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Review Article

Semiochemicals, semiophysicals and their integration for the development of innovative multi-modal systems for agricultural pests' monitoring and control

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With 2 figures

Abstract: Semiochemicals are informative molecules emitted by living organisms that affect the behavior of receivers. As herbivorous insects are primarily thought to depend on olfaction and taste for their intra- and interspecific communication, semiochemicals have been widely studied for pest management applications. However, given that pest behavior does not rely on just one communication modality, stimuli of physical nature, such as light, sounds and vibrations, can also be used to manipulate insect-insect or insect-plant interactions. Moreover, stimuli of different natures can be combined in a multi-modal pest management program to increase the overall efficacy. Besides the widespread use of both chemical and physical signals in multimodal insect communication, the integration of stimuli has hardly been implemented for hardly any crop. This review introduces the term semiophysicals as opposed to semiochemicals and focuses on pest behavioral manipulation by discussing three main approaches; i) manipulation of pest orientation through attractive/repellent stimuli, ii) inhibition or promotion of specific pest behaviors and iii) interference with intraspecific communication through disruptive stimuli. For each approach, we provide examples of use of both semiochemicals and semiophysicals. Lastly, we describe the case study of the vineyard agroecosystem in the Trento province, where a multi-pest management program has been successfully developed, and we discuss future perspectives.

Keywords: chemical ecology, biotremology, insect communication, behavioral manipulation, disruption

1 Introduction

Animals need to communicate to mediate most activities and behaviors critical to their survival, such as reproduction, foraging, and the organization and maintenance of social structures. For this reason, animal communication has been widely studied and the knowledge acquired by basic research has been often applied to pest management. Broadly, communication happens whenever a signaler influences the behavior or physiology of a receiver by sending a signal (Horisk & Cocroft 2013). Many different stimuli have evolved to be signals: such as chemicals, lights, colors, sounds, and substrate-borne vibrations. Among these, chemicals are probably the most studied especially among economically relevant species. Since their discovery in the late 50s, chemical signals have been considered the most relevant and ancient communication channel (Wilson, 1970), to the extent that the term, semiochemicals, was coined to indicate chemicals able to modify the behavior of the recipient animal (Čokl & Millar 2009). Depending on their role in the ecological community, semiochemicals are divided into subcategories: pheromones are used by individuals of the same species to the advantage of both the emitter and the receiver; kairomones benefit a heterospecific receiver; allomones favor the individual producing them to the detriment of the receiver (Brown et al. 1970; Nordlund & Lewis, 1976). Lately, also mechanical signals, in particular substrate-borne vibrations, are beginning to be considered as relevant as chemical signals in terms of diffusion across the insect phylogenetic tree and the term biotremology has been recently coined to indicate the study of vibrational communication (Cocroft & Rodriguez 2005; Hill & Wessel 2016). The more we learn about mechanical signals, the more parallelism between them and semiochemicals we find. Moreover, even if literature on mechanical communication is still scarce compared to semiochemicals, the field of study is rapidly

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developing and we think the time has come for a specific term to be introduced (Hill et al. 2019). We decided to use the term "semiophysicals", as it embodies both mechanical and visual stimuli (Hill et al. 2019; Mazzoni et al. 2018). Thus, in this review we will use the term semiochemicals to indicate gustatory and olfactory signals, and semiophysicals for all physical stimuli, including substrate-borne vibrations, sounds, lights, and colors.

Communication can be pictured as a complex network, in which, besides the intended receiver of the signal, there are many unintended receivers that may eavesdrop on the communication or use the signals to their own advantage (McGregor 2005; Meta Virant-Doberlet et al. 2014). This is the case of conspecific rivals disrupting mating duets, predators and parasitoids eavesdropping on their preys, and parasites influencing the behavior of their hosts. Humans, are no different from other animals and have many opportunities to intercept and exploit such signals to manipulate the behavior of unwanted pests (Čokl & Millar 2009). To develop a successful pest management strategy based on behavioral manipulation, it is critical to identify the communication channel on which the target species relies, to decode its language, and finally to reproduce the signal. For semiochemicals, this process began in the late 50s with the identification of the first pheromone by Karlson and Butenandt: the bombykol of the silk moth, *Bombyx mori* L. (1959). Since then, sex or aggregation pheromones have been identified in thousands of species. For semiophysicals, visual and acoustic stimuli have been used for trapping for a long time, whereas the use of substrate-borne vibrations for pest management (i.e. applied biotremology) is new (Hill et al. 2019). This review aims to analyze the numerous applications of both semiochemicals and semiophysicals in behavioral manipulation of agricultural crop pests. Finally, we describe the case study of a vineyard agroecosystem, in which different control strategies, based on either chemical or physical stimuli, have been integrated to develop a successful multi-pest and multi-modal management program.

2 Behavioral manipulation strategies

The most successful examples of pest control mediated by semiochemicals are found in Lepidoptera and Coleoptera (Agelopoulos et al., 1999; Howse et al. 1998). On the contrary, the exploitation of semiophysicals for behavioral manipulation has often been limited by lack of specificity (e.g. visual stimuli; Foster & Harris 1997) or by difficulties in observing/recording and reproducing the stimulus itself (e.g. acoustic and vibrational stimuli; Mankin 2012; Polajnar et al. 2015). Nonetheless, many insect groups rely, partially or totally, on physical stimuli for a variety of interactions and the latest technical advances have made practical what was considered impractical until few years ago (Cocroft & Rodriguez 2005; Mankin 2012; Mazzoni et al. 2019). Depending on the target pest, therefore, behavioral manipulation tactics based on chemical and physical stimuli can be applied singularly or combined in a multimodal control strategy. Both semiochemicals and semiophysicals can be exploited to orient target organisms (attraction/repellence), to prevent or elicit specific behaviors (inhibition/promotion) or to interfere with intraspecific communication (disruption). In this section, we provide an overview of behavioral manipulation methods that can be used to control insect pests, giving examples of both well-established practices and methods that have only been tested experimentally.

2.1 Attraction/repellence

Orientation behaviors are coordinated movements that occur in response to the perception of an external stimulus (Hager & Kirchner 2019; Murlis et al. 1992). Such orientation can occur towards (i.e. attraction) or away from (i.e. repellence) the stimulus source and therefore can be exploited to implement both monitoring systems and control methods. Monitoring, mass trapping and attract-and-annihilate rely on attractive stimuli to guide the target organism towards a trapping device in order to early detect its presence or to reduce its population on the crop (Foster & Harris, 1997). In push-pull or stimulo-deterrent diversionary strategies (SDDS), a combination of repellent and attractive stimuli is used to divert pest populations away from the crops to be protected, while encouraging pest aggregation in external areas (Agelopoulos et al., 1999). While the above-mentioned approaches act directly on the target pest, attractive stimuli can also be used to influence the behavior of beneficial insects, such as predators or parasitoids, to better exploit their natural population or to increase the effectiveness of artificially released biocontrol agents (Sharma et al. 2019).

2.1.1 Semiochemicals

The use of chemicals to manipulate pest's orientation is probably the most common form of behavioral control, as olfaction is widely used by insects to locate conspecifics (e.g. potential mate) or hosts at a long-range distance through the perception of their emitted volatile organic compounds (VOCs) (Murlis et al. 1992). Despite the terminology denotes the function, it should be known that the distinction between attractants and repellents is not definitive. For example, dose-dependent behavioral studies showed that several compounds are attractive at low concentrations and repellent at high concentrations, this is the case of the potato tubeworm, *Phthorimaea operculella* (Zeller), and the spotted-wing drosophila, *Drosophila suzukii* (Matsumura) to plant volatiles and of the Asian tiger mosquito, *Aedes albopictus* (Skuse), to floral odors, (Hao et al. 2013; Anfora et al. 2014; Revadi et al. 2015). Nonetheless, we will still mention attractants and repellents primarily referring to the functional aspects of those compounds in specific practical contexts.

Generally, naturally occurring olfactive stimuli consist of complex blends of several VOCs (Renou 2014). Receivers are therefore faced with the challenge to identify an odor despite alterations of intensity or composition due to changes in the odor source (e.g. fruit ripening) or in the environment (e.g. temperature fluctuations). To achieve this goal, receivers often rely not only on the presence but also on the ratio of one or few key compounds within the blend that determine the identity of the olfactory stimulus (Reinecke & Hilker 2014). This strategy greatly simplifies the feasibility of behavioral manipulation methods with semiochemicals. In fact, their employment does not imply their perfect match with the chemical profile of the natural stimuli and once the ratios of the key molecules in the odor mixture is respected, the target organism can detect the stimulus against the noise of other compounds in the environment. As an example, the commercial formulations of the sex pheromone of the European grapevine moth, *Lobesia botrana* (Den. and Schiff.), contains only the main pheromone component (*E,Z*)-7,9-dodecadienyl acetate, and Isonet LE mating disruption dispensers aged for 1 year in the field still release a much higher amount of active ingredient per hour than a calling *L. botrana* female (Anfora et al. 2005; Ioriatti et al. 2011).

Sex pheromones, aggregation pheromones and plant kairomones are the three main types of semiochemicals currently employed as attractants. Their use has been implemented for various behavioral manipulation control techniques and for monitoring, thanks to their specificity and ability to elicit long-distance responses (Foster & Harris, 1997). While aggregation pheromones and plant kairomones may act on adults of both sexes (Jurc et al. 2006) and even on juvenile stages (Kirkpatrick et al. 2019), the vast majority of Lepidopteran sex pheromones are produced by females to attract males (Anshelevich et al. 1994; Cross & Hall 2009; Millar et al. 2002). For monitoring purpose, trapping only adult males is not considered an issue, as long as the number of catches can be related to the entire pest population in the monitored area (Witzgall et al. 2010). On the contrary, trapping only adult males could be a strong limitation when applied to mass trapping or attract-and-kill approaches, because the removal of only adult males from the environment is unlikely to have a significant impact on the size of subsequent pest generations (Suckling 2000; Thomson et al. 1999). However, mass trapping techniques using sex pheromone traps may have a potential to suppress or eradicate low density populations (El-Sayed et al. 2006) and several studies showed that the addition of a plant kairomone, which attracts females, can have additive or even synergistic effects on the effectiveness of the behavior-manipulating stimulus (Knight et al. 2019; Schmidt et al. 2007).

The case of codling moth, *Cydia pomonella* L., is illustrative of the evolution of behavioral manipulation strategies. Commercial dispensers containing the pest's main pheromone component, (*E,E*)-8,10-dodecadienol (codlemone; Roelofs et al. 1971), are widely used in apple and pear orchards for monitoring and control (e.g. mating disruption) of the pest. Several additional compounds have been tested through the years to improve the original formulation and to get a standard acceptable for field use (Arn et al. 1985; Barnes et al. 1992; Bartell et al. 1988; Einhorn, et al. 1986). Good efficiency was found using the MSP, a multicomponent sex pheromone (El-Sayed et al. 1999), which has been traditionally used to monitor male populations, but not yet for mating disruption. The latter became possible when a decisive improvement was achieved by adding to the MSP a plant kairomone (e.g. the pear ester (*E,Z*)-2,4-ethyl decadienoate) that allows the catch also of female moths (Knight et al. 2019; Schmidt et al. 2007).

Repellents are generally used to prevent pests from finding a valued resource (Foster & Harris, 1997). Several essential oils and synthetic compounds are commercially produced as repellents and represent the first line of defense against mosquito and other bloodsucking insects' bites (Alzogaray 2016; Benelli & Pavela 2018). Plant-derived volatiles can be used to mask host apparency, as host recognition by insects is often based on specific ratios of key volatiles (Anfora et al. 2014; Natale et al. 2003; Tasin et al. 2006). Pioneering studies with the Colorado potato beetle, *Leptinotarsa decemlineata* (Say), showed that a slight alteration of the host odors ratio resulted in the cessation of directed host orientation (Visser & Ave, 1978). In recent years, similar studies conducted on the European grapevine moth, *L. botrana*, led to the creation of stable grapevine transgenic lines, with altered emission of (*E*)-β-caryophyllene and (*E*)-β-farnesene, the key volatiles used by the pest for host recognition (Anfora et al. 2009; Salvagnin et al. 2018). Besides ratio-specific odor recognition, volatiles from unsuitable or non-host plants can elicit avoidance and repellent behaviors in several pests (Bruce et al. 2005). For example, isothiocyanates of brassicaceous plants are involved in the host location and recognition processes of several pest species. Such compounds elicit attraction in brassica-specialist aphids (Blight et al. 1995; Nottingham et al., 1991), whereas they are associated with active avoidance response in insects for which brassica plants are inappropriate hosts (Nottingham et al., 1991; Stratton et al. 2019). Synthetic green leaf volatiles from non-hosts angiosperms have been shown to inhibit pheromone attraction and to interfere with locating coniferous host plants in several bark beetle species (Guerrero et al., 1997; Huber et al. 2001; Unelius et al. 2014; Zhang & Schlyter 2004).

Integration of attractive and repellent stimuli can have additive or synergistic effects thus enhancing the overall effectiveness of the behavioral manipulation strategy (Cook et al. 2007; Cowles & Miller, 1992). When such an approach is applied using semiochemicals, it requires a complete understanding of the pest's chemical ecology and of its interactions with host and non-host plants. The "push" and "pull" components that protect the harvestable crop consist of either extracted volatile compounds, applied as trap baits, dispensers or sprayable formulations, or whole plants (e.g. intercropping and trap plants) emitting the attractive/repellent stimuli (Agelopoulos et al., 1999). However, in the framework of integrated pest management (IPM), the use of companion plants for push and pull is preferable as they provide additional benefits to the crop such as improved soil fertility, natural mulching, improved biomass, erosion control, refuge areas for beneficial insects and high value animal fodder (Khan et al. 2016; Mutyambai et al. 2019). A mixed approach using synthetic semiochemicals and whole plants is also possible. For example, wheat and pea aphids are repelled by dispensers loaded with (*E*)-β-farnesene or methyl salicylate in oil, while combined intercropping strips of wheat and pea attract beneficial arthropods that contribute to keep aphid populations low (Xu et al. 2018).

2.1.2 Semiophysicals

Even if many insects rely on odors to orient themselves, in some species orientation is mediated by photo- and phonotaxis behavior. In particular, while phototaxis has been known and investigated for the longest time, studies on chemical and acoustic orientation were in their infancy (Jander, 1963). In fact, it is common knowledge that lights attract insects during the night, and we often see streetlamps surrounded by nocturnal moths. Therefore, light as an attractant to trap and to kill insects has been widely used and 'electric insect killers' are a perfect example in which UV-emitting fluorescent tubes attract beetles and moths thus preventing them from entering stores and houses (Shimoda & Honda 2013). This strategy is used mainly in greenhouses and crops to control moths and rice pests; for these species, light traps are used to monitor the population density and predict outbreaks (Shimoda & Honda 2013). The main shortcomings in the use of light for pest control are the low specificity and the narrow range of efficacy, mostly restricted to crepuscular insects (Kim et al. 2019; Shimoda & Honda 2013). To improve the specificity of light traps, one solution is to identify specific wavelengths to which the target species is more sensitive; once the wavelength has been selected it can be replicated by using light-emitting diodes (LEDs) (Johansen et al. 2011; van Grunsven et al. 2014). Insects' attraction to light is a "wavelength-specific behavior" and it highly depends also on the light intensity; but insects show also "true color vision", the ability to discriminate between different hues independently from light intensity (Song & Lee 2018). Thus, colors can be used to attract insects that rely on "true color vision" to locate host plants by using colored targets. Sticky traps are an example of this approach: they are mainly used for monitoring pests and different colors can be used to target specific pest groups, such as thrips (blue) or whiteflies (yellow) (Broughton & Harrison 2012; Hodge et al. 2019). Differential attraction towards specific colors has also been observed among closely related pest species. The western pine beetle, *Dendroctonus brevicomis* LeConte, and the southern pine beetle, *D. frontalis* Zimmermann, exhibit a different response to visual cues during the host searching process, which suggests a differential effectiveness of multi-funnel traps towards the two species (Strom et al. 2001). In nature, the contrast between the target, such as fruit, and the surrounding background, the vegetation, seems to be of much greater relevance than the target's color itself for several insects, therefore traps designed on color contrast are usually more effective in attracting pests (Arnold et al. 2016; Little et al. 2018; Mainali & Lim 2010). For instance, the spotted wing drosophila *D. suzukii* uses color contrast between ripening fruits and surrounding foliage to identify suitable host fruits (Little et al. 2018; Little et al. 2019). The preference of *D. suzukii* for specific colors has also been exploited for the development of commercial monitoring traps (Fig. 1). It has been shown that red, yellow and black are more attractive to the insect as they probably mimic the color of ripening fruit used as oviposition and feeding sites. Traps with such colors have been combined with food attractants in fermentation, such as wine and apple vinegar or with the main volatile compounds emitted by them, providing a further example of the synergistic combination of olfactory and physical stimuli (Cha et al. 2014; Kirkpatrick et al. 2017; Landolt et al. 2012; Rossi Stacconi et al. 2016). Specific wavelengths can mediate repellency too. In these cases lights can be used to interfere with positive phototactic responses, such as in the case of the cigarette beetle, *Lasioderma serricorne* (F.) (Kim et al. 2013) or the greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood) (Johansen et al. 2011). Reflective mulch films, such as light-colored polyethylene plastics and aluminum foil, and UV-absorbing nets have been successfully applied to repel thrips, whiteflies and aphids from ornamental and vegetable crops (Antignus 2000; Legarrea et al. 2010).

Substrate-borne vibrations mediate orientation of several insect species, which use vibrational signals to locate food or a mating partner (Virant-Doberlet et al. 2006). As for the reproductive behavior, usually the female is stationary and attracts the male by emitting species-specific vibrational signals. In some species, such as leafhoppers, stink bugs, and psyllids, males also emit vibrational calling signals with the aim to elicit a female's response and generate an alternation of male-female signals called "duet". The exact mechanism by which insects are able to get directional information from vibrations is yet to be completely understood. To date, it is known that plant-dwelling insects, which encompass most agricultural pests, use the time delay in the perception between legs (where the vibrational receptor organs are located) and the whirling motion of plant stems to assess the source of vibrations (Gibson & Cocroft 2018; Prešern et al. 2018). Detailed knowledge, in terms of spectral and temporal parameters, of the vibrational signal of the attracting sex makes it possible to reproduce a synthetic playback that can be transmitted onto a substrate to attract insects into a trap or to keep them far from a specific area. This is what has been

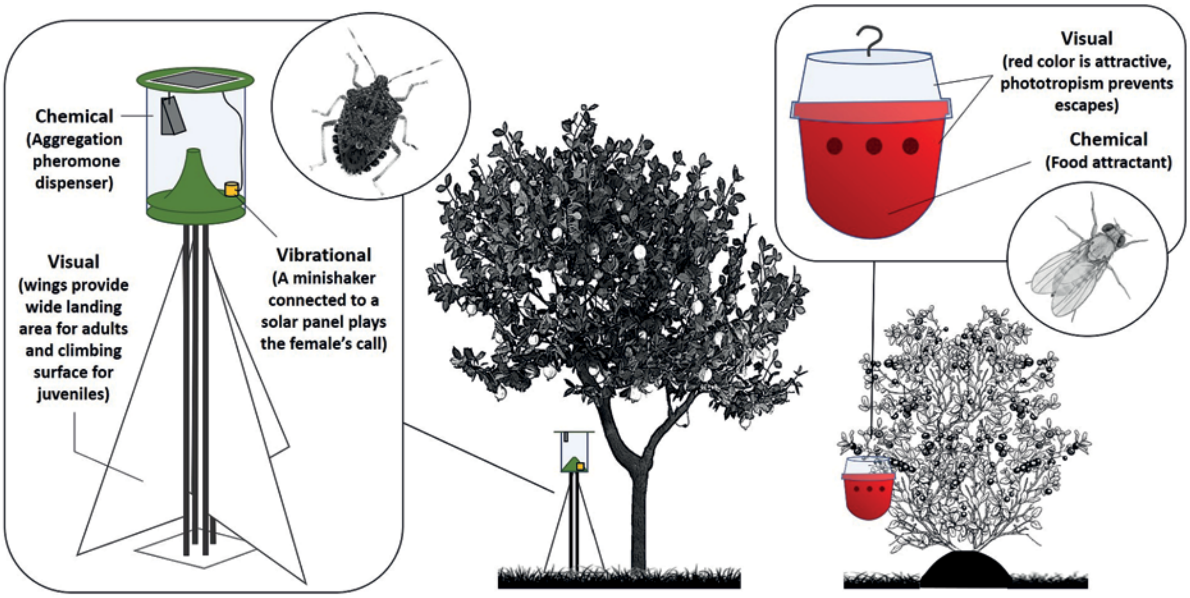

Fig. 1. Two examples of multi-modal traps: on the right a trap for *Drosophila suzukii* uses visual and olfactory stimuli, on the left a trap for *Halyomorpha halys* integrating chemical and vibrational stimuli.

done in laboratory conditions for the brown marmorated stink bug, *Halyomorpha halys* (Stål) (Mazzoni et al. 2017), and for the Asian citrus psyllid, *Diaphorina citri* Kuwayama (Mankin et al. 2013). For both species, the stimulation of males with the playback of the female signal drives them to the source of the vibration. Even though a commercial application of vibrational traps or repellents is not yet available, it is likely that in the near future devices based on the release of vibrational stimuli will be introduced into the farmers toolbox. Two possible major shortcomings of this technology are the sex selectivity and the temporal response of the automated playback. As in pheromones, these signals just attract one gender, usually males, who are searching for the signaling females. To overcome the gender selection, in the case of species that rely also on other stimuli, such as aggregation pheromones, the latter can be added to the trap to synergize their effect with the vibrations. For example, the brown marmorated stink bug is already monitored with commercially formulated lures (Weber et al. 2017; Suckling et al. 2019) (Fig. 1), whereas for the Asian citrus psyllid, the lure should contain plant volatiles (Martini et al. 2014; Zanardi et al. 2018). Although the sex pheromone could also be employed to improve the trap efficacy, kairomones would be necessary to attract also females. The temporal issue concerns the species recognition system. In several species, the time delay between the male signal and the female response is crucial to species recognition (Kuhelj et al. 2015; Polajnar et al. 2014). For these species, the playback should perfectly match the time response of the species to "fool" the male and be attractive. To date, the technology to perceive the male signal and reply with the emission of the attractive signal in the correct timeframe exist, but it is still not economically suitable for field applications (Korinšek et al. 2019).

A special mention is due to the use of sounds and substrate-borne vibrations to monitor insects without altering their behavior. For decades, it has been hypothesized that it could be possible to evaluate the presence and number of insects just by eavesdropping on their calls or movements. However, the needed technology has been recently developed at accessible costs (Mankin et al. 2020). The applicability is particularly relevant for stored commodities, such as grain and flour, and their pests.

2.2 Promotion/inhibition

Insect behaviors, primarily feeding, oviposition and locomotion, can be manipulated for control purposes by using short-range stimuli (Foster & Harris 1997). Such stimuli promote or inhibit behavioral responses of a pest when it comes at close distance or in contact with the crop. Promotors and inhibitors can be further divided into subcategories, since some pestilential behaviors (e.g. feeding) have been demonstrated to be separable into two consecutive phases, initiation and maintenance (Beck 1965). Specifically, incitants are promotors that evoke a reaction (e.g. biting or piercing), while stimulants promote the continuation of a specific response. Similarly, inhibitors that prevent the initiation of a response are called suppressants, whereas those preventing its continuation or hastening its termination are called deterrents. Arrestants designate stimuli that cause insects to cease locomotion. Although an arrestant may have the same final effect of an attractant causing aggregation, the two concepts should not be mixed as they work on different distance ranges and act on different physiological mechanisms (Knipling, 1979).

2.2.1 Semiochemicals

Chemicals promoting feeding activity are commonly used in pest management in combination with insecticidal products to increase pest contact with toxicants and to reduce insecticide exposure to humans. The control programs of the Mediterranean fruit fly (Medfly), *Ceratitis capitata* Wiedemann, initiated in the 1950s in USA are early examples of successful application of phagostimulants for pest management. Insecticides mixed with protein hydrolysate as attractant food bait provided superior control of the Medfly, leading towards the complete eradication of the pest in Florida (Steiner et al. 1961) and later in California (Scribner, 1983). The management of *D. suzukii* still heavily relies on chemical control. Limited numbers of insecticides with different modes of action are effective to control this pest and such reliance on few modes of action increases the risk of resistance insurgence (Gress & Zalom 2019). Non-nutritive feeding stimulants (i.e. erythritol, yeasts) have been tested in laboratory and field settings showing potential to significantly increase pest mortality in marginally effective insecticides (Fanning et al. 2018; Gullickson et al. 2019; Knight et al. 2016). In attract-and-kill strategies, feeding stimulants may be advantageous when used in combination with attractants as they can counteract the feeding inhibition response to the toxin associated with the baits, thus allowing the acquisition of a lethal dose (Gregg et al. 2018). Recently, an attract-and-arrest strategy was tested to mitigate *D. suzukii* damage. A combination of chemical cues from host plants (attractant component) and conspecific frass (arrestant component) was used to develop a non-nutritive lure that causes the pest to spend a significant amount of time away from the ripe fruit, therefore reducing infestations without using toxicants (Rossi Stacconi et al. 2020; Tait et al. 2018).

Unlike feeding stimulants, which mostly consist of common nutritional compounds (e.g. sugars, proteins and fats) or microorganisms that are relatively cheap and easy to obtain, oviposition stimulants are often highly specific. Chemicals acting as oviposition stimulants have been identified for several pests, however their synthesis and application on a large scale are too expensive and no formulation has yet been implemented for a commercial use. Besides pest management, oviposition stimulants can enhance the egg laying activity required for mass production of insects for sterile insect technique programs (Kempraj et al. 2019).

Feeding inhibitors are mostly derived from non-host plants (Isman 2006). A great deal of work has been carried out on antifeedant terpenoids derived from the neem tree *Azadirachta indica* A. Juss, the chinaberry tree *Melia azedarach* L. and several *Citrus* species. Although these compounds are extremely sensitive to degradation caused by environmental factors, the addition of photoprotectors and stabilizers allows their use in commercial bioinsecticides. Azadirachtin and other neem extracts show multiple biological activities of deterrence, toxicity and growth regulation, and have successfully been applied for the control of the fall armyworm, *Spodoptera frugiperda* (JE Smith), and other key pests of corn and cotton (Pinto et al. 2013; Zehnder et al. 2007).

Oviposition inhibitors (i.e. host-marking pheromones, HMPs) are found in exocrine secretions, frass and regurgitations left by ovipositing females or larvae to inform both conspecific females and individuals of other species about a resource that has already been taken (Nufio & Papaj 2001). Field applications of HMPs have been limited to tephritid flies such as the cherry fruit fly, *Rhagoletis cerasi* L. (Aluja & Boller, 1992), the Mediterranean fruit fly, *C. capitata* (Vargas et al. 2010), and more recently the Mexican fruit fly, *Anastrepha ludens* Loew (Birke et al. 2020).

Chemicals produced by microorganisms have also been found to be aversive for oviposition and feeding behaviors when they are associated with microbial species that have direct toxicity to insects or may be a threat to the development of their offspring. As an example, *D. suzukii*, negatively responds to the earthy-smelling sesquiterpene, geosmin, and to the mushroom alcohol, 1-octen-3-ol (Wallingford et al. 2016a). Both molecules are produced by many fungal and bacterial plant pathogens associated with fruit decaying and could be used by the pest as indicators for unsuitable substrates for feeding and oviposition. The two compounds when incorporated into controlled-release matrices (e.g. mineral oil or clay-based substrate) and tested in raspberry field settings caused a reduction of *D. suzukii* infestation up to 4 days after the application (Wallingford et al. 2016b).

2.2.2 Semiophysicals

Light intensity and quality, such as wavelength and polarization, can cause several changes in insect behavior and physiology (Shimoda & Honda 2013; Blake et al. 2019). Artificial lighting can disturb the circadian rhythms of a species, leading a nocturnal species to behave during night as if it was daytime. This phase shift can suppress flight, feeding, mating, and oviposition in nocturnal species that are exposed to bright light at night. This method can be easily applied in greenhouse settings by using artificial lights or LEDs; good results have been obtained to control the cotton bollworm *Helicoverpa armigera* Hübner, the common cutworm *Spodoptera litura* (Fabricius), and the webworm, *Hellula undalis* Fabricius. Also, for diurnal species, such as whiteflies and fruit flies, there is evidence that specific wavelengths or light intensity can inhibit landing, probing, oviposition and egg survival, but long-term studies and applications are still missing (Fountain et al. 2020; Johansen et al. 2011). There are also several effects of light exposure that show potential for pest control, because they can affect insect survival, but they have yet to be applied for pest management. For instance, exposing insects to light for several days can disrupt their photoperiodicity (i.e. the physiological response of insects to the light-dark alternation), thus suppressing crucial behaviors such as diapause (Saunders 2012). Failing to initiate diapause cause the insect to die during winter and can reduce pest populations (Shimoda & Honda 2013). Exposure to ultraviolet (UV) light can be toxic on its own; for example, eggs and larvae of *Trogoderma granarium* Everts are killed by exposure to UV-C (Ghanem & Shamma 2007). However, the effect of UV can be dramatically different even in the same pest species. In *Helicoverpa armigera* (Hübner)*,* larvae have longer developmental time and lower survival when exposed to UV-A with respect to the control, but adults showed increased fertility and oviposition (Zhang et al. 2011). In conclusion, it is difficult and it requires a deep knowledge of the mechanisms of action to balance the light treatments and to develop a successful pest management strategy. To date, such level of comprehension of the basic biology for most species is still missing and this is likely the reason why light is still not in use in agricultural pest management strategies.

Mechanical and electromagnetic waves may act as external stressors on insects and they are potentially good inhibitors of several insect behaviors. At the physiological level, low frequency microwaves, substrate-borne vibrations, and radio frequencies affected immatures and adults: the larval stage was prolonged and the survival rate and fertility of adults was reduced in a variety of species, including Coleoptera, Lepidoptera, and Heteroptera (Hofstetter et al. 2014; Maharjan et al. 2019a; 2019b; 2020; Nelson, 1996). At first, this approach was criticized because the effects seemed to be strictly temperature dependent; in that case it would be extremely unlikely that mechanical or electromagnetic stressors would have been applied as a pest management strategy (Nelson, 1996). However, later studies showed similar effects using sound and substrate-borne vibrations that do not heat the insect's medium (Hofstetter et al. 2014; Jinham et al. 2012). Evidence indicates that mechanical stressors other than heat affect hormone production in insect and the subsequent cascade of biogenic amines release (Hirashima et al. 1993; Hirashima 2009). In particular, the titers of octopamine and juvenile hormone, which are responsible for larval growth, pupation, fat storage, and survival of insects, are modified by the exposure to mechanical stimuli. The exact mechanism of action is yet to be unveiled, but some epigenetic evidence has been found in wasps' physiology, in which substrate-borne vibrations seem to modify the fat metabolism of larvae and thus determine adult survival and caste fate (Jandt et al. 2017).

Sounds and substrate-borne vibrations are also good deterrents. Cerambycids exhibit freezing and startle when exposed to low frequency vibrations (100-500 Hz) (Takanashi et al. 2019) and curculionid larvae shorten their tunneling distance (Hofstetter et al. 2014). Such effect has the potential for the development of new pest control strategies on fruit and ornamental trees. Even though, to date, technology issues are preventing the applicability of this method, several studies are underway to develop effective and accessible technologies, especially in Japan (Takanashi et al. 2019).

2.3 Disruption

The disruption of communication in pest management happens anytime a stimulus is used to interfere with the natural communication occurring between two or more insects. When considering intraspecific behavior disruption for pest control, the great majority of studies in the literature refer to techniques that interfere with sexual communication. Mating disruption (MD) using sex pheromones has been widely investigated and three different mechanisms of disruption have been described: desensitization, competitive and non-competitive attraction (R. Cardé, 1990; Millar 2006). Even though such mechanisms have only been defined for the use of semiochemicals, they apply to all kind of sexual stimuli. Desensitization implies a decreased sensitivity to the sexual stimulus due to continuous exposure to high concentration of such stimulus. The sensory modification can happen at the peripheral nervous system level (i.e. adaptation) or at the central nervous system level (i.e. habituation) (Rodriguez-Saona & Stelinski 2009). Competitive attraction consists of the application of an artificial/synthetic sexual stimulus that competes with that which is naturally emitted by calling partners, thus decreasing the encounter rate between mates. Non-competitive mechanisms comprise camouflage and sensory imbalance. Camouflage uses high concentrations of an artificial sexual stimulus to mask the natural one, assuming that the receiver's sensitivity is unaffected by the continual exposure to the artificial stimulus. Sensory imbalance involves dispensing in the environment large amounts of one or more components of the natural sexual stimulus to alter the ratio of sensory inputs perceived by the receivers, thus disrupting the response.

2.3.1 Semiochemicals

Successful MD with sex pheromones has been achieved for several pest species, particularly moths (Rodriguez-Saona & Stelinski 2009). In this group, comprising more than 120,000 species, mate finding consists of upwind flight by the male towards a pheromone plume released by a female. Since the first pioneering field studies conducted over 50 years ago (Gaston et al., 1967), sex pheromones have now been identified for more than 2,000 species of insects and many synthetic formulations of the pheromones are commercially available for MD applications. To our knowledge, the only examples of non-lepidopteran pest for which commercial formulations of sex pheromone are available are the vine mealybug *Planococcus ficus* Signoret (Hemiptera, Pseudococcidae), the Swede midge *Contarinia nasturtii* Kieffer (Diptera: Cecidomyiidae), the California red scale *Aonidiella aurantii* (Maskell) (Hemiptera: Diaspididae) and the European pine sawfly *Neodiprion sertifer* (Geoffroy) (Hymenoptera: Diprionidae). Starting from simple steel planchettes mounted on stakes to evaporate the active compounds, many technological advances have been achieved on passive release devices through the years. Synthetic pheromones can be released in the environment through hand-applied dispensers, strategically deployed in the crop area considering the prevailing wind direction (EPPO 2019), or through impregnated substrates (e.g. micro-flakes) distributed with specifically adapted blowers (Bohnenblust et al. 2011). Currently, hand-applied dispensers, deployed at rates ranging between 250 and 1000 per hectare, are the most widely used method for dispensing pheromone (Epstein et al. 2006; Stelinski et al. 2009; Trimble 2007). Such dispensers come in different shapes, most commonly as hangable bags/planchettes (e.g. Checkmate-style dispensers) or as polymer tubes containing an aluminum wire that allows positioning by twisting the dispenser around the plant stem (e.g. Isomate-style dispensers). Electrospun mesofibers are a novel approach for MD pheromone application that allow labor saving through mechanical deployment and environmental sustainability, as the small pheromone-loaded fibers (0.6 to 3.5 micrometres) are fully biodegradable within 6 months (Hummel 2017). In recent years, high-release pheromone dispenser systems have been developed, using microsprayers or aerosol puffers (Helsen et al. 2019). Compared to passive dispensers, active systems allow for more rational diel distribution of the pheromone release and reduced labor cost for deployment. For example, Witzgall et al. (1999) reported that only 11% of the total pheromone emission from rope (passive) dispensers used for MD of *C. pomonella* was released during the pest's flight activity time. On the other hand, aerosol dispensers allow programmed releases of the sex pheromones at selected times, covering the intervals when the target species is active thus avoiding wastes of product released outside those periods.

2.3.2 Semiophysicals

Compared to the wide application of semiochemicals as behavioral disruptors, semiophysicals are used much less to disrupt pest communication. Even though, light can modulate several insects' behaviors, such as recognition of conspecifics and oviposition and foraging sites (Owens and Lewis 2018), to date, to our knowledge, vibrations and sounds are the only examples of semiophysicals used for behavioral disruption. Several insect pests rely on vibrational communication, and among them the vast majority use vibrational signals to mediate reproduction (Cocroft & Rodriguez 2005; Čokl & Virant-Doberlet 2003). Probably for this reason, one of the most successful example of mechanical pest management is vibrational MD. This strategy consists of designing a vibrational signal that interferes with the mating duet and prevents the male from locating the female, and thus from mating (Eriksson et al. 2012). Theoretically, it can be developed for most species that rely on the establishment of a vibrational duet for identification and location of the partner, as shown in leafhoppers. Usually, the male begins to emit species-specific calls that trigger the female reply; when the male perceives the female's response signal, then a vibrational duet (the alternation of male and female signals) is established (Čokl & Virant-Doberlet 2003). During the duet, the male acquires information on the location of the female, who remains stationary until reached by the male; when the two individuals are close enough, the actual courtship begins and copulation can occur (Polajnar et al. 2014). However, communication is a complex network and rivals may eavesdrop on mating duets and disrupt them by emitting specific rival signals (Virant-Doberlet et al. 2014). In the American grapevine leafhopper, *Scaphoideus titanus* Ball*,* rival males mask the mating duet and prevent the duetting couple to mate (Mazzoni et al. 2009a). By playing back the rival male's signal into the plants by means of specific transducers (i.e. shakers), mating can be artificially prevented (Eriksson et al. 2012; Mazzoni et al. 2009b; Polajnar et al. 2016). The same process has been applied experimentally in the laboratory and semi-field conditions also to other leafhopper species using naturally occurring rival signals, female signals or artificial stimuli (Gordon, et al. 2017; Mazzoni et al. 2017; Nieri & Mazzoni 2018b). Vibrational MD can be applied also to species that do not rely exclusively on vibrational communication. For instance, psyllids and stink bugs use vibrational signals to locate mates within short distances, whereas they use pheromones for long range communication. Also for these species, vibrational disruption has proved to be effective (Avosani, et al. 2020; Čokl & Millar 2009; Laumann et al. 2018; Mankin 2019). However, to date, the vibrational MD strategy has been applied in open field conditions only to leafhoppers (Mazzoni et al. 2019) and the mechanism of disruption is yet to studied. Probably it depends on the species and the disrupting signal used. For instance, when the rival signal is used, it may be effective because it is a camouflage of the duet. Whereas when using a pure tone, it may cause desensitization in either the male, who is not able anymore to locate the female, or in the female, who stops replying. The hatching behavior is another crucial step for insect survival that it is controlled by vibrational cues and it may be disrupted by means of vibrational stimuli. Recently, it has been shown that some Heteroptera species use vibrations to synchronize hatching. Vibrations can be emitted by the mother while guarding the egg mass, like in the shield bug *Parastrachia japonensis* Scott and in the borrower bug *Adomerus rotundus* (Hsiao) (Mukai, et al. 2012; 2014). Alternatively, the first embryo hatching generates vibrations sufficient to induce the close siblings to hatch, like in the brown marmorated stink bug (Endo et al. 2019; Tanaka & Kotaki 2020). Either way, synchronization in hatching seems to directly affect the survival, so if disrupted it may lead to a reduced population density (Mukai et al. 2018).

3 Integration of stimuli in the vineyard agroecosystem

Pest management in the vineyards of Trento province (Northern Italy) is a shining example of behavioral manipulation integrating semiochemicals and semiophysicals (Fig. 2). In 1998, thanks to the collaboration between growers, stakeholders, and researchers and the government support, pheromonal MD was adopted as a benchmark strategy to control population of the European grape berry moth, *Eupoecilia ambiguella* (Hübner), and of *L. botrana* (Ioriatti et al. 2011). In less than ten years, the land managed with pheromonal MD increased up to 10,000 ha, accounting for the 90% of the entire grape-growing area, and the technique has been the standard technology in this area to control tortricid moths since then. Before large-scale MD adoption, more than 90% of growers relied on insecticides to manage tortricid pests on grape, applying at least one or two treatments per year. After more than 20 years of pheromonal MD, insecticide treatments are no longer required, saving more than 15 metric tons of toxic compounds yearly, with great benefits for the environment and human health (Ioriatti et al. 2011).

Such an achievement was a first step towards the adoption of an integrated management program aimed to control populations of grape's key pests. However, the presence of other important phytophagous insects still required massive insecticide applications. To continue pursuing the reduction of insecticides usage, in 2009, a new technology was tested for the first time on *S. titanus*, a leafhopper vector of the phytoplasma disease Flavescence dorée (Chuche & Thiéry 2014). Leafhoppers rely on vibrational communication for reproduction, thus chemical ecology cannot be used for their management. By playing back in the plants the rivalry vibrational signal emitted by *S. titanus* males, the number of mating was reduced in laboratory and semi-field conditions up to 70% (Mazzoni et al. 2009; Polajnar et al. 2016). In 2017, a 1.5 ha vineyard at the Fondazione Edmund Mach (Trento province, Italy) was set up as the first vibrational vineyard in the world. About 100 transducers were installed on the trellis poles to play back into the trellis system the disturbance

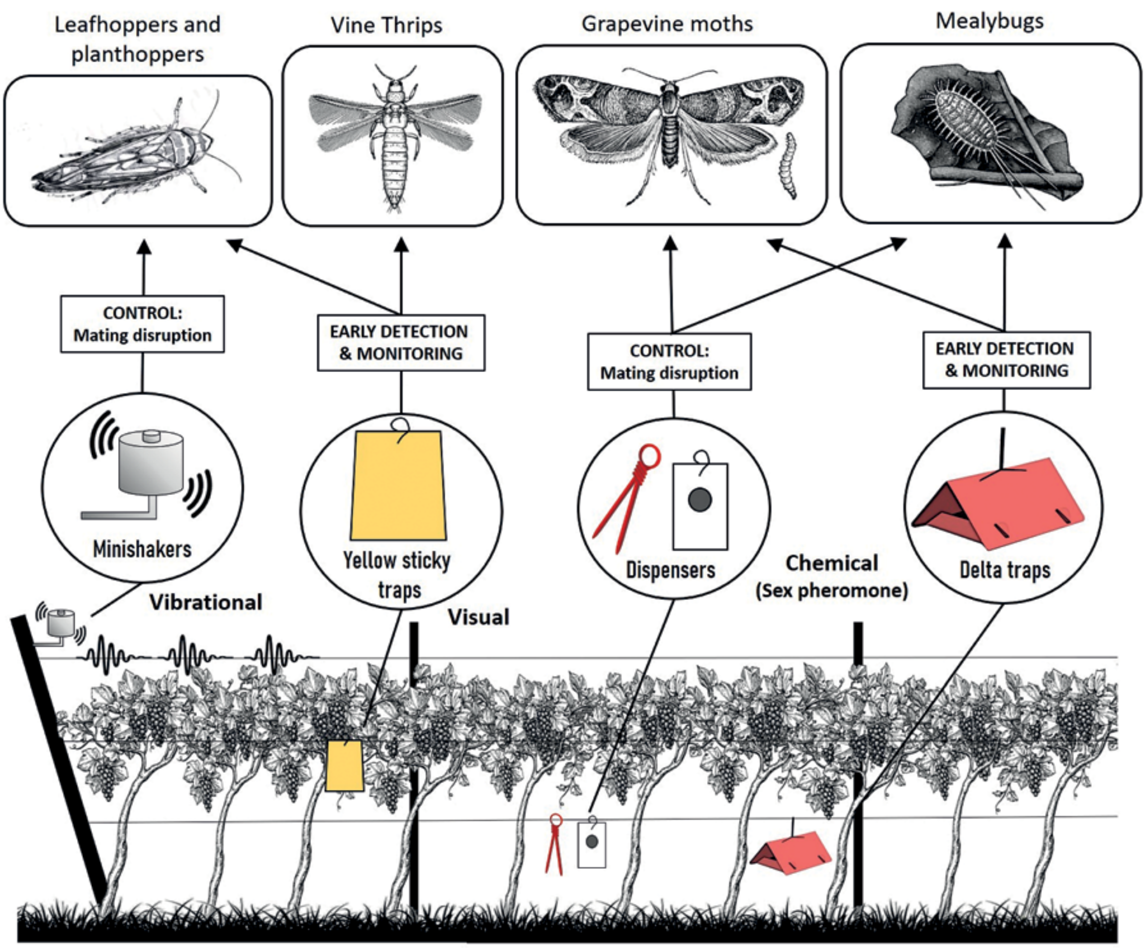

Fig. 2. A multi-modal program for pest control in the vineyard ecosystem. Vibrational, visual, and chemical stimuli are used to monitor and control different pests: leafhoppers, thrips, moths, and mealybugs.

noise specifically designed to disrupt the *S. titanus* communication (Mazzoni et al. 2019). In the subsequent years, the disturbance noise was updated to be effective in controlling also *Empoasca vitis* (Göthe), the green grapevine leafhopper. To design the updated disturbance noise, a pure tone was integrated into the signal for *S. titanus*, according to the evidences of laboratory studies (Nieri & Mazzoni 2018b). In the first two years of testing, no significant effect was detected on predators, such as spiders (Nieri & Mazzoni 2018a); thus, vibrational mating disruption is a promising technique to be added in an integrated pest management approach (Mazzoni et al. 2019). When a commercial product becomes available (a commercial product is currently under evaluation), grapevine will be the first crop in which semiochemicals and vibrations can be used simultaneously.

A different level of integration can be found when the same stimulus is used to control two or more different species. For example, various insect groups that use visual stimuli for orientation are monitored using colored traps for early warning. In particular, leafhoppers and thrips, including the vine thrips *Drepanothrips reuteri* Uzel, are attracted by yellow; thus, monitoring can be done by deploying yellow sticky cards in the vineyard (Jenser et al. 2010; Lessio & Alma 2004). Early detection is crucial for the success of IPM strategies and the possibility to combine the same detection method to several pests facilitates and promotes a timely application of environmentally friendly strategies.

The great potential of behavioral manipulation strategies lies in their high selectivity towards the target species which enables conservation biological control, allowing natural enemies of both target and non-target pests to flourish. However, we need to consider possible countereffects due to the replacement/reduction of broad-spectrum insecticides to control primary pests. The successful application of less impactful control techniques on a large scale, with the principle of Area Wide Pest Management (AWPM), can indirectly favor a resurgence of secondary pest populations, previously controlled by the conventional management. An example of this is the case of harmful tortricid moths in the vineyards of northern Italy. Following the large-scale and long-term application of MD against *L. botrana* and *E. ambiguella*, serious outbreaks of the secondary tortricid pest *Argyrotaenia ljungiana* (Thunberg) were reported. Thanks also to the chemical compatibility between the main pheromone components of the three tortricid species involved, it was possible to rapidly develop a triple pheromone dispenser for the simultaneous control of all three tortricids (e.g. Isonet LA plus), and in this way to safeguard the application of MD on the area (Ioriatti et al. 2004).

Another example of secondary pest outbreak is the Grapevine mealybug, *Planococcus ficus* (Signoret). This species has recently expanded its geographic range to Northern Italy, invading Trentino province and causing both direct damage (limiting production) and indirect damage (virus transmission) to the crop. In the absence of MD, *Pl. ficus* would have been controlled by insecticides applied to control the tortricid moths, but the elimination of these sprays allows local outbreaks of the mealybug. To potentially solve this problem, an integrated MD strategy that targets both tortricid moths and mealybugs is currently under evaluation. *Pl. ficus* sex pheromone, as a lure for pheromone traps, is available since 2006 from Suterra LLC (Daane et al. 2020); thus, researchers are testing passive double-reservoir dispensers (e.g. Isonet LPFX246) combining *L. botrana* and *Pl. ficus* sex pheromones (Ioriatti & Lucchi 2016).

4 Perspectives

In the last half century, there have been numerous advances in pest management strategies as alternative to pesticides and new solutions are still being developed. The possibility to manipulate the behavior of pests has proved to be successful, especially in specific geographic areas, such as Trento province. Nevertheless, in order to be effective, behavioral manipulation strategies need background knowledge about the behavior of target species, signal production and transmission mechanisms, and not less importantly, about the economic planning and marketing to introduce new technologies to the market.

4.1 A clear understanding of pest's behavior

Insect communication is complex and encompasses multiple modalities of communication, which are often used by the same species in one or more contexts (Higham & Hebets 2013). It is crucial to clearly understand the communication of pests to effectively manipulate their behavior. This means that in the future no modality should be overlooked when developing pest control strategies; as it happened before with vibrational communication that has begun to be integrated into pest management just recently. In the same crop system, multiple pests are present; each species may use a specific communication modality, so multiple channels must be considered for the same crop at the same time. In the future, it would be beneficial to have a holistic approach to the crop ecosystem: to target not just one modality of communication, but to adopt multimodal manipulation strategies. In this way, it will be possible to readily develop and apply the most suitable strategy for new pests that may occur in the crop. Climate change, globalization and the resulting increase in the number and impact of invasive alien species make this approach more challenging but also increasingly necessary (Heeb et al. 2019).

4.2 Mode of action and transmission of the signal

Working on multiple communication channels is challenging, because it involves several sets of skills and specializations. Both chemistry and physics are needed to explain how insects perceive and process the information we want to manipulate. Such understanding of insect communication is crucial to develop a commercial product. The studies on insect vision helped to understand what colors really matter in the deployment of traps and studies on the perception of odors enabled the synthesis of highly effective molecules. The knowledge of the active space of a vibrational signal used to disrupt the mating behavior of an insect species has had immediate bearing on the number and positions of transducers to be deployed in the field (Little et al. 2019; Mazzoni et al. 2019; Millar 2006). To be able to integrate the knowledge acquired so far in each field of study, it is important now to bring together the know-how acquired in each field. This will be crucial for the development of strategies that target species with multi-modal communication, such as *D. suzukii* (vision and odor) or stink bugs (odors and vibrations).

4.3 Product development and commercialization

Finally yet important is the socio-economic aspect of integrated pest management. No innovation would have ever be applied if it had not improved current control technologies, most often insecticide applications. The knowledge acquired with basic research provides the specifications that the new technology should use, but the main work to reduce the costs and meet the growers' needs include a multidisciplinary approach where entomologists work together with mechanical and electrical engineers, informaticians, chemists, designers and others. From the identification of the first pheromone it took almost two decades to design an effective dispenser that allowed the development of a mating disruption technique (Cardé & Minks, 1995). In applied biotremology, a rapid development in technology is quickly easing the designing process of low energy consuming and cheap transducers, but their unavailability until a few years ago is likely the main reason why this research field did not flourish until now (Mankin et al. 2011; 2020). Therefore, to ultimately integrate semiochemicals and semiophysicals in the field, an effective collaboration between all disciplines is needed.

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