Sound perception in plants

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\textbf{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 \textit{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 \textit{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 \textit{Arabidopsis thaliana} plants pre-treated 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...
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 sounds 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 kHz 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.

<table>
<thead>
<tr>
<th>Article Year</th>
<th>Species</th>
<th>Growth stage</th>
<th>Sound description</th>
<th>Medium</th>
<th>Duration</th>
<th>Main Result</th>
</tr>
</thead>
<tbody>
<tr>
<td>[35] 2018</td>
<td>Oenothera drummondii</td>
<td>Flowering</td>
<td>Bee recordings of sound of water running through a pipe.</td>
<td>Air</td>
<td>3 min</td>
<td>Sweeter nectar produced in the flowers</td>
</tr>
<tr>
<td>[22] 2017</td>
<td>Pisum sativum</td>
<td>Sprouts</td>
<td>Recorded sound of water running through a pipe.</td>
<td>Soil</td>
<td>5 days</td>
<td>Roots growth towards sound.</td>
</tr>
<tr>
<td>[19] 2017</td>
<td>Arabidopsis thaliana</td>
<td>20-30 days</td>
<td>500 Hz recordings of sound between 500 and 1000 Hz.</td>
<td>Air</td>
<td>103,060,120 minutes</td>
<td>Up-regulation of defense and salicylic acid responsive genes in Botrytis infected Arabidopsis.</td>
</tr>
<tr>
<td>[18] 2017</td>
<td>Arabidopsis thaliana</td>
<td>3 weeks</td>
<td>250, 500, 1000, 2000, 3000 Hz recordings of sound.</td>
<td>Soil</td>
<td>1 hour</td>
<td>Global changes in sensitivity of drought. Proteins were significantly increased.</td>
</tr>
<tr>
<td>[16] 2016</td>
<td>Arabidopsis chilensis</td>
<td>2 weeks</td>
<td>500 Hz recordings of sound between 500 and 1000 Hz.</td>
<td>Air</td>
<td>1 hour</td>
<td>Protein production was significantly increased.</td>
</tr>
<tr>
<td>[15] 2016</td>
<td>Arabidopsis chilensis</td>
<td>2 weeks</td>
<td>500 Hz recordings of sound between 500 and 1000 Hz.</td>
<td>Air</td>
<td>1 hour</td>
<td>Protein production was significantly increased.</td>
</tr>
<tr>
<td>[17] 2012</td>
<td>Arabidopsis chilensis</td>
<td>2 weeks</td>
<td>500 Hz recordings of sound between 500 and 1000 Hz.</td>
<td>Air</td>
<td>1 hour</td>
<td>Protein production was significantly increased.</td>
</tr>
</tbody>
</table>

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 – represents a critical ecosystem service of great value to humanity [53], since 35% of our global food production depends on animal pollination.
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 sounds. Another scenario involves the potential for plants to detect and respond to the sounds of herbivores or their predators, using these sounds as cues to activate defense mechanisms or to coordinate their responses with those of other plants in the vicinity. This could also include coordinating the production of volatile compounds or other chemical signals to attract beneficial insects or deter pests.

The ability of plants to detect and respond to sounds from their environment opens up new avenues for understanding the complexity of plant communication and its ecological significance.
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.

Acknowledgements

We thank Yuval Sapir for discussions, and Tuvik Beker for comments on the manuscript. The research has been supported in part by ISF 2064/18 (LH), by the Manna Center Program for Food Safety and Security fellowships (IK), and by Bixura 2658/18 (LH, YY).

References