Review

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

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Abstract

This review presents an overview of the potential 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. This review therefore focuses on the theoretical background, using it to highlight potential applications in a field environment, and lists the few preliminary studies that have been or are being performed. Conceptual similarities to the use of sound, as well as limitations inherent in this approach, are also noted.

Keywords: bioacoustics; vibrational Communication; disruptive signals; IPM

1 INTRODUCTION

Since the groundbreaking public exposure of the risk to the environment and public health posed by chemical methods of pest control,[1] there has been an ongoing effort to reduce harmful effects of pesticides, either by the development of more targeted compounds that exhibit less side effects or by the 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 that the risks and impacts of pesticide be reduced by promoting the use of integrated pest management (IPM) and alternative approaches or techniques, again by a combination of compatible chemical and non-chemical methods of population control. IPM utilises knowledge of bionomics and population dynamics of pest species to maintain 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] These work, for example, by directly attracting individuals with push-and-pull or lure-and-kill tactics, by concentrating them in an area where they can be conveniently removed and 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 the target's sensory physiology, ecology and behaviour under natural conditions. However, exploiting sensory processes used by animals to guide the above-mentioned 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, of which the most studied at long range are chemoreception and mechanoreception.[7] Therefore, these 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,[5,8,9] but the role of mechanical vibrations in insect behaviour has been largely overlooked owing to technical constraints and other factors.[10] 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 to use this knowledge to highlight potential applications. Firstly, the effect of mechanical vibrations on insect behaviour is described (with particular focus on mating communication). Then, acoustic tools already available to users and the potential for development of innovative solutions are reviewed. Note that publications in which the authors used vibrational signals simply to detect the presence of pests are ignored. Finally, the possible risks associated

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with side effects on non-target organisms and the constraints that still do not allow a wide range of acoustic approaches on a larger scale are discussed.

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 fulfil fundamental needs.[11,12] Mating behaviour is probably the best-studied function of vibrational communication; however, several other functions are known, including attraction (ants), alarm (termites), defence (treehoppers), cooperation and adult/larva communication (wasps).[10] This list is not exhaustive, as vibrations are an important part of the communication in many insect taxa, including Orthoptera, Isoptera, Thysanoptera, Hemiptera, Coleoptera, Diptera, Siphonaptera, Lepidoptera and Hymenoptera.[10,13] Recent estimates put the number of insect species that use vibrational modality for communication at 195 000,[13] whereas it is also used by spiders,[14] numerous crustaceans[15] and other arthropods.

The 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 the environment of their host plant. As a consequence, signalling and signals are optimised according to physical properties of the substrate.[13,16,17]

The fundamental information that any individual needs to extract from the environment concerns the source of signals. This should be identified (who?), located (where?) and evaluated (what?).[18] Indeed, vibrational signals should, in both intra- and interspecific interactions, carry those features that allow the receiver to interpret the signal correctly and modify its behaviour accordingly; otherwise, 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 the age, health, strength and size of the sender. This function is often associated with courtship signals which have evolved to promote mating.[19] 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 owing to antagonists such as predators/parasitoids and mating rivals.[20] Therefore, rival males listening to vibrational signals during mating duets may try to exploit the ongoing communication to take advantage and mate in place of the other male. Possible tactics that a rival male may adopt include signal masking by emitting vibrational signals with specific spectral features (in terms of frequency and intensity) that allow the ongoing duet to be masked, thus blocking the information stream between individuals and delaying or preventing the copulation to his benefit.[21]

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.[22] Such events are unpredictable at short timescales, but some of them may exhibit predictable longer-term variation (i.e. on the scale of hours). Wind in particular is regarded as 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.[13,23,24] 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,[25] whereas elsewhere they emit signals in periods of relative lull in wind speed.[24–26]

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 characterised, it may lend itself to exploitation 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 itself as quiescence (feigning death), rapid shaking of body parts, jumping or flying away. 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* Say, 1824, 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 the amplitude of vibrations), which could be prolonged by a repeated stimulus before the onset of activity.[27] This is probably a generalised 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 investigate* Friauf & Edney, 1969, burrowing and cessation of activity are responses to vibrational cues emitted by its scorpion predator, so as to prevent the scorpion from finding its prey by utilising vibrational sense for localisation.[28]

Herbivorous insects often respond to the approaching predator with dropping behaviour, utilising gravity to achieve sufficient escape velocity.[29] 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* (Walker, 1861), 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.[30] Similarly, foliar-foraging predators trigger the dropping behaviour of pea aphids *Acyrthosiphon pisum* Harris, 1776,[31] which has been proposed as a mechanism behind the multiplicative synergistic effect of foliar- and ground-foraging predators against this species.[32] 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,[33] which should be taken into account, although vibrations indicating the 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,[27,34] which can be at least partly overcome by randomising the timing and other properties of stimuli.[35] For this reason, a better option is to exploit intraspecific alarm signals where possible, as habituation to such signals is diminished or completely suppressed in insects.[36]

Long-term exposure to chronic mechanical vibration is a different question, one that involves less specific physiological mechanisms. Chronic vibration is considered to be a stress factor in animals;[37] however, it may have an unpredictable effect on certain physiological processes, depending on circumstances. By way of illustration, larvae of the red flour beetle *Tribolium castaneum* (Herbst, 1797) vibrated at frequencies of up to 100 Hz and 0.5 W had altered levels of neuroactive biogenic amines, resulting in retardation of larval growth in one study.[38] 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 3 days at 100 Hz and 4 W had elevated juvenile-hormone esterase activity and ecdysteroid levels, resulting in accelerated pupation in crowded conditions.[39] Vibration in both cases had a similar effect to other stressors (optical and thermal stressors, for example). A similar effect on biogenic amines and on physiological state was reported in adult crickets *Gryllus texensis* Cade & Otte, 2000, exposed repeatedly to vibrational cues of a predator over the course of 3 days.[40] 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* (Sulzer, 1776),[41] 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* (Hübner, 1813),[42] rice moths *Corcyra cephalonica* (Stainton, 1866)[43] and two species of flour beetles (*Tribolium* sp.),[44] 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 reduced adult emergence rates, especially at resonant frequencies predicted from the larval physical characteristics.[43] This was recently confirmed in an experiment with red flour beetle larvae.[45] However, some of the studies on the 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 non-specific tool, able to damage other biological materials aside from pest insects.

3 APPLICATIONS

The general approach to developing a method that uses substrate vibrations to evoke a behavioural response is presented in Fig. 1. Early attempts to use vibrations for manipulating insect behaviour go back to the late 1970,s when Saxena and Kumar[46] 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* (Distant) and *Nilaparvata lugens* (Stål, 1854)]. They suggested that music could be used for mating disruption, providing that steps for minimising noise pollution are taken (opportune frequencies, intensities, temporal activation, etc.). No further attention was paid to this subject, and in particular to approaches of mating disruption, for many years.

Most attention in the field has hitherto been directed at acoustic detection of arthropod pests, and several successful solutions have already been implemented and the method extensively reviewed.[47–49] Even more established is the use of sound-producing devices for pest deterrence, although mostly targeting vertebrates.[35,50] Nevertheless, conceptual parallels with sound technology exist and may be useful for understanding the possibilities and limitations related to behavioural manipulation with substrate vibrations. For example, the method of 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, such as Čokl and Millar,[51] have specifically proposed the exploitation of vibrations to achieve control by mating disruption of certain insect groups (in their case pentatomid bugs) and reviewed the

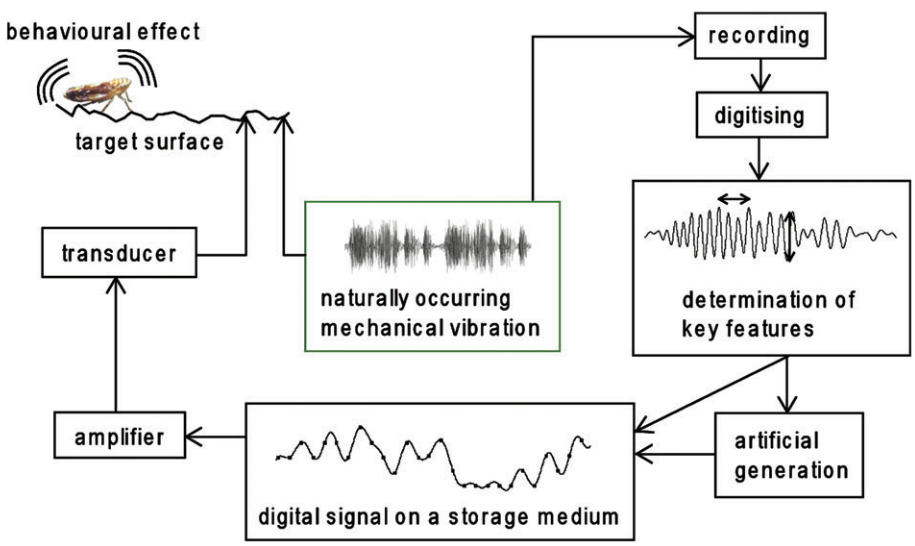

Figure 1. General approach for developing a novel method for exploiting the behavioural effect of mechanical vibrations. Such a process starts with identification of naturally occurring effects of vibrational stimuli. The stimulus is recorded using suitable acoustic equipment (laser vibrometers or contact microphones are normally used) and analysed to determine its key features (amplitude, frequency, modulation, etc.). Complex stimuli can be directly used, or more simple vibration patterns with necessary features can be generated artificially. Playback to the target surface is done with electromechanical transducers that vibrate the target surface; this vibration is then transmitted to target organisms in which it evokes a behavioural effect.

theoretical basis of such a method, but few actual attempts to use this knowledge have been made.

One example is an ongoing study with the intention of reducing the population of the leafhopper *Scaphoideus titanus* Ball, 1932, in European vineyards. This species represents a convenient target because it lives and feeds on only one host plant species in its introduced range (grapevine)[52] and, like other Auchenorrhyncha, uses no modality other than vibrations for mating communication during pair formation.[53] At the same time, it is considered to be a dangerous pest in its role as a vector of the phytoplasma disease Flavescence dorée, and its control is mandatory in the EU.[54] After initial studies on the species' mating behaviour,[55] 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,[21] and then in semi-field conditions with insect pairs placed in cages in an experimental vineyard.[56] The approach was to gather knowledge of basic reproductive biology first, which revealed a naturally occurring disturbance signal that masked the temporal structure of mating calls in antagonistic interactions between males. Knowing and using such a signal by playback has a 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 the temporal structure of signals, which is important for mate recognition,[53] should be effective in other species as well. Another favourable feature of such a system is the suspension of standard wires along the rows in vineyards, which can be used to deliver vibrational energy to individual plants without the need for elaborate technical solutions (Fig. 2).

Another example of the application of substrate vibrations for insect control is the use of stridulation playback to disrupt tunnelling and mating in pine bark beetles (*Dendroctonus* spp.).[57] The authors combined naturally occurring alarm calls of several species in their playback to evoke a flight response in experimental animals and reduce their tunnelling and mating to virtually zero. Although the reported trials were short term, the example of termites[36] gives hope about long-term efficiency as well. The practically applicable solution the authors developed[58] 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 cut logs or structural wood.

Figure 2. The transducer used for field experiments with mating disruption of the leafhopper *Scaphoideus titanus* in a vineyard (Photo: Jernej Polajnar).

The idea of using the phonotactic response to a substrate vibration source to facilitate trapping was first proposed in the early 2000s, with the goal of improving pheromone traps for pentatomid bugs.[51,59] As known from the case of the green stink bug *Nezara viridula* (Linnaeus, 1758), pheromones are used for attraction to the general area, while the final approach is mediated by vibrations,[10] which is a likely reason for the observation that bugs tend to linger in the vicinity of pheromone traps, but do not enter.[60–62] The approach was recently tested in laboratory conditions with the Asian citrus psyllid *Diaphorina citri* Kuwayama, 1908.[63] The authors highlighted some requirements, such as the importance of accurately mimicking the 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 commercialised 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 the precise properties of the vibrations used are not disclosed, the startle response is prone to rapid habituation, so long-term efficiency is questionable, at least in specialised herbivores, but it might work against non-specialists where other hosts are available in the 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 metre or more and spanning air gaps between neighbouring plants.[16,64] 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 metres.

The substrate and excitation techniques both determine the type of mechanical waves that will be evoked when energy is delivered to the point of excitation.[65] Seeing that the subgenual organs are by far the most sensitive to the component of motion perpendicular to the surface,[66] there are two types of wave that merit attention: Rayleigh waves in the ground and bending waves in plants.[67] In both types, movement is perpendicular to the plane of propagation,[68,69] and they are biologically relevant in that the propagation velocity is low enough to enable localisation of the source.[68,70] 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.[23] On the other hand, high frequencies (from 500 Hz upwards) are rapidly attenuated in solid elastic structures such as herbaceous plant tissues,[68] and therefore less useful at long range.

In the context of arthropod communication, Rayleigh waves have been studied mainly in sand, and, while the physics of wave dispersion in granular media is highly complex, a general property has been noted: attenuation is fairly low in the frequency range 0.1–5 kHz, especially in the range 300–400 Hz, and decreases with distance from the source.[70–73] The propagation of Rayleigh waves in soil depends on particle stiffness, where attenuation is inversely proportional to stiffness and proportional to frequency.[74,75] Apart from the ground, Rayleigh waves might occur in large and relatively flat plant parts, such as woody trunks of appreciable diameter.

Bending waves are the most biologically important type of wave in herbaceous plant parts in which the diameter is small compared with the wavelength. Free-moving plant parts are resonant structures,[68] and pure-tone vibrations that travel along these structures exhibit cyclic changes in amplitude that are consistent with the material properties of these parts. The changes are caused by reflections from endpoints, resulting in constructive or destructive interference at different locations.[76,77] 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.[77] It is still unclear how those insects that use pure-tone signals themselves avoid this problem, but preliminary evidence suggests active tuning,[78] 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 substrate such as small-diameter woody stems, where frequency-dependent variability of attenuation is less drastic.[79] Aside from resonance, a part of the variation in amplitude is also caused by the directional nature of excitation, where the amplitude will naturally be highest in the plane of excitation and lowest perpendicular to it. However, owing to the complex shape of most plant substrates, such variation is only noticeable very close to the source[80] and is therefore of little importance.

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. These include harmoniums[46] and small loudspeakers[81,82] producing airborne sounds picked up by the substrate, or directly attached devices, such as electromagnetic shakers[21,83,84] and piezoelectric actuators.[85] Non-electromechanical methods usually involve striking the substrate with a dropped object, such as a small metal ball or a lead weight.[27,74,75,86] 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 vibrated in parallel with multiple transducers. The favourable 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 the physiology of affected plants and consequently affect yield. Growth response to mechanical perturbation, i.e. thigmomorphogenesis, has been recognised in various plant species, although usually in the context of incidental mechanical perturbation, such as that caused by the wind.[87,88]

Generally, chronic mechanical stress promotes hardening of plants[87,88] not only against that stress but also against frost and drought,[89] although most studies hitherto have focused on the effect of wind, which evokes chaotic and high-amplitude vibrations in plants by flexing and rubbing plant parts together.[23,87] Nevertheless, several authors have reported on the effect of less intense, sinusoidal vibrations in controlled conditions. Sinusoidal vibrations with a frequency of 50–100 Hz promoted seed germination in wild-type *Arabidopsis thaliana* (L.) Heynh. when the displacement was in the 0.5 mm range.[90] 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 *A. thaliana* mutants showed that ethylene response is not required for expression of thigmomorphogenesis.[91] An older study showed the promotion of seed germination and root elongation in rice (*Oryza sativa* L.) and cucumber (*Cucumis sativus* L.) on a plastic plate vibrated at 50 Hz, although the amplitude of vibration was not well characterised (clearly visible to the naked eye and could also be felt by hand) in that case.[92] 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* (L.) Medik., 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.[93] Therefore, lower-amplitude vibrations or airborne sounds picked up by plants appear to be a better choice. In fact, these 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.[94,95] The stimulating device, the QGWA-03 plant acoustic frequency generator, has been patented[96,97] 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 to be universal, thereby potentially influencing the behaviour of many insects, including beneficial ones. Likewise, a disturbance signal designed to drown out vibrational signals will affect all insects that utilise 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 the behaviour of honeybees 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 honeybees with artificial pure-tone vibrations of between 100 and 6000 Hz,[98] where frequencies of between 500 and 1000 Hz had the lowest amplitude threshold. The sound intensity needed to evoke a response was 108 dB SPL, so the triggers are 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.[14] Spiders use vibrations in many important contexts, including prey capture, mating behaviour and predator avoidance. At the same time, spiders are considered to be beneficial in agricultural environments, where promoting their abundance is actively pursued by IPM methods.[99,100] 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* (Hentz, 1844) stopped courting and froze in response to simulated birdsong or beak tapping,[101] although the latency until resuming normal behaviour was shorter than

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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 birdsong and transient tapping evoked response, continuous white noise did not. A recent study connected insect vibrational communication with spider behaviour,[20] showing that the tangle-web spider *Enoplognatha ovata* (Clerck, 1757) is attracted by vibrational songs of male leafhoppers *Aphrodes makarovi* Zachvatkin, 1948, 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^{-1}.[102] A similar response may be expected in parasitoids, but experimental evidence is again scarce.[103,104]

To summarise, artificially induced vibrations may produce synergistic effects by disrupting the behaviour of pest species and also attracting their natural enemies, or may have unwanted side effects, such as disrupting the behaviour of beneficial organisms. Therefore, careful planning and research is needed before implementation, and the actual effect will likely depend on the 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 increasingly 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. In light of 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 in 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 (Table 1). However, in order for a technique to be adopted by the 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 the cost of the device (purchase + maintenance). One fundamental issue is the power consumption, which 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) that are entirely cable-free for open field applications, which implies the maximisation of energy efficiency (by improving the mechanical properties of the system and the materials that form the trellis system of a crop, for instance poles and wires of the vineyard). On the other hand, integrating the device with smart functions such as environmental sensors (e.g. leaf wetness, light and temperature) will also increase the desirability for users. From this it follows that the constraints are mostly related to current technological limits and are likely to be solved in the near future with targeted effort in development.

In conclusion, the present authors believe 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 are already available. The lack of solutions would be overcome if more directed efforts were made to unify and optimise knowledge already available and to study and

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. The distribution of species across the insect class demonstrates the breadth of potential, while the low number of species demonstrates how underutilised this approach is

Order	Family	Species	Reference(s)
Blattodea	Rhinotermitidae	*Coptotermes acinaciformis* (Froggatt, 1898)	34
Orthoptera	Acrididae	*Schistocerca gregaria* Forsskål, 1775	32
Hemiptera	Aphididae	*Acyrthosiphon pisum* Harris, 1776	29–31
		Myzus persicae (Sulzer, 1776)	39
	Cicadellidae	*Amrasca devastans* (Distant)	44
		Aphrodes makarovi Zachvatkin, 1948	19
		Scaphoideus titanus Ball, 1932	20, 54
	Delphacidae	*Nilaparvata lugens* (Stål, 1854)	44
	Liviidae	*Diaphorina citri* Kuwayama, 1908	61
	Membracidae	*Echenopa binotata* (Say, 1824)	25
Coleoptera	Buprestidae	*Agrilus planipennis* Fairmaire, 1888	56
	Cerambycidae	*Anoplophora glabripennis* (Motschulsky, 1853)	56
	Chrysomelidae	*Leptinotarsa decemlineata* Say, 1824	26
	Curculionidae	*Dendroctonus frontalis* Zimmerman, 1868	55
		Dendroctonus ponderosae Hopkins, 1902	56
	Tenebrionidae	*Tribolium castaneum* (Herbst, 1797)	36, 42, 43
		Tribolium confusum Jacquelin du Val, 1863	42
		Tribolium freeman Hinton, 1948	37
Lepidoptera	Geometridae	*Macaria* (*Semiothisa*) *aemulataria* Walker, 1861	28
	Pyralidae	*Corcyra cephalonica* (Stainton, 1866)	41
		Plodia interpunctella (Hübner, 1813)	40

develop new solutions for practical application according to the peculiarities of any crop–pest system where an acoustic based approach is feasible.

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