Manipulating behaviour with substrate-borne vibrations – potential and use for insect pest control

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Abstract

This review presents an overview of potential and use of substrate-borne vibrations for the purpose of achieving insect pest control in the context of integrated pest management. Although the importance of mechanical vibrations in the life of insects has been fairly well established, the effect of substrate-borne vibrations has historically been understudied, in contrast to sound *sensu stricto*. Consequently, the idea of using substrate-borne vibrations for pest control is still in its infancy. Our review therefore focuses on theoretical background, using it to highlight potential applications in field environment, and lists the few preliminary studies that have been or are being performed. We also note conceptual similarities with the use of sound, as well as limitations inherent in this approach.

1. Introduction

Since the groundbreaking public exposure of the risk to the environment and the public health posed by chemical methods of pest control [1], there has been an ongoing effort to reduce harmful effects of pesticides, either by development of more targeted compounds that exhibit less side effects, or development of non-chemical methods of pest management. As a recent example, the EU directive on the sustainable use of pesticides (2009/128/EC) urged to reduce the risks and impacts of pesticide by promoting the use of integrated pest management (IPM) and of alternative approaches or techniques also by a combination of compatible chemical and non-chemical methods of population control. The IPM utilizes knowledge of bionomics and population dynamics of pest species to maintain the damage below the economic threshold while reducing the risk of pesticide poisoning [2]. Insects comprise numerous economically important pests, and IPM practices have historically been focused on controlling harmful insects in agricultural environments [3,4].

Broadly speaking, most of the non-chemical methods for pest management involve manipulation of the target organism's behaviour using different external stimuli [5]. Those work, for example, by directly attracting individuals with push and pull or lure and kill tactics, by concentrating them at an area where they can be conveniently removed, by repelling individuals from the protected area, or indirectly, by disrupting key behaviours such as host finding, feeding, mating, and oviposition, resulting in population decrease. To achieve this, the stimulus design must incorporate knowledge about target's sensory physiology, ecology and behaviour under natural conditions. However, exploiting sensory processes used by animals to guide the abovementioned behaviours is a robust approach that can be successful even with imperfect knowledge of underlying mechanisms [6], although likely with diminished efficiency.

Insects sense their environment using various modalities, the most important of them being chemoreception and mechanoreception. Therefore, those two modalities should be regarded as primary targets for control by behavioural modification. Behavioural manipulation of insects using odours, either natural or synthetic, is already quite established and has been reviewed extensively before (e.g. [5,7,8]), but the role of mechanical vibrations in insect behaviour has been largely overlooked so far due to technical constraints and other factors [9]. Consequently, IPM practice using this modality is virtually non-existent.

The present paper aims to review current knowledge about the various roles of substrate vibrations in insect behaviour and use this knowledge to highlight potential applications. We first describe vibrational signals and their importance in insect communication (with particular focus on the mating communication) but also in other aspects of their life. Then, we review the applicative acoustic tools already available for the users (few) and the potentials for development of innovative solutions (many). Finally, we discuss the possible risks associated to side effects on non-target organisms and the constraints that still do not allow a wide range of acoustic approaches on larger scale. Constraints are mostly related to current technological limits and are likely to be solved in the near future.

2. The role of mechanical vibrations in the life of insects

2.1. Vibrational communication

In animals, signal emission and reception are crucial to survival and reproduction; for this reason, only a correct interpretation of sensory cues coming from relevant sources make it possible to fulfill fundamental needs [10,11]. The mating behaviour is probably the best studied function of vibrational communication, however, several other functions are known. Some of these are attraction (ants), alarm (termites), defence (treehoppers), cooperation and adult/larva communication (wasps) [9]. The list is not exhaustive, since vibrations are an important part of the communication in many insect taxa including Orthoptera, Isoptera, Thysanoptera, Hemiptera, Coleoptera, Diptera, Siphonaptera, Lepidoptera, and Hymenoptera [9,12]. Recent estimates put the number of insect species that use vibrational modality for communication at 195,000 [12], whereas it is also used by spiders [13], numerous crustaceans [14] and other arthropods.

Behaviour of arthropods that rely on plant-borne vibrational signals is strongly influenced by the physical characteristics of their acoustic environment which often coincides with their host plant. As a consequence, signalling and signals are optimized according to physical properties of the substrate [12,15,16].

The fundamental pieces of information that any individual needs to extract from the environment concern the source of signals. This should be identified (who?), located (where?) and evaluated (what?) [17]. Indeed, vibrational signals should, in both intra- and interspecific interactions, carry those features that allow the receiver to correctly interpret the signal and modify the behaviour accordingly; otherwise any interference by either environmental noise and/or non-target species is likely to occur. For example, in mating communication, signal characteristics may also transmit fitness cues, such as age, health, strength and size of the sender. This function is often associated to courtship signals which have evolved to promote mating [18]. In addition, it is important to use vibrations also for orientation. Directionality and the distance from the source (but also if the source is on the same plant/leaf) may help an individual to make the correct decision in order to conserve energy and reduce eavesdropping risks. The latter is a possible setback due to antagonists such as predators/parasitoids and mating rivals [19]. Therefore, rival males who are listening to vibrational signals during mating duets may try to exploit the ongoing communication to take an advantage and thus to mate in place of the other male. Among the possible tactics that a rival male can adopt, is signal masking by emitting vibrational signals with specific spectral features (in terms of frequency and intensity) that allow to cover the ongoing duet thus blocking the information stream between individuals and delaying or preventing the copulation [20].

Environmental noise is an external factor limiting the efficacy of vibrational signals. Vibrations are produced by a range of environment factors, including wind, rain, movement of other animals on the same substrate, and even human activity [21]. Such events are unpredictable at short time scales, but some of them may exhibit predictable longer-term variation (i.e. on the scale of hours). Wind in particular is regarded a major source of noise in both sound and vibrational communication of animals. It induces vibrations mostly in the low-frequency part of the spectrum, but also contains energy in the KHz range [12,22,23]. There is observational and experimental evidence for behavioural adaptation to this limiting factor, to achieve either spatial or temporal release from masking. Insects appear to prefer sheltered locations in areas with constant wind [24], whereas elsewhere, they emit signals in periods of relative lull in wind speed [23-25].

2.2. Scenarios not involving communication

Naturally, intentional communication is not the only context in which insects respond to substrate vibrations. For example, in elastic structures such as herbaceous plant parts, organisms produce incidental vibrations by moving, which can be used as a cue, most notably in predator-prey interactions. If the response is well characterized, it may lend itself to exploiting by artificial means.

One such behaviour is the startle response evolved to fend off an approaching predator or make an escape, which implies ceasing with normal activity to focus on the perceived threat. It may manifest as quiescence (feigning death), rapid shaking of body parts, jumping or flying away, etc. Startle response to incidental substrate vibrations has been documented in many species throughout the class of insects. For example, quiescence as a response to substrate vibrations has been demonstrated in the Colorado potato beetle (*Leptinotarsa decemlineata*) where dropping a metal weight on a plant or a surface connected to it induced cessation of activity ranging in duration from 12 to 500 s (depending on amplitude of vibrations), which could be prolonged by a repeated stimulus before the onset of activity [26]. This is probably a generalized response against the many arthropod predators of the Colorado beetle, although the authors did not venture a guess on the cause. In the desert cockroach *Arenivaga investigata*, burrowing and cessation of activity is a response to vibrational cues emitted by its scorpion predator, so as to prevent the scorpion finding its prey by utilizing vibrational sense for localizing [27].

Herbivorous insects often respond to the approaching predator with dropping behaviour, utilizing gravity to achieve sufficient escape velocity. The behaviour may simply involve releasing the hold on the plant and plummeting to the ground, or a more elaborate escape mechanism. Dropping and hanging on a silk thread as a specific response to vibrational cues produced by an insect predator has been demonstrated in the geometrid moth caterpillar *Semiothisa aemulataria*, while movement of a herbivorous insect triggered this response far less often, and movement of a foraging bird or abiotic noise (wind) never triggered it [28]. Similarly, foliar-foraging predators trigger the dropping behaviour of pea aphids (*Acyrthosiphon pisum*) [29], which has been proposed as a mechanism behind multiplicative synergistic effect of foliar- and ground-foraging predators against this species [30]. Dropping or otherwise moving away from a feeding site incurs a mortality risk, especially in less mobile insects such as the wingless form of aphids. Response to a cue may therefore be situation-dependent [31], which should be taken into account, although vibrations which indicate proximity of a predator are expected be more effective than indirect signals such as alarm pheromones in aphids.

On the other hand, repeated vibrational cues have been shown to induce rapid habituation of response [26,32], which can be at least partly overcome by randomizing timing and other properties of stimuli [33]. For this reason, a better option is to exploit intraspecific alarm signals where possible, since habituation to such signals is diminished or completely suppressed in insects [34].

Long-term exposure to chronic mechanical vibration is a different question, one that involves less specific physiological mechanisms. Chronic vibration is considered a stress factor in animals [35], however, it may have an unpredictable effect on certain physiological processes, depending on circumstances. To illustrate, larvae of the red flour beetle (*Tribolium castaneum*) vibrated at frequencies up to 100 Hz and 0.5 W had altered levels of neuroactive biogenic amines, resulting in retardation of larval growth in one study [36]. Unfortunately, the authors only reported the rated power of their stimulus, but it is interesting to note that at 8 and 10 W, all the larvae in their trials died. On the other hand, larvae of *T. castaneum* vibrated for three days at 100 Hz and 4 W had elevated juvenile-hormone esterase activity and ecdysteroid levels, resulting in accelerated pupation in crowded conditions [37]. Vibration had in both cases similar effect as other stressors such as optical and thermal. Similar effect on biogenic amines and physiological state was reported in adult crickets *Gryllus texensis* exposed repeatedly to vibrational cues of a predator during the course of three days [38]. The specimens had increased levels of octopamine and decreased weight gain, or increased weight loss if they were starved.

Intense sound picked up by organisms is also effective, as demonstrated in a study on the green peach aphid (*Myzus persicae*) [39] where sound stimuli between 66 and 90 dB SPL at frequencies between 100 and 10.000 Hz suppressed phloem feeding. The same approach was used in experiments to disrupt development in larvae of Indian-meal moths (*Plodia interpunctella*) [40], rice moths (*Corcyra cephalonica*) [41] and two species of flour beetles

(*Tribolium* sp.) [42], which are pests of stored grain. In the case of rice moths, it has been suggested that direct physical damage from sound energy is the reason for the reduced adult emergence rates, especially at resonant frequencies predicted from the larval physical characteristics [41]. This was recently confirmed in the experiment with red flour beetle larvae [43]. However, some of the studies on damaging effect of sound are difficult to interpret, because the authors do not supply sufficient information about sound amplitude, giving only the voltage or electrical power supplied to the transducer. Additionally, intense sound is a nonspecific tool, able to damage other biological materials aside from pest insects.

3. Applications

Early attempts to use vibrations for manipulating insect behaviour go back to late 70's when Saxena and Kumar [44] showed that airborne sounds of 200 Hz picked up by plants were able to interrupt the mating communication of a leafhopper and a planthopper (*Amrasca devastans* and *Nilaparvata lugens*). They suggested that music could be used for mating disruption, providing that steps for minimizing noise pollution are taken (opportune frequencies, intensities, temporal activation etc.). No further attention had been dedicated to the subject and in particular to approaches of mating disruption for many years.

Most of the attention in the field has so far been directed at acoustic detection of arthropod pests, where several successful solutions have already been implemented and the method has been reviewed extensively before [45-47]. Even more established is the use of sound-producing devices for pest deterrence, although mostly targeting vertebrates [33,48]. Nevertheless, conceptual parallels with sound technology exist and may be useful for understanding possibilities and limitations related to behavioural manipulation with substrate vibrations. For example, attraction and trapping is similarly restricted to actively searching individuals, while deterrence is more universal, but prone to habituation. Technological challenges are also similar, such as delivering acoustic energy to targets from a point source. Some authors like Čokl and Millar [49] have specifically proposed exploitation of vibrations to achieve control by mating disruption of certain insect groups (in their case Pentatomid bugs) and reviewed the theoretical basis of such a method, but few actual attempts to use this knowledge have been made.

One of the examples is an ongoing study with the intention of reducing the population of the leafhopper *Scaphoideus titanus* in vineyards. This species represents a convenient target because it lives and feeds on only one host plant species in its introduced range – grapevine [50] and, as other Auchenorrhyncha, uses no modality but vibrations for mating communication during pair formation [51]. At the same time, it is considered a dangerous pest for its role as a vector of the phytoplasma disease Flavescence dorée and its control is mandatory in the EU [52]. After initial studies on the species' mating behaviour [53], attention was focused on the possibility of achieving mating disruption by playback of vibrational signals. Efficacy of playback with sufficient amplitude was first demonstrated in laboratory trials [20], then in semi-field conditions with insect pairs placed in cages in an experimental vineyard [54]. The approach was to gather knowledge of basic reproductive biology first, which revealed a naturally occurring disturbance signal that masks temporal structure of mating calls in antagonistic interactions between males. Knowing and using such a signal by playback has distinct advantage over synthetically generated waveforms, because its features have evolved for efficiency, so amplitude, temporal and spectral features are expected to be optimal for this function. Although *S. titanus* is one of the few species known to use acoustic disruption, masking temporal structure of signals which is important for mate recognition [51] should be effective in other species as well. Another fortunate feature of the target system are the standard wires suspended along the rows in vineyards which can be used to deliver vibrational energy to individual plants without the need for elaborate technical solutions (Fig. 1).

Another example of application of substrate vibrations for insect control is using stridulation playback to disrupt tunneling and mating in pine bark beetles (*Dendroctonus* spp.) [55]. The authors combined naturally occurring alarm calls of several species in their playback to evoke a flight response in experimental animals and reduce their tunneling and mating to virtually zero. Although the reported trials were short-term, the example of termites [34] gives hope about long-term efficiency as well. The practically applicable solution the authors developed [56] consists of a transducer attached to a target surface, which can be a tree trunk or even other structures vulnerable to bark beetle infestation, such as a cut logs or structural wood.

The idea of using the phonotactic response to a substrate vibration source to facilitate trapping was first proposed in the early 2000, with the goal of improving pheromone traps for Pentatomid bugs [49,57]. As known from the case of the green stink bug (*Nezara viridula*), pheromones are used for attraction to the general area, while the final approach is mediated by vibrations [9], which is a likely reason for the observation that bugs tend to linger in vicinity of pheromone traps, but do not enter [58-60]. The approach was recently tested in laboratory conditions with the Asian citrus psyllid (*Diaphorina citri*) [61]. The authors highlighted some requirements, such as the importance of accurately mimicking spectral properties of original insect signals, but no field trials have been published so far with this or any other pest.

Finally, an application based on the principle of the startle response has been commercialized recently (BugVibe LLC) in the form of a battery-powered vibrating device targeting a wide variety of pests, including various insect species and birds. Although exact properties of vibrations used are not disclosed, the startle response is prone to rapid habituation, so long-term efficiency is questionable, at least in specialized herbivores, but it might work against non-specialists where other hosts are available in vicinity.

4. Technical considerations

Technical difficulties must be overcome before a technique is viable. In most solid materials, attenuation is rapid and a method of distributing vibrational energy at relevant scales is key. A point source will induce vibrations whose amplitude will decrease (attenuate) with distance. Certain plant-dwelling insects have overcome this limitation by inducing vibrations at or close to the resonant frequencies of their substrate, enabling communication across distances in the range of a meter or more and spanning air gaps between neighbouring plants [15,62]. This is a remarkable achievement for an animal the size of 1 cm or less, but for agricultural application, the required distances are in the range of dozens or hundreds of meters.

Substrate and the excitation technique both determine the type of mechanical waves that will get evoked when energy is delivered to the point of excitation [63]. Seeing that the subgenual organs are by far the most sensitive to the component of motion perpendicular to the surface [64], there are two types of waves that merit attention: Rayleigh waves in the ground and bending waves in plants [65]. In both types, movement is perpendicular to the plane of propagations, and they are dispersive, i.e. velocity of propagation is frequency-dependent, increasing with increasing frequency [66,67]. They are also biologically relevant in that the propagation velocity is low enough to enable localization of the source [66,68]. For the most part, insects use mid-range frequencies for vibrational communication which should be regarded as the primary target for exploitation of this modality. Low-frequency vibration is common in the environment, usually induced by wind, rain, other environmental factors, or human activity [22]. On the other hand, high frequencies (from 500 Hz upwards) are rapidly attenuated in solid elastic structures such as herbaceous plant tissues [66], and therefore less useful at long range.

In the context of arthropod communication, Rayleigh waves have been studied mainly in sand and, while physics of wave dispersion in granular media is highly complex, a general property has been noted: attenuation is fairly low in the frequency range 0.1 to 5 kHz, especially in the range 300 to 400 Hz, and decreases with distance from the source [68-71]. Propagation of Rayleigh waves in soil depends on particle stiffness, where attenuation is inversely proportional to stiffness and proportional to frequency [72,73]. Apart from the ground, Rayleigh waves might occur in large and relatively flat plant parts, such as woody trunks with appreciable diameter.

Bending waves are the most biologically important type of waves in herbaceous plant parts in which diameter is small compared to the wavelength. Free-moving plant parts are resonant structures [66], and pure-tone vibrations that travel along those structures exhibit cyclic changes of amplitude consistent with material properties of those parts. The changes are caused by reflections from end points, resulting in constructive or destructive interference at different locations [74,75]. Consequently, the amplitude of artificial pure-tone signals may drop below the effective threshold at regular intervals, even disregarding average attenuation, and those missing the resonant frequency will require higher energy input for the same effect. Broad-band signals attenuate more steadily [75]. It is still unclear how those insects that use pure-tone signals themselves avoid this problem, but preliminary evidence suggests active tuning [76], which might not be practical for field use. On the other hand, reflections do not seem to be an issue in some other types of substrates like small-diameter woody stems, where frequency-dependent variability of attenuation is less drastic [77]. Aside from resonance, a part of variation in amplitude is also caused by directional nature of excitation, where the amplitude will naturally be the largest in the plane of excitation and smallest perpendicular to it. McNett et al. [78] showed that the motion of a small-diameter stem is highly eccentric close to a point source, but the eccentricity approaches zero at the range of 10 cm or even less if there is a crossing in the path of wave propagation.

There is a wide variety of methods for inducing vibrations in solid materials that have been used in laboratory or semi-field settings for experimental purposes. Those include harmoniums [44] and small loudspeakers [79,80] that produce airborne sounds picked up by the substrate, or directly attached devices, such as electromagnetic shakers [20,81,82] and piezoelectric actuators [83]. Non-electromechanical methods usually involve striking the substrate with a dropped object, such as a small metal ball or a lead weight [26,72,73,84]. However, scaling is an issue not yet sufficiently explored. To induce vibrations, target surfaces must either be continuous, vibrated in parallel using a common medium with a single transducer or in parallel with multiple transducers. The fortunate situation in vineyards is an exception and even there, each row would require a separate transducer. The technology might be more easily applicable in a greenhouse environment, vibrating trays with seedlings or installing loudspeakers at suitable intervals.

5. Side effects of vibrations on non-target organisms

5.1. Plants

Control methods that cause the plant substrate to vibrate, either directly or incidentally, might influence physiology of affected plants, and, consequently, affect yield. Growth response to mechanical perturbation, i.e. thigmomorphogenesis, has been recognized in various plant species, although usually in the context of incidental mechanical perturbation, such as that caused by the wind [85,86].

Generally, chronic mechanical stress promotes hardening of plants [85,86], not only against that stress, but also against frost and drought [87], although most studies so far have focused on the effect of wind which evokes chaotic and high-amplitude vibrations in plants, by flexing and rubbing plant parts together [22,85]. Nevertheless, several authors reported on the effect of less intense, sinusoidal vibrations in controlled conditions. Sinusoidal vibrations with the frequency between 50 and 100 Hz promoted seed germination in wild-type *Arabidopsis thaliana* when the displacement was in the range of 0.5 mm [88]. The authors also provided evidence that the mechanism for this effect is increased ethylene production in vibrated seeds, but a later study with ethylene-insensitive *Arabidopsis thaliana* mutants showed that ethylene response is not required for expression of thigmomorphogenesis [89]. An older study showed promotion of seed germination and root elongation in rice (*Oryzum sativa*) and cucumber (*Cucumis sativus*) on a plastic plate vibrated at 50 Hz, although the amplitude of vibration was not well characterized (»clearly visible to the naked eye and could also be felt by hand«) in that case [90]. More intense sinusoidal perturbation in the growing period (displacement between 30 and 120 mm at 60 Hz) mimicked the effect of wind in *Capsella bursa-pastoris*, causing increased biomass allocation to the root system and reduced the dry weight of reproductive structures at maturity, delayed flowering and fruit formation, and promoted senescence [91]. Therefore, lower-amplitude vibrations or airborne sounds picked up by plants appear to be a better choice. In fact, those can have a positive effect on plant physiology as well. Although the effect is still controversial, stimulation by pure-tone airborne sound reportedly increased yield and various physiological parameters in several species of crop plants [92,93]. The stimulating device, Plant Acoustic Frequency Generator

QGWA-03, has been patented [94,95] and is produced commercially for this purpose. It produces low- to medium-range frequencies largely overlapping with the range of insect-produced signals, however, precise amplitude is not disclosed.

5.2. Non-pest arthropods

Not much is known about the effect of vibrations on other, potentially beneficial arthropods, but at least stimuli evoking startle response may be considered universal, thereby potentially influencing behaviour of many insects, including beneficial ones. Likewise, disturbance signal designed to drown out vibrational signals will affect all insects that utilize this communication channel. Understanding life cycles and activity patterns of both detrimental and beneficial arthropods in agroecosystems is therefore also important in this case.

Most importantly, any stimulus influencing behaviour of honey bees and other pollinators would have to be carefully researched before implementation in flowering plants. There is an old report about evoking a freeze response in honey bees with artificial pure-tone vibrations between 100 and 6000 Hz [96], where frequencies between 500 and 1000 Hz had the lowest amplitude threshold. Sound intensity needed to evoke the response was 108 dB SPL, so the trigger is probably substrate vibrations where the threshold was estimated at around 0.05 µm. However, more comprehensive research is lacking.

Spiders (order Araneae) form another large grouping of arthropods whose behaviour is guided by vibrations, even more so than insects [13]. Spiders use vibrations in many important contexts, including prey capture, mating behaviour and predator avoidance. At the same time, spiders are considered beneficial in agricultural environments, where promoting their abundance is actively pursued by IPM methods [97,98]. As with bees, research on exposure to vibrations that may be considered noise or a predator proximity cue is lacking in spiders. In one such study, the wolf spiders *Schizocosa ocreata* stopped courting and froze in response to simulated bird song or beak tapping [99], although the latency until resuming normal behaviour was shorter than when exposed to visual cues. By placing the subjects on a granite slab, the authors proved that vibrational, not acoustic cues evoked this response. Interestingly, while narrow-band bird song and transient tapping evoked response, continuous white noise did not. A recent study connected insect vibrational communication with spider behaviour [19], showing that the tangle-web spider *Enoplognatha ovata* is attracted by vibrational songs of male leafhoppers *Aphrodes makarovi* and uses them as a cue for foraging, suggesting a possible synergistic effect of simulated songs if they were used for attraction. On the other hand, simulated low-frequency anthropogenic noise has been shown to decrease spider sensitivity to prey cues, but the effect only started at amplitudes above 0.1 mm/s [100]. A similar response may be expected in parasitoids, but experimental evidence is scarce as well [101,102].

To summarize, artificially induced vibrations may produce synergistic effect by disrupting behaviour of pest species and also attracting their natural enemies, or have unwanted side effects, such as disrupting behaviour of beneficial organisms. Therefore, careful planning and research is needed before implementation, and actual effect will likely depend on spectral characteristics, amplitude and temporal pattern of activation.

6. Future direction

There is a strong market demand for alternatives to chemical pesticides in agriculture for several reasons. Consumers are more and more careful about potential risks from chemicals and chemical residues in fruit and vegetables, so large food retailers are imposing more stringent limits than those in current legislation on residues. Current EU legislation is moving in the direction of finding alternatives to chemicals. Due to regulation 1107/2009, which imposed re-registration of pesticides, many old active ingredients are no longer available on the market. The adoption of strategies based on acoustic tools would enable medium to long term reduction of the use of chemical pesticides, which fits well within the IPM concept. The present review illustrates in part the breadth of potential across the insect class (Tab. 1). However, in order for a technique to be adopted by public, it must become accessible and commercially viable. Such tools should therefore be (economically) competitive with other solutions already available on the market, beginning with cost of the device (purchase + maintenance). One fundamental issue is the power consumption that in relation to the working distance (from which derives the density of installation) may be problematic. The state-of-the-art energy harvesting methods still impose a limit, so a duty cycle principle must be taken into account. It will in particular be crucial to develop tools with rechargeable batteries (i.e. solar lights), and entirely cable-free for open field applications, which implies the maximization of energy efficiency (by improving the mechanical properties of the system and the materials which form the trellis system of a crop, for instance poles and wires of the vineyard). On the other hand, by integrating the device with smart functions such as environmental sensors (e.g. leaf wetness, light and temperature) this will also increase the desirability for users.

In conclusion, we think that the use of acoustic devices for IPM in a sustainable way for growers is still to come but that the technology and also a good part of the biological knowledge to make it work is already there. The lack of solutions would be overcome if more directed efforts were made to unify and optimize already available knowledge and to study and develop new solutions for the practical application according to the peculiarities of any crop-pest system where an acoustic based approach is feasible.

Figures

Figure 1: Transducer used for field experiments with mating disruption in the leafhopper *Scaphoideus titanus*. Photo: Jernej Polajnar.

Tables

Table 1: Pest species in which behavioural or physiological manipulation with vibrations has been researched experimentally, mentioned specifically in this review or just referred to by the references. Distribution of species across the insect class demonstrates breadth of potential, while the low number of species demonstrates how underutilized this approach is.

Order	**Family**	**Species**	**Ref(s)**
Blattodea	Rhinotermitidae	*Coptotermes acinaciformis*	34
Orthoptera	Acrididae	*Schistocerca gregaria*	32
Hemiptera	Aphididae	*Acyrthosiphon pisum*	29-31
		Myzus persicae	39
	Cicadellidae	*Amrasca devastans*	44
		Aphrodes makarovi	19
		Scaphoideus titanus	20,54
	Delphacidae	*Nilaparvata lugens*	44
	Liviidae	*Diaphorina citri*	61
	Membracidae	*Echenopa binotata*	25
Coleoptera	Buprestidae	*Agrilus planipennis*	56
	Cerambycidae	*Anoplophora glabripennis*	56

	Chrysomelidae	*Leptinotarsa decemlineata*	26
	Curculionidae	*Dendroctonus frontalis*	55
		Dendroctonus ponderosae	56
	Tenebrionidae	*Tribolium castaneum*	36,42,43
		Tribolium confusum	42
		Tribolium freemani	37
Lepidoptera	Geometridae	*Macaria* (*Semiothisa*) *aemulataria*	28
	Pyralidae	*Corcyra cephalonica*	41
		Plodia interpunctella	40