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Sound perception in plants

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ABSTRACT

Can plants perceive sound? And what sounds are they likely to be "listening" to? The environment of plants includes many informative sounds, produced by biotic and abiotic sources. An ability to respond to these sounds could thus have a significant adaptive value for plants. We suggest the term *phytoacoustics* to describe the emerging field exploring sound emission and sound detection in plants, and review the recent studies published on these topics. We describe evidence of plant responses to sounds, varying from changes in gene expression to changes in pathogen resistance and nectar composition.

The main focus of this review is the effect of airborne sounds on living plants. We also review work on sound emissions by plants, and plant morphological adaptations to sound. Finally, we discuss the ecological contexts where response to sound would be most advantageous to plants.

1. Introduction

Living organisms need to sense their environment and respond to it in order to survive. Plants have been shown to sense and respond to different types of stimuli, including light [1,2], volatiles [3], and touch [4,5]. In recent years, the ability of plants to respond to sound has been revealed as well [6–8], and plant sound emissions have also been documented [9]. We suggest the term *Phytoacoustics* to describe the new and growing research field that explores the ability of plants to emit sounds and to respond to sounds.

Sound reception can have significant selective advantage for plants. Sounds travel fast, are naturally present in the environment, and carry important information about the presence of pollinators, herbivores, frugivores, weather conditions and essential resources such as water. Thus, if plants possess even a rudimentary ability to respond to sounds, natural selection would be expected to favor such traits, and evolution should lead to improved plant hearing.

Here we review the latest works showing plants' physiological responses to sound stimuli, examining morphological adaptations of plants to acoustic signaling, and demonstrating sound emissions by plants. We conclude our review by discussing the ecological scenarios in which responding to sound could be adaptive for plants. We will distinguish (see Fig. 1) between responses to: (1) direct mechanical vibrations (e.g., as a result of a caterpillar crawling on the plant), and (2) medium-borne sound waves (including soil- water- and air-borne sounds). In both cases (1 and 2) the ultimate result is a vibration of the plant. However, while sensitivity to direct vibrations depends on very close stimuli and requires direct contact with the plant, sensitivity to medium-borne sounds would allow a plant to respond to distant events and stimuli in its surroundings. Moreover, while responses to direct vibrations have been demonstrated and studied [10–12], convincing evidence for a response to medium-borne sounds (be the medium air, water or soil) is still far less common.

2. Plant sound reception

2.1. Direct vibrations

Plant's response to touch and its underlying mechanisms have been demonstrated [4]. It is thus not surprising that a plant can respond to the vibrations created by a herbivore, such as a caterpillar chewing its leaves [13]. Appel et al. showed that *Arabidopsis thaliana* plants pretreated with vibrations representing the vibrations of caterpillars chewing on a leaf, had increased levels of glucosinolate and anthocyanin in comparison to untreated plants. Moreover, the plants in the study responded to the vibrations caused by chewing but not to

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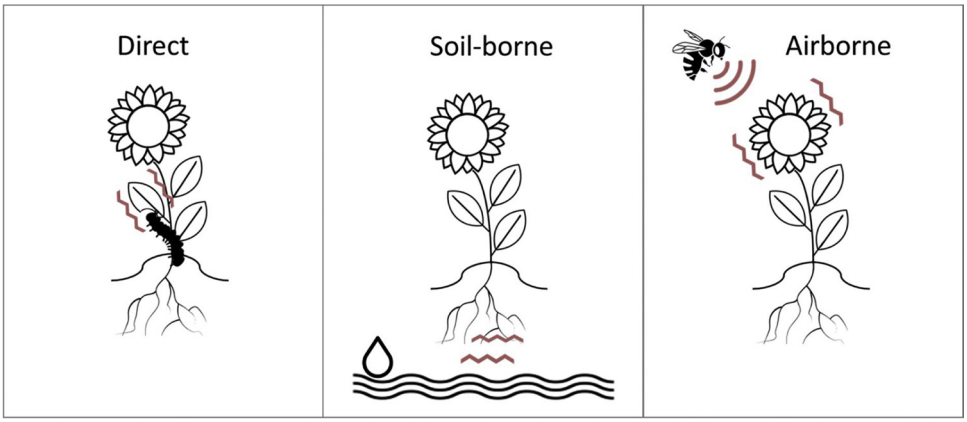

Fig. 1. Modes of vibration sensing in plants. Direct vibrations (a) where the vibration source (e.g. caterpillar chewing) touches the plant [13], and medium-borne vibrations – where the sound waves travel through a medium, that can be water, soil (b) [14,15] or air (c) [35], before reaching the plant.

vibrations caused by wind or insect song. A possible mechanism for plant responses to such vibrations may be through some sort of touch receptors [11].

Even though they do not demonstrate a response to medium-borne sound, these results exemplify that plants can respond even to very gentle touch producing micrometer-scale vibrations. The ability to respond to these vibrations could have been favored by natural selection, through its effect on resistance to pathogens, and could have led to sensing of medium-borne sound.

2.2. Water-borne and soil-borne sounds

Although acoustic communication in a terrestrial environment intuitively evokes thoughts of airborne sounds, sound can also propagate via water and soil (see Fig. 1). Two studies that examined the effect of natural sounds on plants tested plant responses to sound waves that propagate through the soil or through plant tissues. The sound of running subterranean water, for example, mostly travels through soil and could have important implications for a plant. Recently, it was shown that young *Pisum sativum* roots tend to grow towards sounds of running water [14]. In another study, *Arabidopsis thaliana* plants were shown [15] to grow towards a sound at 200kHZ, a frequency included in the spectrum of the sound of running water. These studies demonstrated that plants can respond to informative sounds that are present in their natural environment. Nevertheless, most of the sounds that a plant is exposed to are airborne, and so the question arises – can plants respond to airborne sounds?

2.3. Airborne sounds

Recently, evidence has been mounting that plants can respond to airborne sounds. Table 1 summarizes the main results of 11 studies that were published since 2009 and examined plant responses to sound stimuli, 8 of which investigated the effects of airborne sounds on plants. These studies reveal several types of responses to sound stimuli. First, it was shown that *A. thaliana* plants can change their gene expression patterns [16] and their protein production [17] in response to sound, with more than 150 genes affected following 1 h of exposure. Expression of some sound responsive genes and mechanosensitive ion channel genes differed between plants exposed to sound and plants that experienced direct touch [18]. Second, several specific responses were observed in different organisms: *A. thaliana* plants were shown to increase their tolerance to *Botrytis cinerea* infection when exposed to 1000Hz sound for 10 days, 3 h per day [19]. Both *A. thaliana* [20] and *Oryza sativa* [21] showed an improvement in their resistance to drought when exposed to sound stimuli for 1 week (10 h a day, white noise) or 1 h (pure tones at 0.8, 1.0 and 1.5 kHz), correspondingly. *Medicago sativa* sprouts exposed to 1000 Hz frequency sound for 2 days (2 h a day), were shown to increase their ascorbic acid content by approximately 50% [22].

Sound stimuli played repeatedly over long periods of time (hours per day for several days) have been shown to induce different responses in different plants, including stimulation of seed germination [23], plant growth [12,24–26], delay of ripening [27], increase in cell energy balance [28], change in endogenous hormone levels [29], cell cycle [30], enzyme activities [31], root metabolism [32] and more [33,34].

Most of the current literature in the field concentrated on prolonged stimuli of either white noise or pure tones in the 200–3000 Hz range. Such long and constant sounds are useful in demonstrating that plants can respond to sound, but they are unlikely to be common in natural scenarios. Recently, we and others have demonstrated that plants can respond rapidly to ecologically relevant sounds from their environment. It was shown that *Oenothera drummondii* plants produce sweeter nectar after exposure of just 3 min to playback of bee buzzing or to synthetic sound at similar frequencies [35]. In our opinion, understanding the effect of ecologically meaningful sounds on plants is one of the most important, and still largely overlooked, goals of phytoacoustics.

After examining the extant literature in the field, some practices for better phytoacoustics can be recommended: First, for better reproducibility and easier comparison of results, a standard (and absolute) scale should be used when reporting sound intensity (e.g., dBSPL), in addition to reporting the sound frequency (or frequency spectrum) and duration. Second, using ecologically relevant sound signals – sounds that can be found in the plant's environment and that are played-back at intensities that a plant would actually experience in nature – is helpful in determining whether a response could have a functional role or is merely an artifact of another mechanism. A third recommended practice, which can help understand the specificity of the response and hence its functionality, is to use a different sound stimulus (in addition to a silent treatment) as a control.

3. Plant morphological adaptations to sound

The environment of plants is full of sounds. If plants can benefit from receiving and responding to these sounds, then they might have evolved to "hear" better. Selection would act on the shape, size, and structure of the plant parts that are involved in the hearing – the plant "ear" – and also on the transduction mechanism which translates external mechanical vibrations into internal signals. Flowers, for example, could serve as very efficient sound receivers. Large bowl-shaped flowers could function similarly to the mammalian external ear, helping to amplify sound and also to selectively amplify certain sound frequency ranges. In the case of hearing pollinators, we suggest that the external ear might be the flower itself. The expected frequency response of the

Table 1
Summary of research pertaining to plant response to sound.

Article	Year	Species	Growth stage	Sound description	Duration	Medium	Main Result
[35]	2018	*Oenothera drummondii*	Flowering	Bee recordings	3 min	Air	Sweeter nectar produced in the flowers
[14]	2017	*Pisum sativum*	Sprouts	Recorded sound of water running through a pipe.	5 days	Soil	Roots growth towards sound.
[22]	2017	*Medicago sativa*	Sprouts	250, 500, 800, 1000, 1500 Hz	1-6 days for 2 hours per day	Air	Change in L-ascorbic acid content.
[20]	2017	*Arabidopsis thaliana*	6 weeks	White noise	7 days for 10 hours per day	Air	Increase in drought resistance. Drought genes response.
[19]	2017	*Arabidopsis thaliana*	2 weeks	500, 1000, 3000 Hz	10 days for 3 hours per day	Air	Up-regulation of defense and salicylic acid -responsive genes in Botrytis infected Arabidopsis.
[18]	2017	*Arabidopsis thaliana*	20-30 days	500 Hz	103,060,120 minutes	Air	Gene expression differed between sound-exposed and touch-treated plants.
[15]	2017	*Arabidopsis thaliana*	2 weeks	200Hz	2 weeks	Soil	Roots growth towards sound source.
[16]	2016	*Arabidopsis thaliana*	3 weeks	250, 500, 1000, 2000, 3000 Hz	1 hour	Air	Global transcriptomic, proteomic and hormonal changes.
[21]	2014	*Oryza sativa*	3 weeks	0, 0.25, 0.5, 0.8, 1.0, 1.5 kHz	1 hour	Air	Enhanced stomatal conductance and quantum yield of PSII in drought stress environment.
[13]	2014	*Arabidopsis thaliana*	4 weeks	Caterepiller recordings	2 hours of repeated 10-minute pattern.	Leaf	Aliphatic GSs were higher in plants that had previously experienced chewing vibrations.
[17]	2012	*Arabidopsis thaliana*	2 weeks	250, 500 Hz	1 hour	Air	Protein production was significantly affected

evening primrose flower (*Oenothera drummondii*), based on the flower shape and physical properties [35], suggests that it could exhibit frequency specificity, mainly amplifying the frequency range that includes the sounds emitted by pollinator wingbeats and not responding to higher- or lower-frequency vibrations. The vast literature on the functionality of animal ears [36] could stimulate a new direction of research on this topic.

In the special case of bat pollination, several extraordinary examples are known for specific plant morphological adaptations, resulting in acoustic functionality. Specifically, certain adaptations evolved to reflect loud and distinct echoes in response to the echolocation signals of bats. There are many plant parts that produce distinct echoes, which could be used by echolocating bats in order to detect them (even if they did not specifically evolve for that purpose [37,38]). Two species of bat-pollinated Central-American rainforest vines (*Marcgravia evenia* and *Mucuna holtonii)* evolved special dish-like leaves, which reflect loud echoes from a very wide range of angles [39,40]. These leaves act as a sonic beacon that stands out among the general clutter of the forest, allowing the bats to find the flowers and guiding them towards the nectar.

4. Sound emission by plants

One important class of sounds that might be relevant for a plant to respond to are sounds emitted by other plants. Plants emit a wide range of sounds. Famously, leaves rustle in the wind and broken branches can crack under pressure, but these are just some of the sounds that plants emit. It has been known for decades that plants produce acoustic emissions, especially when they experience drought stress [41]. These acoustic emissions may result from cavitation, the process whereby water bubbles are formed and then rapidly collapse in the xylem, producing a shock wave accompanied by detectable acoustic emissions [41]. While such acoustic emissions have been recorded since 1966 [42–48], they have only been recorded using a sensor attached to the xylem – by cutting a hole in the bark and removing the underlying phloem and cambium, so the sensor can be attached directly to the xylem (see Fig. 2 in [44]). Such recordings do not indicate whether these sounds produced by the plants can travel through air and therefore can be detected by other organisms (plants or animals) that are not in physical contact with the plant. Considering that vibrations are created in the plants' xylem, it is very interesting to study the propagation of plant sounds through air by *remotely* detecting and recording them (see Fig. 2). In a recent work [9], we have shown that plant sounds can indeed be detected remotely, and furthermore, that they contain information about the state of the plant. Specifically, it is possible to identify dry or cut plants based on their sounds.

5. The potential advantages of plant responses to sound

Plant sound perception has many potential advantages (see Fig. 3), in the context of plants' interaction with pollinators, herbivores, frugivores, water, and other plants.

5.1. Pollination

The majority of flowering plants are pollinated by insects and other animals [49]. By presenting conspicuous colors and releasing attractive fragrances, plants can signal their pollinators, whose visits are critical for the plants' reproduction and survival [50,51]. The ability of pollinators to receive and react to the plants' signals is advantageous for the pollinators because plants are providers of nectar and pollen, which are important sources of energy and amino acids for the pollinators. Plant-pollinator communication is also extremely important for humans. The pollination of flowering plants by animals – primarily bees [52] –represents a critical ecosystem service of great value to humanity [53], since 35% of our global food production depends on animal pollination

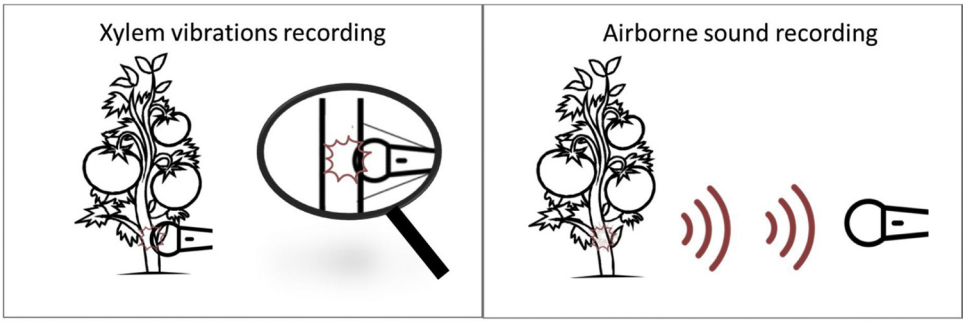

Fig. 2. Methods of detecting plant sound emissions. Sounds can be detected by attaching the sensor directly to the xylem (a), after removing the cambium and phloem layers covering it. Plant sounds can also be recorded from a distance (b), which indicates that they are likely to be perceived by other nearby organisms that have the relevant hearing ability.

[54].

The wingbeat of flying pollinators often produces sounds with detectable intensities. Plants' ability to sense sound suggests that they might be able to perceive these sounds in particular, and react to them rapidly. One form of reaction is improved reward [35], but others may be increased secretion of volatiles or even changes in gene expression to mediate longer-term responses.

5.2. Herbivory

A major threat to a plant's life is being eaten by animals. When plants are consumed by herbivores, multiple sounds are produced: the sounds of the herbivore itself walking or vocalizing, and the sounds of the chewing process, which might directly vibrate the plant [13], as well as travel through the air. When attacked by herbivores, certain plants are known to emit volatile organic compounds (VOCs) that alarm nearby plants [3]. Could the sounds of a herbivore's attack be detected by nearby plants and elicit such a response? More intriguingly, could nearby plants emit 'alarm' sounds in response?

5.3. Frugivory

Fleshy fruits are produced to be consumed by frugivores and allow seed dispersal [55]. However, the ripening of fruits is a delicate optimization: a fruit that is ripe too early is likely to be consumed by bacteria, whereas a fruit that is not yet ripe when its disperser arrives would often not be dispersed. Synchronizing fruit ripening with frugivore presence could thus have a significant adaptive value. Many frugivores are noisy, and even very noisy (e.g. parrots), and a plant responding to their sounds, e.g. by increasing ethylene production [56], could increase its rates of dispersal and reproduction.

5.4. Water

Water is a major limiting factor for plants [57,58], and plants invest significant resources in locating water and growing towards it. Sound reception can help plants obtain water in several ways: First, the water itself produces sounds, which can travel through the soil. Indeed, roots have been shown to grow towards the sound of water [14]. Above ground, the presence of available water might vary greatly in time, especially in dry areas that depend on sporadic events such as rain. The atmospheric events that predict high and transient levels of water are accompanied by thunders, whose sound travels through air. Plants could hypothetically benefit from responding to the sound of thunder and preparing themselves to take up as much water as possible in a short period of time, especially in desert or sub-desert areas. In contrast, flowering plants could also be damaged by heavy rains, and may benefit from acting rapidly to close their flowers and protect their pollen from the rain.

6. Plant-plant acoustic communication?

One of the most intriguing ideas, resulting from plants' ability to receive sounds and from their emission of sounds, is that of plant-plant acoustic communication. Could plants respond to the sounds produced by other plants? This could be beneficial in multiple scenarios: First, plants could listen to the sounds of stressed plants. We have shown [9] that plants increase sound emission both when suffering from drought and when cut. In these cases, neighboring plants could benefit from up-regulating genes relevant to the stress experienced by the plant emitting

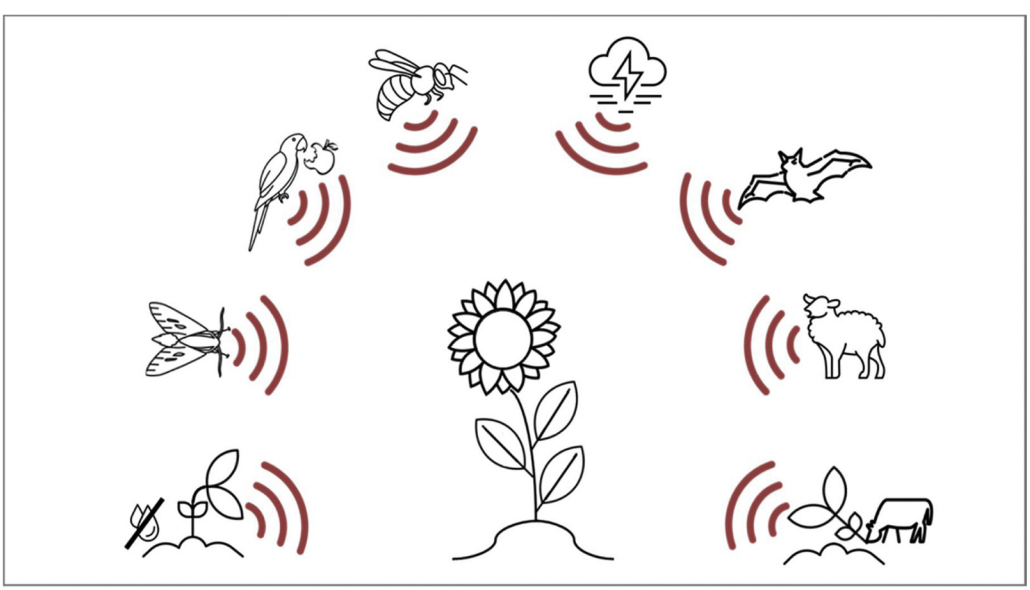

Fig. 3. Ecologically relevant sounds that plants could benefit from sensing. Informative sounds include (counter clockwise): the sounds emitted by a drying plant, suggesting drought threat; the wingbeats of a moth, which might represent either a herbivore or a pollinator, depending on the plant; the vocalizations and eating sounds of a frugivore, suggesting it is a good time for fruit ripening; the sounds of a potential insect pollinator; thunders, implying likely rain in the near future; the sounds of bats, which might serve as either pollinators or predators of herbivores; the sounds of herbivores, moving or vocalizing, which could evoke the activation of different defenses; and the sounds resulting from a herbivore's attack, including the chewing sound itself and possibly also sounds emitted by plants.

the sounds. A plant could, for example, benefit from up-regulating drought resistance genes [59,60], or closing its stomata [61] when exposed to the sounds of a drought-stressed plant [9], as the sounds can serve as indicators of increased short-term risk of drought for the hearing plant. Similarly, a plant could also benefit from upregulating herbivory resistance genes [62,63] in response to the sounds emitted by nearby plants that are being attacked by herbivores.

7. Future directions in phytoacoustics

The exciting field of phytoacoustics is still in its infancy. There is a need for new studies that would investigate different plant responses to sound, and we see particular potential in the study of rapid responses to realistic airborne sounds. These may include the sounds of animals, water, and other plants. Similarly, there is a lack of studies investigating plant sound emission, especially under natural conditions. The exciting question of plant responses to the sounds of other plants is nearly unexplored. There is also a need for complementary studies examining the bio-mechanics of sound reception, the signal transduction and down-stream signaling to other plant parts. We expect that research in these directions would revolutionize our understanding of the interaction of plants with their environment, and that many known plant responses may actually contain a phytoacoustic component.

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