, and applying the pheromone just before the second male flight

820 can generate at least the same efficacy. Furthermore, considering that there is a period of

821 30-40 days without male activity, between the first and the second CRS male flights,

822 dispenser deployment before the first flight will originate a wasting of about 2 months of

823 pheromone emission, when compared with the application before the second male flight.

824 Therefore, according to the results obtained by Vacas et al. (2015), between the two timing

825 options for MD of CRS, i.e., disrupting the first generation or completely disrupting the

826 third or even the fourth generation, the last one seems to be the optimal management tactic.

827 Another point to consider is the cumulative effect of MD. One of the main advantages of

828 MD is the reduction of pest populations year after year (Cardé & Minsk 1995). This

829 cumulative effect can only be achieved if MD is acting during the main part of the pest

830 population growth. For this reason, when the cost of the pheromone or the lifespan of the

831 dispensers do not allow keeping them active in the field during the whole year, the

832 deployment of pheromone dispensers should be timed to cover the generations that are

833 most responsible for population growth, that is the third and fourth generations, in the case

834 of CRS.

835 **7.2.4. Plot shape and size requirements for mating disruption**

836 The minimum size of the treated plots and the distance to untreated areas are also important

837 factors for MD success. Although the migration of fertile females from outside the

838 pheromone-treated plots is not an issue in CRS, as the females are sessile, the airborne

839 pheromone concentration is lower in the edge of the treated plots, and thus males may be

840 able to find receptive females and mate. In field trials conducted by Vacas et al. (2009), a

841 buffer area of 15 m around the treated plot was delimited to obtain the best performance of

842 CRS MD. However, in the case of plots treated with MD at the lowest pheromone doses, a

843 higher fruit damage was observed in the buffer area. For this edge effect, MD treatment is

844 not recommended in plots of less than 0.5 ha and it is necessary to avoid narrow and

845 elongated shapes that do not allow fulfilling the requirements of the edges.

846 **7.2.5. Compatibility of mating disruption with biological and chemical control**

847 It is important to know whether and how MD treatment can influence mortality caused by

848 parasitoids (mainly *A. melinus*) and predators (e.g., *Rhyzobius lophanthae* (Blaisdell)) of

849 CRS. As mentioned earlier, the hypothesis raised by Sternlicht (1973) that CRS sex

850 pheromone could attract *Aphytis* species was confirmed for *A. chrysomphali*, an endemic

851 parasitoid of the Mediterranean area (Pekas et al. 2015). In contrast, no attractant effect was

852 detected for the main *Aphytis* species, *A. melinus* and *A. lepidosaphes*. In the same way,

853 Morgan & Hare (1998) and Vacas et al. (2012) demonstrated that the presence of CRS

854 pheromone in the environment does not affect *A. melinus* mating behaviour or its capacity

855 to parasitize or feed on CRS. Moreover, the presence of the pheromone in MD plots was

856 reported to delay the development of CRS, allowing a higher parasitism rate compared with

857 untreated plots and a significant higher total predation and parasitism in MD plots (Vacas et

858 al. 2012, Vanaclocha et al. 2012)

859 Another important point to highlight is the high compatibility of MD with chemical control.

860 In fact, several studies demonstrated that MD efficacy is always higher with low to medium

861 pest pressure due to the accidental encounters between males and females that occur when

862 the populations are very high in competitive mating disruption, as it has been described in

863 section 6 (Sharon et al. 2016). In such high populations, Vacas et al. (2010) showed that a

864 chemical treatment (e.g., mineral oil) in the first CRS generation, combined with MD in the

865 second and third generations engendered better results than chemical or MD treatments

866 alone.

867 **8   Actual worldwide use of mating disruption against scales**

868 Mating disruption is currently applied worldwide in about 184,500 ha against VMB

869 (129,500 ha) and CRS (55,000 ha). Suterra formulations for the VMB (CheckMate®VMB-

870 XL, CheckMate®VMB-F) are used in ca. 120,000 ha, mostly (more than 100,000 ha) in

871 California, but also in Argentina, Uruguay, South Africa, Spain, and Italy, among other

872 countries. In California, the most used product is the microencapsulated formulation

873 CheckMate®VMB-F. CheckMate®VMB-XL has been available since 2010 and was the

874 first registered product worldwide in California (Suterra LLC, pers. comm. 2020). In

875 Europe, MD of VMB using Shin-Etsu formulation Isonet®PF is employed in 9,500 ha,

876 namely in Italy (6,000 ha), Spain (3,000 ha), and Greece (500 ha) (Shin-Etsu Chemical Co.

877 Ltd, pers. comm. 2020).

878 In relation to CRS, Suterra formulations are applied in ca. 50,000 ha worldwide. Most of

879 that area is covered by CheckMate®CRS, especially in the USA. In California, where it has

880 been registered since April 2016, this product has been used in more than 40,000 ha. It is

881 available or under registration process in the main citrus-producing countries of Latin

882 America and South Africa and is expected to be also available soon in some Southern

883 European countries. Suterra produces another passive dispenser that is commercialised only

884 in Spain, as well as an aerosol formulation that is seldom used in California (Suterra LLC,

885 pers. comm. 2020). In Spain, MD is applied against CRS in ca. 5,000 ha, using different

886 trademark formulations, such as Dardo (Syngenta), Scalebur (EPA SL) and Masslure

887 (Massó). MD formulations for CRS have been registered in Europe since December 2016

888 (EPA SL, pers. comm. 2020).

889 **9   Future prospects**

890 The expansion of MD as a sustainable approach for the management of scale pests depends

891 on future developments on technological, scientific and legal aspects, such as economic

892 synthesis of pheromones, availability of efficient formulations, clarification of MD

893   mechanisms, and suitable registration procedures. That is, all aspects that may improve MD

894   effectiveness facilitate its practical application and reduce the costs.

895   The cost of synthetic pheromones is often regarded as the key limiting factor for MD. In the

896   case of scales, several species have pheromones that are structurally complex and difficult

897   to synthesize at the industrial level, which may compromise practical application of MD

898   (Rodriguez-Saona et al. 2009; Tabata 2020). Therefore, technological advances simplifying

899   the methods used for the synthesis of scale pheromones, such as the invention of a new

900   synthetic method for the lavandulol-related pheromones, e.g., VMB and *Planococcus*

901   *krauniae* (Kuwana) (Tabata 2020), can be of critical importance. The level of purity in

902   synthetic pheromones may also influence production cost, as increasing purity requires

903   more rigorous distillation processes (Hinkens et al. 2001). Daane et al. (2020) recently

904   obtained similar efficacy in field trials using 99% and 95% chemically pure racemic

905   lavandulyl senecioate in MD against the VMB.

906   The development of more efficient formulations, less temperature-dependent and with a

907   longer effective lifespan, should be further explored. For example, the release rate of

908   pheromone from dispensers can be adjusted through membrane permeability (Daane et al.

909   2020). Multispecies formulations, such as Isonet® LPF (Ricciardi et al. submitted), are

910   another approach, which may contribute to reducing application costs of MD. Suckling et

911   al. (2016) reported an average return on investment of six to one in the use of a

912   multispecies formulation (ISOMATE® 4-Play™) for MD of the codling moth *Cydia*

913   *pomonella* (L.) and several leafrollers in New Zealand. The use of aerosol spray cans for

914   MD in scales deserves further investigation, as this type of formulation has advantages over

915   passive formulations, including lower application cost, and the possibility of synchronizing

916   the pheromone release with the period of circadian activity of the target pest (Benelli et al.

917   2019; Daane et al. 2020). As mentioned earlier, male flight activity and female emission of

918   pheromone in scales are limited to a few hours per day.

919   Further studies are also needed for optimising the pheromone dose (e.g., dependent on the

920   number of dispensers per ha and pheromone load of each dispenser; or the number of

921   applications per season and the application rate, in the case of flowable formulations), and

922   better defining the seasonal coverage of MD in scales (i.e., identification of critical periods,

923   optimisation of coverage strategy; Daane et al. 2020).

924   The elucidation of MD mechanisms in scales, besides the scientific interest per se, has

925   important practical implications. For example, in competitive disruption, which is pest-

926   density-dependent, the suppression of pest reproduction is not expected in high population

927   densities, whereas in non-competitive disruption mating will be strongly suppressed even in

928   high pest pressure. Further related examples are discussed by Miller & Gut (2015).

929   Finally, further developments in legal aspects related with MD formulations are still needed

930   to facilitate their registration and use, as part of the global trend aiming to reduce our

931   dependence on pesticides (Lechenet et al. 2017; Brühl & Zaller 2019; Möhring et al. 2020).

932   Regulatory requirements for pheromones should take into consideration the expected low

933   risk for human health and environment of these semiochemicals, due to their specific

934   properties, namely the specificity, the use in low doses close to natural concentrations, and

935   the rapid dissipation and/or degradation (European Commission 2016). In the USA,

936   pheromones are considered biopesticides, which generally require much less data to register

937   than a conventional pesticide. In fact, new biopesticides are often registered in less than a

938   year, compared with an average of more than three years for conventional pesticides (EPA

939   2020). However, in Europe, pheromones are classified as Plant Protection Products and fall

940   under Regulation 1107/2009, which has been mainly designed for classical synthetic

941   pesticides and does not completely consider the specific nature of pheromones, although

942 the registration process of Straight Chain Lepidopteran Pheromones has been simplified

943 (European Commission 2014). Nevertheless, this is not the case for other groups, including

944 scale pheromones. For example, the registration process for the approval of the VMB

945 pheromone for MD in Europe started four years ago and is still in progress (EFSA 2020).

954

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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				

Species	Compound	Reference	Ester type	Formula
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
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-trimethylcyclopentane	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-tetramethylcyclopentane	C12H22O2

1 **Table 2.** Worldwide application of mating disruption in the control of the vine mealybug

2 (VMB) and California red scale (CRS): formulations and grape-growing areas.
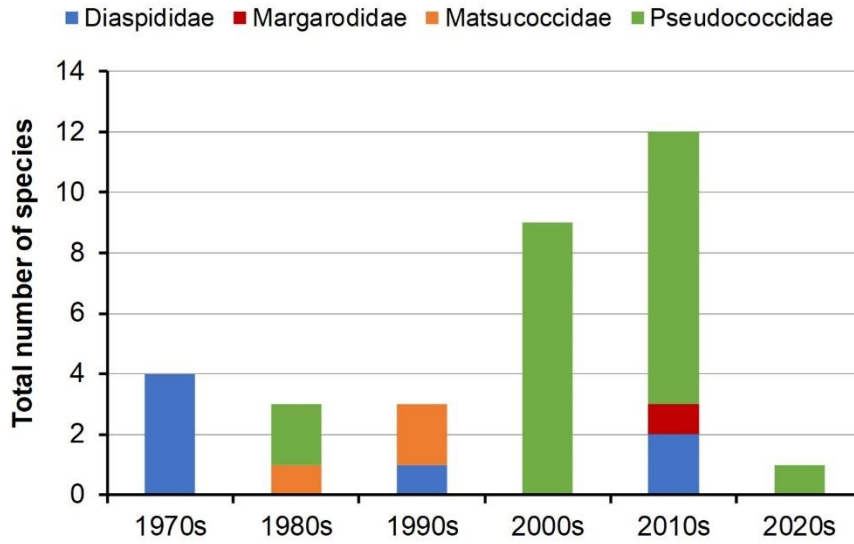
3

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)	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)

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6 **Fig. 1.** Evolution of the total number of sex pheromones described for scale species

7 reported by families, from seventies to date.

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