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REVIEW

A tuning point in plant acoustics investigation

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ABSTRACT

In a very recent book called *Sensory Biology of Plants*, published by renowned publisher Springer Nature, the authors stated that the scientific literature gathered so far regarding knowledge around the field of Plant Acoustics allows us to divert the focus from the question "whether plants perceive sound" toward the questions "how and why they are doing it" Some phenomena are well known: roots perceive the sound of flowing water and display a sound-mediated growth toward the water source, while the buzz pollination process allows plants to minimize the pollen lost and maximize which is collected by true pollinators. But plants are far more perceptive and responsive to their environment than we generally consider them to be, and they are communicating far more information than we realize if we only took all their signals (VOCs, sound, exudates, etc.) into a greater picture. Could Volatile Organic Compounds (VOCs) be involved in mediating more responses than we imagine? VOC synthesis and release is known to be elicited also by electrical signals caused by mechanical stimuli, touching and wounding being among these, serving as info-chemicals in the communication between plants ("eavesdropping"), and within the organs of the same plant, in order for it to get synchronized with its surroundings. This paper is an overview of the discoveries around plant perception with a focus on the link between mechanical stimuli, as sound vibrations are, and changes in plant physiology leading to VOC emission.

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Introduction

In his movie *Nomad: In the Footsteps of Bruce Chatwin*, German film director Werner Herzog reports to the viewer the theory of nomadism by the English writer Bruce Chatwin, and says: "Of course, I have a similar worldview that with nomadic existence, with the demise of nomadic life, city-sedentary life, would come in place and involve huge amount of human beings and technology, all of which is now probably working on the destruction of the human race".

Unlike us, human beings, who have made sedentary life our norm, Plants, a kingdom not too far from ours, have made the most of their sedentary-sessile lifestyle. From the adjustments that necessarily came with this choice, they built the key to the evolutionary success that led them to colonize almost every terrestrial environment. The way plants survive, live, and thrive, in the process of finding their ecological niche in the same dynamic and complex world that we live in, represents another branch of the phylogenetic tree, an alternative evolutionary pathway, the other side of the coin, another "mind" set of which we, human beings, should make ourselves better observers, and to which we should open our mind to better comprehend Nature's lessons. The differences between animals and plants are not so relevant, in terms of genetics; hence it is not inconceivable to compare animal biology to plant biology, as the American-born plant geneticist Daniel Chamovitz writes in his awarded book *What a Plant Knows* .[1] The scientist and his research group found that the light-dependent signalosome COP9, which belongs to the Thale cress (*Arabidopsis thaliana*) and it is crucial for the repression of photomorphogenesis growth in darkness, [2] and the *Drosophila melanogaster*'s regulator that causes the entrainment of the molecular clocks in light-dark cycles are alike .[3] This reveals how both plant and animal kingdoms can have similar structures involved in light-dependent responses, i.e. key reactions to a switch mechanism.

World plant's perception

Plants and Animals, like any other living organism, have a common goal: to fine-tune their growth by dealing with a clamorous number of multiple stimuli and an enormous combination of diverse situations, in order to ensure the reproduction of their species (i.e. the continuity of their genotypes). Animals achieve this through their exceptional nervous system, which adjusts and synchronizes internal metabolism in response to the outer environmental conditions. Even if plants do not exhibit a fight-flight response, they surely perceive harmful events or threats to survival and are perfectly capable of arraying different, event-specific defense mechanisms.

At first, plant sensitivity studies were held back due to the human-forma-mentis-bias that, since plants do not own a nervous system, they cannot sense their surroundings. However, some nonscientific works, *The Secret Life of Plants*[4] and *The Sound of Music and Plants*[5] paved the way for the investigation into a plant's unique means to perceive this visible, olfactory and audible world, and for the breakthrough of the echo-chamber that nailed us down to such an extent that we were delayed in scrutinizing some plant features that needed to gain more attention.

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One outstanding example of plant sight is provided by the Chilean plant *Boquila trifoliolata*. This climbing woody vine is capable of sensing shapes and colors, via plant-specific ocelli [this concept was first worked out by Gottlieb Haberlandt in 6], in a way that it is able to mimic the leaves of its supporting trees in terms of size, shape, color, orientation, petiole length, and/or tip spininess. Moreover, the plant leaf mimicry is impeccable even in the absence of any direct contact between the vine tree and mimicked host trees .[7] It was speculated that this mechanism is set out by the vine to avoid leaf herbivory, thus this hypothesis was demonstrated: on unsupported vines the leaf herbivory was greater than that on vines climbing on trees but was greatest on vines climbing onto leafless trunks. It is suggested that we can strike off the chance that the plant-host plant mimicry is VOC-mediated, as researchers in 2016 said: they made the claim that Boquila possesses the sense of sight, this being the least thrifty explanation for this complex phenomenon.[8]

Instead, one clear evidence of a VOC-mediated response is the scent-perception that the Dodder plant displays. It was demonstrated that the parasitic plant *Cuscuta pentagona* (dodder) uses volatile cues for host location. Finding a host is a crucial aspect for dodder survival because, being free from chlorophyll pigments, it cannot absorb solar energy that transforms light into sugar and oxygen, hence it must derive its nutritional requirement from another living plant, the host plant. The dodder seedlings exhibit VOC-mediated growth toward nearby tomato plants (*Lycopersicon esculentum*) and toward extracted tomato-plant volatiles presented in the absence of other cues. Moreover, there is compelling evidence that the dodder seedlings can distinguish tomato and wheat (*Triticum aestivum*) volatiles and preferentially grow toward the former .[9] It is astonishing that, as these findings suggest, a mechanism for the observed preference is possible: the volatile blend produced by the tomato, the preferred host, is recognized and distinct from that produced by wheat. Plant biology is full of these types of chemical communicational exchanges among the kingdom Plantae (between conspecifics and not) and between plants and other kingdoms, as in the case of attractive (pollinators) and repellent (pests) ecological relationships.

Volatile Organic Compounds (VOCs) are defined as any organic compound with high enough vapor pressures to be vaporized into the atmosphere in normal conditions .[10] It is known that plants produce an amazing variety of metabolites. Only a few of these are involved in "primary" metabolic pathways, thus common to all organisms; the others, called "secondary" metabolites, are plant-group specific. Among such "secondary" metabolites, VOCs play a dominant role. Being released by any kind of tissues or type of vegetation (trees, shrubs, grass, etc.) as green leaf volatiles, nitrogen-containing compounds, and aromatic compounds, plants can emit constitutive stored VOCs or synthetize and release them in response to a variety of stimuli, being involved in a wide class of ecological functions as a consequence of evolutionary adaptations of plants with biotic and abiotic factors.

A glaring example of synthetized and released VOC as a reaction to stress was demonstrated in the 1980s on the Limpopo Savanna in South Africa. At the time, there was a terrible ongoing drought, and the Acacia tree was the only plant that was acceptably adjusting to the dry conditions. An animal that heavily relied on this tree for its survival was the greater kudu, a woodland antelope. About 3.000 kudus were reported to suddenly be dead for no apparent reason .[11] Later, it was discovered that the kudus were dying due to excess tannin, defense molecules produced by Acacia trees being eaten by the kudus. However, it was also discovered that Acacia plants that had not yet been affected by kudu grazing were also producing excess tannins. This led scientists to gather that there must be a strategic signaling among trees causing them to increase their tannin production. Since then, several scientists have been describing and analyzing similar case studies.

In 2007, Heil and Silva Bueno showed that, when exposing Lima Bean plants (*Phaseolus lunatus*) to volatiles of beetle-damaged conspecific shoots, they reduced herbivore damage and increased their growth rate .[12] This study not only demonstrates that the quality and quantity of volatiles released by induced leaves are sufficient to elicit another indirect defense in yet-undamaged plants under natural conditions, but it also underlined that VOCs might serve as a rapid and efficient external signal for within-plant signaling.

Sound perception

Apart from the airborne transport of leaf volatiles from damaged tissues to undamaged ones, there are several other defense mechanisms that have been proposed. Localized feeding causes the induction of chemical defenses in undamaged tissues by signaling molecules that move within the plant (phloem-borne signals) and by signaling pathways that rely on electrical signals. Vibrational signals are likely to complement other signals that plants receive from herbivory; however, none of these mechanisms has been shown to transmit signals to all plant parts as rapidly as mechanical vibrations (10–100 m/s) .[13] In this last study, scientists wondered whether acoustic energy generated by the feeding of the *Pieris rapae* (L.) caterpillar was detected by the *Arabidopsis thaliana* plants. Evidence reveals and reports that the Thale cress plants exposed to chewing vibrations produced greater amounts of chemical defenses (glucosinolate and anthocyanins) and that the plants distinguished chewing vibrations from other environmental vibrations such as wind and insect (leafhopper) song.

Sound Vibrations (SV) introduced in the afore-mentioned investigation not only leads to bringing in another type of plant-perception, but it also leads to highlight how plants have developed a sophisticated mechanism for perceiving SVs of variable, ecologically relevant frequencies. SVs as a stimulus have only started receiving attention relatively recently, as a 2016 opinion paper by Mishra and colleagues divulges .[14] In 2012, in the above-mentioned book *What a Plant Knows*, the writer ends the chapter about plant hearing with some critical words: "plants thrived for hundreds of million years on Earth and the nearly 400,000 plant species have occupied every ecological niche without ever hearing a sound".[1] It was not until 2016, just four years later, that he had to reconsider the concept and stated: "music is not ecologically relevant for plants, but there are sounds that could be advantageous for

Figure 1. Buzz-pollinating bumblebee (Bombus lapidarius) on purple thistle (*Cirsium tuberosum*) by Luca Forti.

them to hear".[14] A 2019 study brought off by Veits and his research team, featuring Chamovitz among others, assessed and illustrated how flowers respond to pollinator sound within minutes by increasing nectar sugar concentration.[15] They exposed petals to different sound frequencies, both pollinator recordings and synthetic sounds at similar and different frequencies, within 3 minutes, and analyzed their effects by measuring petal vibration and nectar sugar concentration. The time range in which they played the sounds was that short because the research aim was to test rapid responses in plants that until now have only been associated with carnivorous (Venus flytrap) and sensitive (*Mimosa* L.) plants. They observed that plants quickly respond to specific airborne sound frequencies in a way that could potentially increase their chances of pollination.

This is not the first known example of flowers that use sound as a medium to increase the chances of cross-pollination. Sonicating bees – so called because of the audible component of the vibration they produce, use the rapid contraction of their thoracic muscles to transmit vibrations that resonate in the floral anthers causing pollen grains to gain energy and be expelled through the apical pores. This is an enchanting widespread phenomenon called buzz pollination, where pollen from anthers is released only against a distinctive SV and was overviewed in 2013. The fascinating aspect is that the duration and the amplitude of produced SVs correlate positively with the quantity of pollen release, which suggests that there is a species-specific relation between pollen removal by vibrations and stamen characteristics (more pollen is released in multi-layered, rigid anthers and with bigger size of the anther pore vs single-layered, flexible anthers and smaller size of the anther pore).[16] It is suggested that only a specific range of pollinators – buzz pollinators – who produce the right amplitude can imprint the necessary energy on the anthers for them to expel the pollen. Hence, non-buzzing visitors, such as flies and some bees, merely extract small amounts of pollen through inserting their mouthparts, for instance, while large quantities of pollen are meant for buzzing bees. This phenomenon is likely to be linked to the minimization of pollen thieves (visitors that collect the pollen without depositing it on stigmas, i.e. without pollinating) and maximization of pollen dispersal thanks to "functionally specialised" sonicating bees.

Sound Vibrations are not only caused when buzz pollination occurs, but they are also caused by wingbeats of flying pollinators. It was found that when pronubial insects hovered above flowers, these vibrated mechanically in response to those specific sounds, suggesting a plausible mechanism where the flower serves as an auditory organ (Figure 1).[15] The astonishing facet of this study is that the flowers only vibrate if the airborne sound is at pollinator's frequency range; in fact, when they vibrated less or did not respond at all it was because higher or lower frequencies (glass covered flowers) than the pollinator's frequency range were applied.

Sound emission

Assuming that flowers may be the "ear" through which plants listen, the Canadian-born composer Mort Garson, pioneer of electronic music featuring the Moog synthesizer, might have been very glad to know about this study, since he recorded a music album in 1976 named *Plantasia* that on its front cover recited «Warm earth music for plants . . . And the people who love them». The artist surely did not mean to make the claim of disclosing the idea that plants could hear, whereas he perhaps merely wanted to follow the fashion of the time when the environmentalist movements were blossoming. At any rate, when Garson called one of his delightful compositions "Concerto for Philodendrum and Pothos", he had no idea that plants could also produce sounds.

Plants exposed to drought stress have been shown to experience the phenomenon of cavitation: this is the mechanical breakage of the continuous xylem water column that occurs when the tensile strength of the column is exceeded (Jackson G, Grace J 1994)[17] and is accompanied by the buildup of mechanical pressures which, upon release, lead to elastic wave propagation away from the stressed zone. These waves are acoustic emissions and Milburn and Johnson first detected them as audible vibrations (< 20 kHz) by fixing petioles of dehydrating leaves of diverse plant species on a phonograph pick-up needle.[18] Past research and the current state of the art about detection of acoustic emissions as a measure for drought-induced cavitation have been reviewed by De Roo et al. and what arises from this review is that vibrations have always been recorded by means of connection of the recording device directly to the plant; thus we cannot reveal the extent to which these vibrations could be sensed at a distance from the plant.[19]

The possibility that plants emit airborne sounds had slightly been explored until an investigation by Khait and colleagues came to light in 2019: plants emit ultrasounds ranging between 20 and 150 kHz when exposed to drought and stress from cutting. The scientists found that tobacco (*Nicotiana tabacum*) and tomato (*Solanum lycopersicum*) plants, when stressed, produce remotely detectable ultrasonic sounds that could potentially be heard by other organisms (they could be detected from a distance ranging between 3–5 m by mammals and insects).[20] Furthermore, the researchers also showed that the emitted sounds carry information about the physiological state of the plants; thus, by developing and training machine learning models, they achieved high accuracy (about 99,7%) in detecting a plant condition from a distance by listening to its sound emissions. This could evidently have significant impact on agriculture, especially since the tested plants were tobacco and tomato, which are broadly farmed.

The joint link

Previous studies have already shown that trees or plant organs produce sounds through cavitation when exposed to drought stress,[14,21] and this signal is like an alarm to nearby plants of the possible risk of water shortage. The roots can sense that water is lacking and transmit the signal to the plant so that it prepares itself by lowering the water potential to draw more water from the soil, or by sending hormonal protection signals such as ABA. But, as mentioned above, they also seem to be able to move toward a source of water following the vibration, if its presence is perceived.[22]

On the other side, mechanical stimulus (i.e. mechanical damage or the pressure gradient generated by the wind) is another signal like drought to which the plant can respond in many ways. The response to this physical stimulus involves the mechanical sensor system. A thorough review by Farmer et al. argues that mechano-stimulation, due to touching and wounding, induces an electrical activity that causes a rapid collapse of the membrane potential (i.e. a decrease of electrical field strength across membranes) that can be coupled to the production and/or action of jasmonate or ethylene.[23]

Given that sound is a wave of pressure (therefore akin to the mechanical stress) that can be propagated through a solid, liquid or gaseous medium, there can be recognized similarities in the physical properties of touch and sound. So far, although it is not yet fully understood whether plants can respond to sound by perceiving it for what it is, or by perceiving it as a mechanical wave transmitted through the air or soil, some similarities also in the responses can be noted. When the Arabidopsis hair cells are pressed and brushed in several ways to mimic insect alighting on a leaf or crawling over it, they showed an active mechano-sensing function: in fact, they display an early warning system based on toxin synthesis and perhaps release that are enhanced above constitutive levels, so as to trigger a rapid buildup of toxins in the presence of herbivore attack and at the same time to minimize the costly accumulation of toxins in the absence of it.[24]

Unlike thigmo-responses, which have been investigated since Darwin's time, studies on plants' sensitivity toward sound have only recently gained attention. The idea that sound and music can have beneficial or harmful effects on living beings is known since the Greek and Roman times.[25] To unravel the specific physiological/molecular induced response to sound in plants, they often are subjected to a single-frequency stimulus. Researchers agree in thinking that a single sound frequency is un-natural, but it represents a good way to observe changes in metabolic activities such as enzyme activation and hormonal changes,[26,27] and to lead to a better knowledge of the ecological significance of sound perception in plants' life.

Conclusion

For further research, VOC emissions should be considered a viable mechanism that plants display in response to sound stimuli, this being of mechano-nature. This paper illustrated the information available on plant mechano-sensing systems, emphasizing the apparent discrepancy between subjecting plants to touching and wounding stimuli and subjecting plants to sound waves. As elucidated so far, both mechano-stimuli result in changes in plant physiology that sometimes lead to VOC emissions. The airborne signals could serve as a vocabulary that might help us gain better insight into plant sensory biology and, by comparison, into animal biology. From an applicative point of view, in-depth knowledge of the "VOC language" could be proficiently harnessed to bio-monitor and stimulate the biosynthesis of target metabolites thus obtaining clean and bioactive enriched products.

Disclosure of Potential Conflicts of Interest

No potential conflicts of interest were disclosed.

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