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REVIEW ARTICLE

Disrupting pest reproduction techniques can replace pesticides in vineyards. A review

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Abstract
Today, we are faced with an increase in the impact of pesticides on the environment, which is becoming a real concern for most agricultural production systems, including vineyards, for a number of reasons, such as the resistance of pest populations to pesticides, the lethal and sublethal effects of pesticides on non-target species, the increase in new invasive pests, the extension of the geographical range of pests due to climate change, and, finally, human health problems. Against this backdrop, the adoption of solutions based on the reproductive behavioral ecology of pests is a subject of prominent (major) interest for the coming decades. Crop pests and, more specifically, disease vectors use sensory cues throughout their life cycle for many fundamental behaviors and in particular for mating, the critical step in population growth. In particular, a large proportion of arthropod crop pests rely on chemical and/or vibroacoustic communication to mate. Several thousand sex pheromones have been identified in insects, most of which can be used either as synthetic baits to trap pests or as behavioral modifiers (e.g., pheromone-mediated mating disruption). Applied biotremology is also emerging as a new discipline for sustainable pest control. Field experiments on vibratotional mating disruption against grapevine leafhoppers are currently ongoing, with promising results. Here we present mating disruption strategies that can be implemented in crop protection, in particular against the main pests and vectors present/occurring in grape production.

Keywords Grape moths · *Lobesia botrana* · *Eupoecilia ambiguella* · *Scaphoideus titanus* · Flavescence dorée · Biological control · Mating disruption · Green pest management

1 Introduction

Pesticides are extensively used in modern agriculture (Deguine et al. 2021), and in 2020, the global pesticide usage has been estimated to be 3.5 million tons (Sharma et al. 2019), while pesticide trades have been estimated to be over 5.9 million tons in 2018 (Sabzeravi and Hofman 2022), an amount that tripled between 1990 and 2010 (FAO 2020). This FAO survey revealed a general (all families) insecticide trade of 6,362 tons in France and of 10,400 tons in Italy, among which 20% was estimated to be used for viticulture. Legislation on pesticide use is, however, rapidly evolving worldwide following the concern of both producers and consumers. As a result, many countries have restricted the use of pesticides inciting growers to adopt alternative methods (Hillcocks 2012), for example by using green pest management approaches (see Ivaskovic et al. 2021). This is the case in the EU, which enacted the pesticide authorization directive, PAD 91/414/EEC, in 1993, reviewing over 1000 active ingredients (Hillcocks 2012). Consequently, EU country members promote more or less strictly integrated pest management (IPM), sustainable agriculture, or organic farming as production approaches (Muneret et al. 2018), and recent legislations regulate more controversial products such as neonicotinoids (Jactel et al. 2019). IPM, in its broad

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definition, is an ancient approach that can be traced back to more than a century and half ago (Kogan 1998), before the advent of a generalized use of synthetic pesticides in agriculture after the first world war. Interestingly, the evolution of IPM over time followed several paths, which depended on the progress of entomological and agronomical research (see Kogan 1998 for a review). As a result, nowadays, IPM comprises a multitude of complementary measures that can be implemented for crop protection (Walker et al. 2017; Han et al. 2022) and more specifically for grape protection (Pertot et al. 2017). Among these measures, sciences of behavioral ecology, such as chemical ecology and biotremology, have a prominent place for future insect pest management (Fig. 1).

Pest insects with sexual reproduction mostly use two types of communication between mating partners: chemical such as pheromones and mechanical such as sounds and vibrations. So called semiochemicals and semiophysicals mediate different steps of reproduction (Nieri et al. 2022). Semiochemicals for mating are mostly sexual pheromones produced by one partner (Karlson and Lüscher 1959; Wyatt 2009), while semiophysicals are mostly substrate borne vibrations, which travel along the surface of plant tissues (Strauß et al. 2021) and are usually emitted by both partners that establish vibrational duets. Semiophysicals have been recently defined as physical signals and cues that have the potential to elicit a behavioral response in animals. Colors, lights, sounds, and vibrations are typical examples of semiophysicals, and their action can interfere with a wide range of different behaviors, such as mating, feeding, host and prey searching, alarm, aggregation, and several others (Nieri et al. 2022). A large number of pheromonal compounds (> 2000) have been isolated in insect pests and vectors (Ujvary 2010), and sex pheromones have been identified so far in over 500 arthropod species (Pherolist 2022), a large proportion of which can be used in crop protection, either for monitoring as lures in traps or for mating disruption (MD). On the other hand, substrate borne communication concerns species which rely on vibrational signals, and the number of insect species that are estimated to use this channel is approximately 200,000 (Cocroft and Rodríguez 2005). Biotremology is the discipline that studies how animals, including vertebrates, can communicate by means of substrate borne vibrations (Hill and Wessel 2016). The evident homology between semiochemicals and semiophysicals are motivating scientists to develop techniques of behavioral manipulation based on semiophysicals, which are quickly becoming of great interest for industries that operate in the pest control market.

Beside colored sticky traps and light traps, which are classic examples of semiophysicals that have been used in pest control for many years, a new concept of applied research has emerged over the last decade based on insect vibrational communication to manipulate and/or interfere with insect behaviors (Polajnar et al. 2014a; Mazzoni and Anfora 2021). This approach is in its infancy but is quickly spreading among scientists while industries in the crop protection sector are starting to invest in biotremology to develop new solutions. It seems clear that vibrations as semiophysicals have many points in common with semiochemicals but also peculiarities that needs to be substantiated. This article reviews what is currently known about the two mating disruption (MD) strategies, pheromonal and vibrational, that can be implemented in crop protection, especially against the current major pests/vectors occurring in grape production. World grape production is estimated to be above 7 Mha (OIV 2022), which makes it an interesting case study to achieve significant insecticide reduction. The historical background and the perspectives of the mating disruption techniques as alternatives to insecticides are discussed.

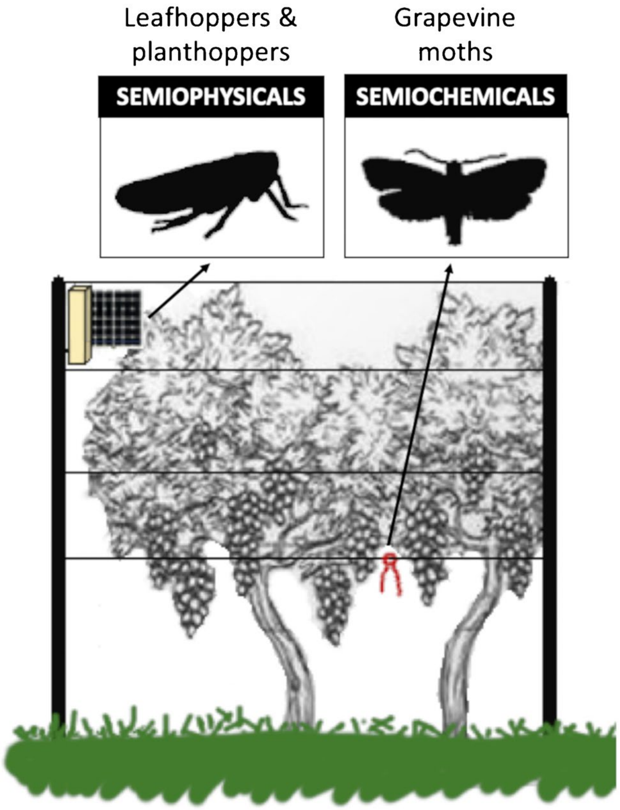

Fig. 1 Integration of semiochemicals and semiophysicals for the control of vineyard insect pests

2 Historical facts regarding behavioral manipulation

The existence of sex pheromones had been suspected for centuries, already by Darwin, then by Fabre and even by the Nobel von Frisch, but only in the years 1958–1959 a hard scientific race led for the first time to the identification of two insect pheromones: the honey bee queen substance (Butler et al. 1959; Barbier and Lederer 1960) and the bombykol, the silk moth sex pheromone (Butenandt et al. 1959). This knowledge opened the door to the use of synthetic pheromones in crop protection as behavioral control agents to disrupt inter-sexual communication. In this regard, the first clear description of the principles of mating disruption was done by Beroza (1960): "…one interesting prospect for control without the use of toxicant, is the spraying of the natural sex attractant over a wide area in order to confuse males in their attempts to locate females of their species."

Interestingly, he clearly proposed something resembling pheromone spray (see below the analogy with microencapsulates), a principle which was therefore developed rather early (Campion 1976; Dubey 2009). Wright (1964) clearly stated the use of pest behavior control agents to replace pesticides "… I believe that in the long run the use of behavior control agents offers a better, safer, more effective, and cheaper means of pest control than is likely to be achieved by pesticides …. For this reason, I think that research in this field needs to be greatly expanded but it must also be properly directed. I think I have shown that the obvious things to do are not necessarily the best things to do." This sparkled a lot of research, both in the field and in the laboratory, to describe the mechanisms of action of pheromones that was greatly assisted by advances in aerodynamics (e.g., wind tunnels) and electrophysiology of the olfactory systems (antennas and antennal lobes in the brain). A first control of the oriental fruit moth, *Cydia molesta* (Tortricidae), was indeed obtained on a large surface in Australia (Rothschild 1975), and assays of pheromonal mating disruption (PMD) were extended against several other pest moths (e.g., Campion 1976), especially tortricids, which are among the main pests of fruits. PMD became very popular in the late 1990s, when Gut and Brunner (1998) and Evendem and co-authors (1999) obtained very promising results in controlling the codling moth, *Cydia pomonella*, and two other orchards tortricids. However, the real turning point was the experiment conducted in the biennium 1991–1992 in the Tulbagh valley (South Africa). Here, 1200 ha of peach crops was treated with PMD allowing for an impressive drop in damage from 49%, despite 13 applications of organophosphates, to 0% (Barnes and Blomefield 1997). This outstanding result gave much popularity to PMD that was registered for grape use in UE in 1995. Since then, PMD has spread worldwide and nowadays, approximately 800,000 ha of crops are managed with this technique (Witzgall et al. 2010; Benelli et al. 2019; see Ready and Guerrero 2010 for crop examples).

As for pests that rely on substrate borne vibrations for mating communication, it was only in 1949 that the Swedish entomologist Frej Ossiannilsson (1949) first hypothesized the existence of this channel of communication, which is inaudible to the human ear. Only in the 1970s was the first evidence of vibrational communication in insects found by Gogala and co-authors (1974) in Cydnidae bugs, while first pioneering experiments in applied biotremology date back to 1980, when sounds transmitted to plants by means of different types of musical instruments disrupted mating of a leafhopper and a planthopper species (Saxena and Kumar 1980). The most important finding of this early experience was that pure frequency airborne vibrations (i.e., sounds) transferred to the substrate can significantly reduce the mating success rate of the target species, provided that (I) specific frequencies are transmitted to the plant and (II) a minimum amplitude (measured as velocity of the vibrated substrate) is guaranteed. If these two requisites were not respected, then the disruption efficacy decreased. After more than 40 years, these principles are still considered the key to achieve vibrational mating disruption (VMD). VMD is therefore a technique of pest control based on the release into the plants of vibrational disturbance signals with the aim to interrupt the vibrational mating communication between a male and a female (Eriksson et al. 2012).

3 Sexual pheromones in vineyards to control moths: attraction *vs* mating disruption

The grape berry moths *Lobesia botrana* and *Eupoecilia ambiguella* have been the most important grapevine insect pests worldwide for centuries (Marchal 1912; Ioriatti et al. 2011, Thiéry et al. 2018; and see a recent review in Benelli et al. 2023). Their larvae attack and feed on berries causing injuries and thus favoring the spread of different fungi, some of them being responsible of ochratoxins production that can be toxic or carcinogenic (Cozzi et al. 2006; Delbac and Thiéry 2016). Females of the two grape moths produce few amounts (range of 2–15 ng, our personal unpublished data) of sex pheromone. At dusk, and only for a few hours, the female extrudes the pheromone from the abdominal gland to emit it, while fanning the wings in a typical posture (Fig. 2).

Such minute amounts of pheromone can attract males from a long distance. Males follow the smell to reach the calling female or, alternatively, any emitting source of synthetic pheromone. Several systems of pheromone dispensers may be used to release enormous amounts of pheromone in the air onto the crop (Fig. 3). As an example, in grapes, 500 Rak dispensers per ha are usually placed (Ioriatti et al. 2011), each one diffusing throughout the grape growing season, 250 mg of formulated substance. Hence, one dispenser corresponds to approx. 10 million emitting females. At the dose of 500 dispensers, the pheromone release of five billion females equivalent can be expected per ha; males are not able to find females, and thus the behavioral processes leading to mating are disrupted.

Fig. 2 Typical posture of *Lobesia. botrana* female emitting her sex pheromone at dusk. Photo by Stefan Rauscher

3.1 Behavioral mechanisms behind PMD in moths

The behavioral sequence that leads a male to find a mate is known in detail and well described in the literature (Mafra-Neto and Cardé 1994; Cardé and Knols 2000; Miller and Gut 2015). The disruption of this behavior involves sensory interference, camouflage, competition, and impairment of orientation. In pheromone saturated clouds, males are unable to perceive either the longitudinal or lateral plume gradients. The latter are necessary to perform the classical orientation behavior that keeps the male within a pheromone plume released by a female (e.g., lateral casting and counterturning visualized as a sort of zigzag within the plume boundaries) (Cardé and Willis 2008). Saturation of olfactory receptors and antennal lobe interneurons are also involved. The consequences of these two mechanisms are that males lose the odorant path and are unable to find the precise source of the odor. The competition between natural female sources and synthetic lures, which conduct males to follow false trails, has been described as well. In most cases, PMD against grape moths is more efficient in large spatial scale application (i.e., area-wide) (See Ioriatti et al. 2011), but, in a few cases, oviposition was also reduced in small plots if they were isolated and treated with high concentration of synthetic pheromone just before mating (our unpublished data). Interestingly, Harari et al. (2011) tested the "handicap principle" evolutive theory (Zahavi 1975) in the pheromonal system of *L. botrana*, finding that the sex pheromone is a costly "honest signal." In this work it was proved that females detect and respond to their own pheromone and also to its major synthetic component, and that signaling is costly for females in that associated to a significant reduction of female lifespan and egg laying. Another important characteristic of PMD is that females tend to move more and eventually to escape from PMD treated plots, a behavior that reinforces the efficiency of the method (Harari et al. 2014). Altogether, these results suggest that the optimal efficiency of the PMD technique is linked to a homogeneous cloud structure of the pheromone in a treated area especially when applied to area-wide surfaces. Therefore, the optimization of PMD efficiency could be achieved in different ways. Developing and placing several pheromone physical sensors in the vineyard to help regulate the concentration and build mathematical models of spatial diffusion for correct release on the crop could be an issue (Ivaskovic et al. 2021).

3.2 Specificity of PMD based on pheromones chemical structure and insects neurophysiology responses

Sex pheromones are commonly known as species specific messengers, and nearly all of the 140,000 known species of moths have one. However, there are some exceptions, and sometimes different species, even if distantly related, share the same major pheromonal compounds. In this regard, the anecdote of the Asian elephant, *Elephas maximus*, is well known and rather spectacular. Elephant females excrete looplure ((z)-7-dodecen-1-yl acetate) in their urine as a sex pheromone to signal their readiness to mate to males

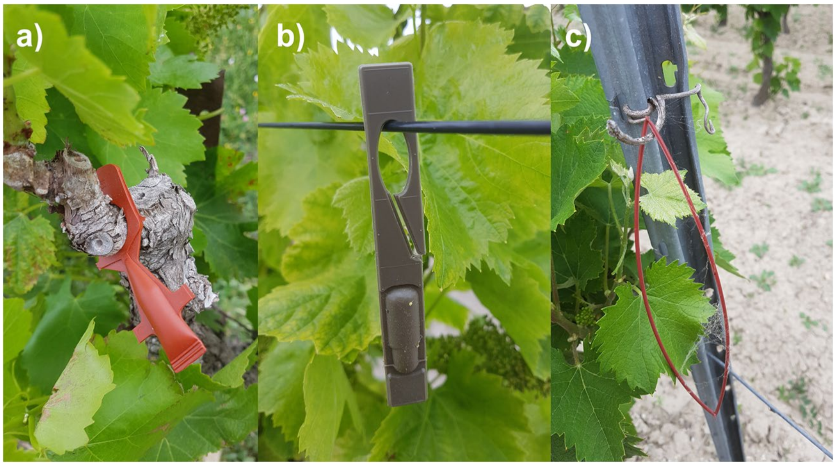

Fig. 3 Three examples of porous polymers passive dispensers recently developed for viticulture (trade marks not specified, pictures of D. Thiery). The following two main types of dispensers are presented: **a**–**b**) ampoules and **c**) tubes filled with pheromone. Hanging position may vary. Older versions of passive dispensers traditionally used since the 1990s (Raks© and Isonet©) and active dispensers ("Puffers" type) are not presented here

(Rasmussen et al. 1982); however, looplure is also used by more than 126 moth species for the same reason (Rasmussen et al. 1996; Mitchell 1975; Wyatt 2014). Active ingredients typically comprising the pheromone blend in Lepidoptera are fatty acids derivatives, mostly C12–C14 chains, and unsaturated esters, alcohols, or aldehydes with more than one chemical components. Single components may differ due to their structure and geometry (i.e., chain length, isomers) or due to the different position of double bonds (Tumlinson 1990 and see the Pherolist 2022 for an extensive database).

Most insects, including moths, have a very sensitive olfaction, and both environmental odors and sex pheromones are well detected by the olfactory system. The peripheral and central structures and their organization have been studied for three decades in different model insects (Ochieng et al. 1995; Kurtovic et al. 2007; Couto et al. 2017; Liu et al. 2021). Early works identified strong sexual dimorphism in both peripheral and central structures, and the neural activity of peripheral sensory cells innervating the tens of thousands trichoid sensilla on male moth antennae has been largely studied (Van der Pers and Den Otter 1978; Kaissling 1996 and refs herein). These works were made possible thanks to two main techniques: electroantennography (EAG) and single cell recording (SCR). Both are still the basis of electrophysiology; EAG is now being applied directly in the field to measure fine variations in the pheromone concentration in the air (Pawson et al. 2020). The antennal lobe structures in the brain were also deeply studied and characterized together with the macroglomerular complex, a specific channel for processing pheromone information, found only in males (Todd et al. 1995; Berg et al. 2002). Recent advances and flourishing research concern the biochemical nature of olfactory receptor proteins or ligands, which enables odors to reach the dendritic surface of the nerve cell (e.g., Missbach et al. 2014; Wicher and Miazzi 2021; Zhou 2010).

3.3 Current technologies to dispense pheromones in the air

Sex pheromones can be released into the air in three different ways: (1) passive diffusion, by means of porous polymers (small polymers dispensers hanged in the vineyards) (Fig. 4); (2) sprayers or microencapsulates of polysaccharides or polymers that can be sprayed on the crop (Dubey 2009; Stelinski et al. 2007); (3) the combination of the two techniques. Example of passive release is the small jars (e.g., Raks) and tubes (Isonet) that were developed and homologated in the 1990s and are still in use in large areas of vineyards where they ensure a season-long control of grape moths from April to harvest. Aerosol devices, instead, are active dispensers that can be programmed to ensure the pheromone release in the proper time of the season and of the day to maximize PMD efficiency. An advantage of this method is also that few dispensers can be positioned in the plots thus sparing time and money fort their application. However, there is still debate about their efficacy in comparison with passive dispensers (Benelli et al. 2019). The principle of microencapsulated pheromones has already existed for several decades (Campion 1976), and a substantial amount of field and laboratory research has been dedicated to it (e.g., Trimble et al. 2004; Waldstein and Gut 2004; Stelinski et al. 2005; Benelli et al. 2019), but, surprisingly, it has not been so far satisfactorily developed for large crop areas.

Fig. 4 Female of *Scaphoideus titanus*, the first insect studied to be controlled by vibrational mating disruption, on a grapevine leaf. Photo by Umberto Salvagnin

3.4 Pheromonal mating disruption side effects

Comparing to the rather long time use of PMD in crop protection, and the million ha crop area involved (Witzgall et al. 2010), research considering the side effects on the local entomofauna appears rather limited, and publications are rather rare (Thomson et al. 2001; Martinez and Mgocheki 2012 for a review). The development of PMD was always viewed as minimizing the negative effects of classical insecticide control; however, side effects were already reported. Because selective against the targeted pests, outbreaks of secondary pests may occur and have been recorded in apple orchards as a consequence of PMD (Walker and Welter 2001). Alternatively, PMD may have some positive side effects on other pests. Martinez and Mgocheki (2012) studied five species of in galling aphids in the surroundings of 130 ha apple orchards PMD treated with codlemone for 18 years and found reduction of these galling aphids population in the trees surrounding the crop. This type of long-term study is however too limited and should be extended in the next years to vineyards areas. One interesting issue should for example test if moth's egg parasitoids or predators are attracted by the female sex pheromone which may represent an "honest" signaling of host presence.

In our present review, we did not consider the effect of a large amount of sex pheromones released in crops under PMP on human health. To our knowledge no convincing long-term databases or publications exist. However, cases of lasting headaches have been observed in practicians involved in dispenser hanging in the crops. The extension of PMD areas should however open the gate for epidemiological studies.

4 Vibrational mating disruption of grapevine leafhoppers

4.1 Role of vibrational signals in the mating behavior of Scaphoideus titanus

Phloem and xylem feeding insects (e.g., aphids, leafhoppers, scales) infest many crops and can sometimes transmit viruses, bacteria, or phytoplasmas, causing significant damage to agricultural production. Among these, there are many species that use vibrational communication to mate (Cocroft and Rodríguez 2005), and in the case of grapevine, one of them is the American grapevine leafhopper, *Scaphoideus titanus* (Fig. 5), which is the main flavescence dorée vector in Europe (Schvester et al. 1961; Chuche and Thiéry 2014).

Pair formation in *S. titanus* is mediated by species- and sex-specific vibrational signals that allow males to make first contact with females, thus establishing a vibrational duet with them. The process of pair formation passes through four distinct phases, each of them characterized by different signals and strict duet rules (Polajnar et al. 2014b). The first phase, called call-fly, consists of males actively searching for females within the vine canopy. A male emits a "calling song" made of a train of pulses (MP1) to elicit a female reply. In case of no replies, males fly away to another leaf and resume calling. This strategy is an adaptation used by insects in search of a mate within the environmental constraints of vibrational communication, in order to increase their active space network (Hunt and Nault 1991; Mazzoni et al. 2014). When a female replies to the male call, the "identification" phase can start. A vibrational duet is established, led by the male that emits relatively shorter trains of MP1 to which the female replies with her own pulses (Female Pulse, FP). During the third phase, the "location" phase, a male keeps on emitting MP1, while alternating signal emissions and walking along the plants in the direction of the replying female (Mazzoni et al. 2009a; Polajnar et al. 2014b).

The male search is driven by the perception of the FP, which gives to the male information of direction and distance (Eriksson et al. 2011). The directionality of the *S. titanus* male's search has been demonstrated by means of laboratory experiments where the number of "correct" male decisions (i.e., towards the female) were found to be significantly higher than the "wrong" ones (i.e., towards other directions) (Polajnar et al. 2014b). This finding proved that the perception of the female signal is a prerequisite for males to take decisions while searching. Another important piece of information for the male is the perceived amplitude of the female signal. This is a crucial element that triggers the passage from "location" to "courtship" phase, which is the fourth and last phase before mating (Polajnar et al. 2014b).

4.2 Physical properties of vibrational signals emitted by leafhoppers

Vibrational signals consist of bending waves, whose attenuation (i.e., reduction of amplitude) is frequency dependent (Michelsen et al. 1982). This means that certain frequency components of a signal better tune with the plant structure and that low-frequency components are transmitted over longer distances than high-frequency ones. MP1 has a dominant frequency between 150 and 200 Hz, which could be considered well-tuned with grapevine tissues and thus can be transmitted efficiently for a relevant distance, covering a full grapevine shoot of 50 cm (Eriksson et al. 2012; Mazzoni et al. 2014). However, as soon as males reach the female's leaf, they immediately change their behavior and start to

Fig. 5 Prototypes of shakers for the transmission of DN in the vineyard. **a**) Version of 2017 powered with cable, currently installed in the"vibrational vineyard" of San Michele all'Adige (Italy); **b**) newest standalone version, with built-in solar panel, available from 2023. Photos by Rachele Nieri.

emit a specific courtship signal characterized by a second strong pulse (MP2) and a harmonic sound called "buzz" with frequency span between 600 and 1200 Hz (Mazzoni et al. 2009a). Given this high-frequency pattern, the "buzz" would dissipate very easily along the plant to the point that it would be detectable only in the leaf where it is emitted by the male, even by highly sensitive sensors like laser Doppler vibrometers. Not surprisingly, males never emit the courtship signal when they are not on the same leaf as a female, thus avoiding a waste of energy: the higher the frequency of the vibrations, the higher the energy consumption (Hill 2008). The activation of the courtship signal is independent from the sight of the female because males start to emit it even if the female is on the opposite side of the leaf. It is relevant to note that there is a sudden drop of about 10 dB in amplitude between the leaf (including the petiole), from which the female signal is emitted, and the nearby stems and leaves (Eriksson et al. 2011 and 2012; Polajnar et al. 2014b). This fact suggests that the leaf of the emitting individual is characterized by signal amplitude values clearly superior to any other part of the plant; therefore, when the signal perception is above a certain amplitude threshold, males switch from searching to courtship behavior. Such a value is the highest amplitude that a *S. titanus* signal can reach on a grapevine leaf. The "safety threshold" is defined as the amplitude value that makes the disturbance noise (see next section) able to mask the natural *S. titanus* signals even when a male and a female occur on the same grapevine leaf (Mazzoni et al. 2019; Polajnar et al. 2016). This value has been experimentally defined, and it is approximately 10 μm/s of surface vibration velocity (Polajnar et al. 2014b).

4.3 Male rivalry behavior and VMD early trials

The above described behavior happens when a male and a female establish a vibrational duet in the absence of any external disturbance. However, the cornerstone that unveiled the possibility to apply VMD to *S. titanus* was the discovery that *S. titanus* males rival one other to gain access to females by emitting the "disturbance noise" (DN) (Mazzoni et al. 2009a, b). In practice, a male that eavesdrops on an ongoing duet between another couple has two main choices: (1) satellite behavior, which means to eavesdrop the FP emitted during the duet with another male, hoping to reach the female before the duetting male and without emitting a single MP; (2) emission of DN to mask the FP and hide the information regarding the distance from the female and direction to take from the other male (Mazzoni et al. 2009a). In fact, the DN is a vibrational signal that has the immediate effect to interrupt an ongoing mating duet. When the male resumes calling, there is another DN emission that frustrates the attempt. The duel can go on for long time, with also role reversals between caller and disrupter. The reason of the DN efficacy is that it has a spectral pattern very similar to the FP and, at the same time, the rival male can emit the DN in the same time window as the FP, thus overlapping it perfectly (Mazzoni et al. 2009a; Eriksson et al. 2012).

Once the mechanism of male-male rivalry had been described and understood (Polajnar et al. 2014a, b), the next step was to turn this knowledge into practice by means of laboratory bioassays. In a sound-vibration insulated environment, the DN was played back into grapevine leaves, by means of mini-shakers, to test the potential to prevent mating in *S. titanus* pairs. In these controlled conditions, it was possible to disrupt the mating of pairs of virgin individuals (Mazzoni et al. 2009b), and similar results were obtained in semi-field trials, testing pairs released on caged potted plants (Eriksson et al. 2012), and in field trials, testing pairs released in net sleeves wrapping grapevine shoots (Polajnar et al. 2016). In the first case, *S. titanus* virgin pairs were placed on five caged potted plants connected to one another through a metal wire, thus simulating a real trellis condition. In the second case, a shoot of 20 leaves, from the middle part of each of five grown plants in a commercial vineyard, was isolated in a nylon-netting sleeve. In both cases, a custom-made electromagnetic shaker, which was attached directly to the wire, was used as a source of disruptive signals (i.e., DN) and all plants were at a maximum distance of 10 m.

Field trials were replicated with different diel operation patterns that revealed how the VMD is consistently efficient as long as the DN is transmitted to the plants. This holds true even if the emission is interrupted for some hours around 12 AM to 5 PM, in correspondence to the highest peaks of daily temperatures. Conversely, any other DN interruption failed to prevent mating (Polajnar et al. 2016). The explanation of such results is that *S. titanus* is a crepuscular insect, and its activity of flying (Lessio and Alma 2004) and mating (Mazzoni et al. 2009a) is concentrated at sunset and continues during the night. In a recent paper (Akassou et al. 2022), recording sessions with a laser vibrometer in semi-field and field conditions confirmed that *S. titanus* males call mainly in the evening.

4.4 Application of VMD in commercial vineyards

Once the possibility to disrupt the mating communication of *S. titanus* was assessed in laboratory and semi-field conditions, it was then time to validate the VMD technique in a real setting that is a commercial vineyard with a natural *S. titanus* population. Thanks to the semi-field trial (Polajnar et al. 2016), it was ascertained that a continuous transmission of the DN with a specific frequency profile and above a certain amplitude threshold was crucial to effectively disrupt *S. titanus* mating; however, how to satisfy both requisites for larger applications (i.e., a whole vineyard) was still unknown. Several custom prototypes of electrodynamic shakers and the respective installation systems were tested in field conditions to check their capability to transmit the DN. The working distance of a shaker for vibrations is constrained by the dampening of the intensity due to the material characteristics and coupling of the system elements (trellis and plants) (Mazzoni et al. 2019). In 2017, the prototype that guaranteed the longest working distance (Fig. 5a) was selected, and the first "vibrational vineyard" was established at the campus of Fondazione Edmund Mach at San Michele all'Adige (Northern Italy) (Mazzoni et al. 2019). In total, 110 shakers, pre-set with the DN, were installed to cover an area of about 1.5 ha of organic cabernet franc (2 arms guyot rearing system). The shakers were attached to the metal poles of the existing trellis system, positioned along the row to ensure the possibility to perform all the maintenance activities of the vibrational vineyard, so that productivity was not affected and growers could continue their practices.

One of the main technical problems was to ensure that the DN was transmitted above the safety threshold of 10 µm/s of substrate displacement velocity. To accomplish this task, two shakers were deployed for each row at 50-m intervals.

4.5 Technical assessment of VMD effectiveness

The method of efficacy assessment was performed by monitoring the vibrational vineyard from both a technical and a biological point of view. From the technical side, the DN intensity was measured from the wires of the trellis system and from the leaves of the plants by means of laser vibrometers and high-sensitive accelerometers (Nieri et al. 2023). The signal analysis showed that the safety threshold was ensured for most of the treated plants the same year of the installation. However, it is important to notice that the plant growth during summer progressively reduced the working distance; similarly, the device wear due to the years of operation (from 2017 to 2022) significantly affected the prototype performance and thus the DN propagation. In fact, the weight of the canopy in grapevines changed dramatically during the growing season, and consequently the DN dampening progressively increased, thus reducing the measured amplitude from the leaves in the course of the summer. On the other hand, use and climatic conditions affected the materials of the shakers, stressing the coupling between the shakers and the poles to which they were coupled and reduced the transmission capacity of the system. Nevertheless, the results of the biological monitoring were satisfying for at least 3 years after the first application (see below the section *Biological assessment of VMD effectiveness*). In this regard, it is worthy to mention that the system was purposely turned on in continuous mode (12 months a year, 24 h a day) from day one of installation to assess its durability, and, for this reason, we can expect much longer durability of the device, if used with rationality.

Another important point of concern is the energetic demand of the shakers. The "vibrational vineyard" at San Michele all'Adige was cabled for the entire treated area. But in 2018, groups of prototypes assisted by a solar panel were successfully tested in two other vineyards in Northern Italy (in Piedmont and Trentino, respectively), and the newest stand-alone version (available from 2023) is a shaker associated with a small solar panel (Fig. 5b).

Durability and energy supply can be better managed if the DN emission is regulated, for instance, by optimizing the shaker activity. This can be done by coupling the system with climatic sensors, because the calling activity of *S. titanus* depends also on environmental temperature and wind (Akassou et al. 2022). Moreover, a constant maintenance, which is required over the years to prevent loss of efficacy, can be achieved with internal monitoring sensors to promptly intervene if a shaker is not able to ensure the safety threshold. In fact, even if only one shaker fails to perform correctly, it would determine a space of silence in the canopy that could be exploited by the insects to resume calling and eventually mate (Polajnar et al. 2016). In this regard, in order to estimate the exact disruption coverage of the treated vineyard by monitoring the shakers installed in the area, it would be necessary to understand the correlation between the signal intensity at the source (i.e., on the shaker or on the adjacent wire) and the intensity of the DN measured from the plant.

5 Biological assessment of VMD effectiveness

To measure the VMD effectiveness, from 2017 to 2022, the *S. titanus* population density in the "vibrational vineyard" was estimated by performing visual monitoring to count the number of immature individuals (about 500 leaves were checked weekly from mid-May to the end of August) and placing yellow sticky cards to check for adults (about 5 traps replaced weekly from June to October) (Nieri et al. 2023). The same monitoring activities were performed in an adjacent organic vineyard of control, with the same variety and the same management. *S. titanus* is a univoltine species, and for this reason the VMD efficacy assessment was done by counting the individuals emerging during the next year. In 2018, 2019, and 2020, the overall number of immature stages in the area exposed to DN was significantly lower compared to the non-vibrated area. The reduction was 63%, 36%, and 43% each year, respectively. In 2021 and 2022, we did not observe any significant difference in the number of individuals between the two areas. This could be explained by the reduced ability of the shakers to ensure the safety threshold of the DN on all the plants in the treated area. The number of individuals captured by the yellow sticky cards did not show the reduction that would have been expected after the visual monitoring of the immatures. In all years, a higher number of individuals were captured in the treated area compared to the control, even if the difference was not always significant. The contrast between the results of the two monitoring systems is probably due to a side effect of VMD on the flight activity of *S. titanus* adults that bias the monitoring system (see below the section VMD side effects).

5.1 Extension of VMD to other target pests

Studies on VMD against *S. titanus* paved the way to the investigation of new target species and in general of new biotremology applications in agricultural pest management. For instance, the green leafhopper, *Hebata* (= *Empoasca*) *vitis*, and the glassy-winged sharpshooter, *Homalodisca vitripennis*, rely on a male-female vibrational duet (Nieri and Mazzoni 2018a; Nieri et al. 2017), which is susceptible to disruption by means of species-specific disturbance signals, as in the case of *S. titanus* (Nieri and Mazzoni 2019; Gordon et al. 2017; Mazzoni et al. 2017).

Hebata vitis is the most common species in European vineyards where it can cause severe leaf damages thus requiring in some cases insecticide treatments (Pavan and Picotti 2009; Fornasiero et al. 2016; for this reason the extension of VMD to this species seems to be very convenient for field applications. In spring 2018, the shakers installed in the "vibrational vineyard" were adjusted to play back in the trellis system an upgraded DN version, which was able to interfere with both the leafhoppers, *H. vitis* and *S. titanus*. The results were almost immediate on *H. vitis*, which, unlike *S. titanus*, has two/three generations per year (Alma 2002), with a reduction of about 30% immatures in the first year of application between the control and the treated area (Mazzoni et al. 2019). Such a difference was found to be significant until 2020, having been 54% and 43%, in 2019 and 2020, respectively. In this case, even though the population was still lower in 2021 and 2022, the difference between treated and untreated areas was not significant (Nieri et al. 2023).

Homalodisca vitripennis is only present in America, where it is of great concern for wine growers, being that it is the vector of the bacterium *Xylella fastidiosa* which causes Pierce's disease in grapevines (Davis et al. 1978; Krugner et al. 2019). Unlike *H. vitis* and *S. titanus*, glassy-winged sharpshooter males do not emit a masking rival signal to disrupt antagonist males but rather they mimic the female signals to attract their rivals and disrupt them from mating (Nieri et al. 2017). The acquisition of this knowledge took scientists to synthetize artificial female signals that were capable to manipulate males' behavior (Mazzoni et al. 2017). Subsequent studies in semi-field situations showed that when exposed to a disruptive vibrational playback, less than 1% of females mated, thus supporting the hypothesis that the VMD may integrate other management tactics to suppress GWSS populations (Krugner and Gordon 2018). These results are of high relevance, because they suggest that VMD strategies have a large spectrum of target species being theoretically applicable towards all plant-dwelling insects that rely on vibrational signals for intraspecific communication.

5.2 VMD side effects

The field-scale experiment in Northern Italy has been of great importance also to investigate side effects of the transmission of DN in the vineyard agro-ecosystem on (1) non target species and on (2) non target behaviors of the target species.

When developing new control strategies, particular attention must be paid to detrimental effects on beneficial arthropods. Spiders and parasitoids are the main natural enemies of leafhoppers, and in many cases, they rely on vibrational cues to detect their preys/hosts (Murphy et al. 1998; Virant-Doberlet et al. 2011, 2014). An important research question was whether the DN could negatively affect their presence in the "vibrational vineyard." For this reason, they were an object of constant monitoring. The response given by the first 5 years of application in San Michele all'Adige was that the density of spiders and parasitoids did not differ between the "vibrational vineyard" and the control (Nieri and Mazzoni 2018b). In this case, however, more in-depth studies are needed in order to exclude any harmful effect on no-target invertebrate species, in terms of their fitness, ability to find their prey/hosts, and in terms of population composition. In fact, the continuous presence of DN could play in favor of certain species and against others, thus modeling the community.

The unexpected higher number of captures on the yellow sticky traps of both *H. vitis* and *S. titanus* in the treated area compared to the control was in clear contrast with the number of immatures counted during the visual monitoring. This is probably due to side effects of the DN towards the leafhoppers' behavior. A laboratory study showed that vibrations affect *S. titanus* oviposition and flight activity. In particular, females laid fewer eggs, and the flight activity of both males and females was significantly increased when individuals were exposed to the DN (Zaffaroni-Caorsi et al. 2022). The oviposition trial, however, was only 10 days long, a time too short compared to the life cycle of *S. titanus* females, which can be up to 2 months long (Chuche and Thiéry 2014; Bocca et al. 2020). This result must be further investigated with a longer experiment. As for the flight trials, as above mentioned, males display the call-fly behavior when they do not perceive a female response to enhance their possibility to find a mate. It descends that when the VMD works, males do not establish a duet with the females and tend to fly more. Consequently, they become more susceptible to be caught by yellow sticky cards. On the other hand, the increased flight activity of both sexes seems to support the hypothesis that the DN induces stress in the individuals in that they tend to remain on the plants for shorter periods of time, and possibly, in the long term they eventually escape from the vineyard, similarly to what observed in grapevine moths exposed to PMD (Harari et al. 2014). This phenomenon could also affect the feeding behavior and, in turn, the ability to transmit agents of plant diseases, like phytoplasmas and viruses. In this direction, a recent paper demonstrated that the exposition of males of the spittlebug *Philaenus spumarius* to playbacks of female signals significantly modified their feeding behavior (Avosani et al. 2021). If this effect is true also for *S. titanus*, its ability to transmit the flavescence dorée phytoplasma from an infected vine to a healthy one might also be negatively affected. Research is currently investigating this interesting topic that could potentially attribute to vibrations and VMD a totally new relevance.

As a general consideration, besides the mere mating disruption, VMD seems to reduce the fitness of *S. titanus* by targeting multiple behaviors at the same time. This phenomenon is known also for PMD (Torres Villa et al. 2002), thus confirming the similarities between the two methods.

6 Concluding remarks

Sixty years ago, scientists had already advocated the idea of using behavior control agents for a better, safer, more effective, and cheaper means of pest control compared to insecticide use. Over the years, an enormous amount of knowledge has been accumulated from these fields of research and has resulted in methods of control currently in use or in advanced developmental stages for many different insect pests. These innovative methods based on behavior modifications are targeted against pest reproduction, but they may impact also other behaviors, such as oviposition, in a synergistic way. For this reason, they represent powerful alternatives to insecticide use against the major pests in the agricultural field including grape production. Our review shows that so far, few side effects have been observed, but large investigations are now needed to evaluate the environmental risks. Even so, techniques based on pheromones and vibrations are expected to contribute to a better and safer crop protection in the near future.

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