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CORRESPONDENCE

The complex interaction between plants and acoustic signals: friends or foes?

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Plant emit acoustic signals under stress conditions

Plants exhibit significant alterations in their phenotypes, including in shape, color, and smell, in response to stress (Potters et al. 2007). Several signals through which plants communicate with their environment are already known. Plants constantly communicate with each other and their surroundings in order to adjust their morphological and physiological characteristics (Kessler et al. 2023). During stressful situations, plants release root exudates and different volatile organic compounds (VOCs), which mediate the plant-plant interactions (Khashi u Rahman et al. 2019, Ninkovic et al. 2021). Like other organisms, plant research has also entered into the world of acoustics, which suggest that plants could also be using sound signals to communicate (Hussain et al. 2023; Khait et al. 2023; Son et al. 2024). However, acoustic vibrations, which act as important cues between plants and their environment, have, to date, not been studied in depth. Importantly, plants sense certain acoustic signals and respond to them accordingly (e.g., flowers produced sweeter nectar when exposed to playback sound) (Veits et al. 2019) (Fig. 1). Vibrations in plants can trigger cellular signaling mechanisms in response to both abiotic and biotic stimuli (Demey et al. 2023; Appel and Cocroft 2023). When plants are exposed to drought stress, a cavitation process takes place due to air bubbles forming, expanding, and finally rupturing in the lumen of xylem vessels, causing vibrations (Cochard et al. 2013). A loss of cohesion between water molecules in the volume of xylem conduits (homogenous cavitation) or a loss of adhesion between conduit walls and water (homogeneous cavitation) could be the potential mechanisms for the initiation of cavitation. During wound stress, plants emit vibrations in accordance with the gas dynamics process, in which a quick and significant air-seeding through all the trachea in the cut plant occurs. Such plant-emitted airborne vibrations can trigger a quick response in nearby plants and animals (Hussain et al. 2023).

Until recently, the ability of plants for airborne sound emission under stress remained enigmatic. A recent ground-breaking discovery showed that plants emit informative airborne sound (20–100 kHz) under stress, providing environmental information to nearby organisms (Khait et al. 2023). Influencing the behavior of nearby organisms may in turn benefit the plant emitting the signal (Khait et al. 2023).

These ultrasonic clicking or popping sounds are beyond human perception but could be detected by other mammals and insects from a distance of 3–5 m (Khait et al. 2023). Also, there is remarkable proof that the vibrations released by insects spark defense reactions in plant leaves (Appel and Cocroft 2014). For further verification, Khait et al. (2023) subjected two plant species, *Solanum lycopersicum* (tomato) and *Nicotiana tabacum* (tobacco), to cutting (wounding) and drought stress in a controlled acoustic chamber. Two microphones placed 10 cm apart were directed at each plant to investigate their sound emissions. Acoustic sounds from the plants were detected both in the acoustically isolated environment and in a greenhouse. The plants exposed to drought and cutting injury emitted airborne sound with a respective average of 35.4 and 11.0 kHz for tomato and 25.2 and 15.2 kHz for tobacco plants. Interestingly, no airborne

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Key message Plants emit sound signals when exposed to stress according to severity and type. External sounds significantly affect plant growth, development, and environmental adaptation.

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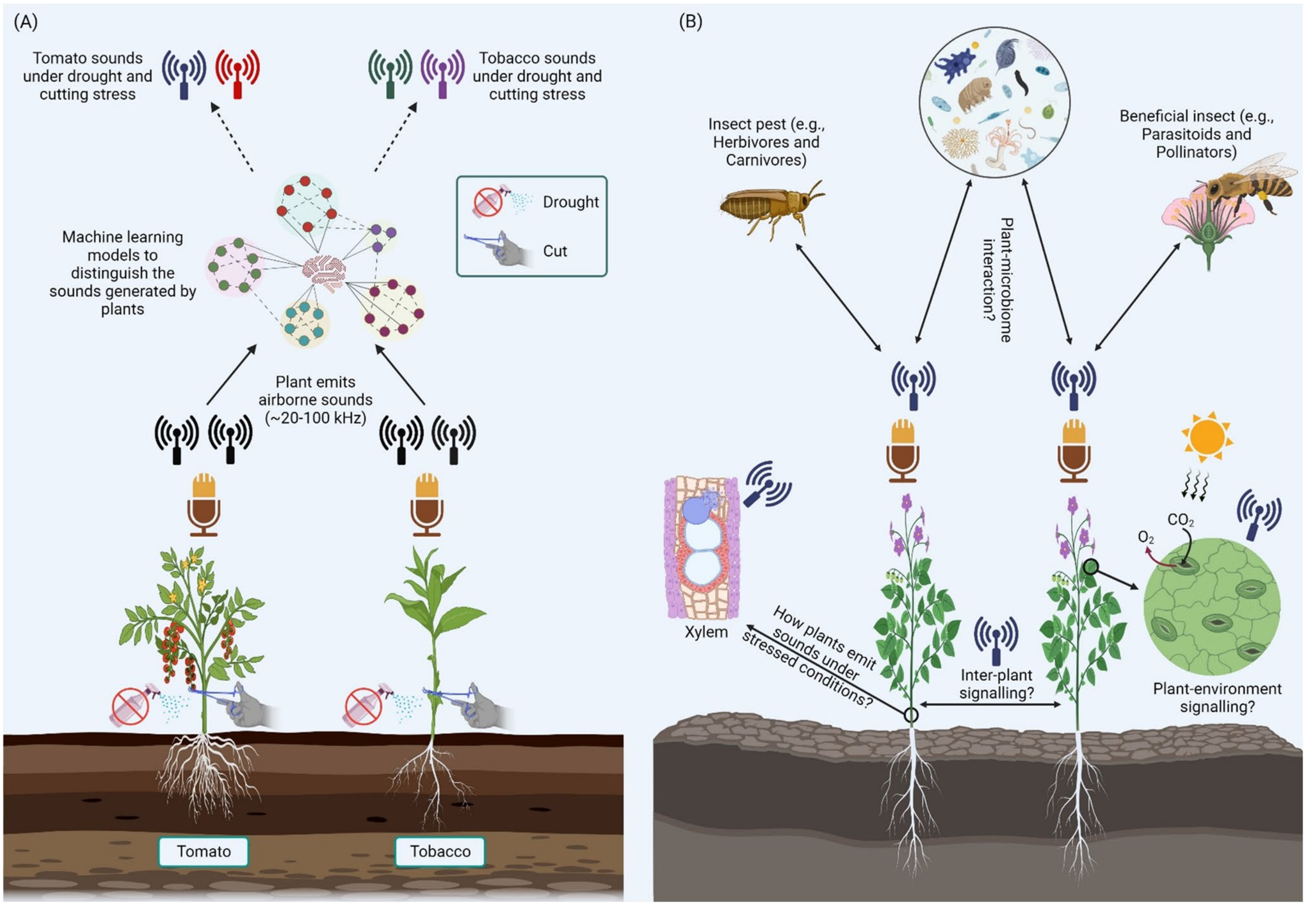

Fig. 1 Plants emit airborne sound signals in response to different stressors, which may be heard by insects or other organisms. **A** Tobacco and tomato plants were grown and subjected to drought and cutting stress. Both plants were exposed to these stresses; they emitted ultrasonic airborne sound signals with the range of ~ 20–100 kHz. A machine learning algorithm model system was applied to identify the emitted sounds by stressed plants. Sound waves with different colors represented the specific sound frequency linked with stress conditions and plant species. **B** What is the full extent of mutualistic interactions of the sound perception mechanism? It remains unanswered whether plant communication through emitted ultrasonic sounds under stress conditions may, in response, induce alterations in neighboring plants and other organisms such as insects and pollinators. Stressed plants help in the induction of the cavitation process, resulting in the sound emission; however, the detailed mechanism of this sound emission remains unanswered. Images prepared with BioRender (www.BioRender.com)

sounds were detected in the control plants over 500 h of recordings. In tomato plants, the average peak sound intensity was 61.6 dBSPL (decibels sound pressure level), and for tobacco plants it was 65.6 dBSPL under drought stress. The average peak sound intensity emitted by cut plants was 65.6 dBSPL and 63.3 dBSPL for tomato and tobacco plants, respectively (Khait et al. 2023). Sounds were emitted with a range of intensities by corn and wheat plants under dry stress, and in henbit, grapevine, and cactus plants, also under cutting injury. Moreover, similar sound emissions were also recorded in tobacco mosaic virus (TMV)-infected tomato plants (Khait et al. 2023). However, a limited number of plant species and conditions (cutting, drought, and TMV infection) were explored in the study. A wider range of plant diversity from different families with other potential conditions must be tested for the same. Overall, the perception in the mode of mechanism of sound emission is at a preliminary stage and requires further investigation.

There is startling proof that plants respond to sound emissions that increase their resistance against drought and diseases, thereby enhancing agricultural production (Demey et al. 2023). These unique vibration sounds released by different plant species could have novel evolutionary and ecological inferences for plant development in biological communities. Recently, the application of a machine learning approach has revolutionized the field of bioacoustics monitoring (Neito-Mora et al. 2023; Kyalo et al. 2025). Machine learning models developed algorithms to distinguish the sounds generated by drought-stressed, cutting injured, and control plants as well as background greenhouse noises.

The generated sounds showed a bimodal peak pattern along the day, with a main peak during the morning (8:00–12:00) and a smaller peak during the afternoon (16:00–19:00), representing the estimated hours of natural daylight (Khait et al. 2023). Previous studies have shown that such "midday depression" may be potentially linked to stomatal conductance (Gosa et al. 2022). Most emitted plant sounds were recorded when the volumetric water contents (VWCs) of the soil were < 0.05, whereas no emission sound was recorded when the VWCs were $^{>}0.1$, suggesting that these two are strongly associated. A high correlation was found between the plant transpiration rate and the number of sound emissions per hour (Khait et al. 2023). A similar pattern occurred in grapevines (Dayer et al. 2021).

Cavitation in the stem can be a potential mechanism for the emission of sounds. Plants exposed to cut wounding, drought, and TMV infection displayed xylem cavitation. During cavitation, air bubbles form, expand, and move through the xylem, causing sound vibrations which can be identified by specific instruments (Jackson and Grace 1996). In different plant species, the trachea diameter is potentially associated with the sound frequency, with lower sound frequency being released with larger tracheas (Khait et al. 2023). Previous studies support this negative association between resonance frequency and xylem dimension (Dutta et al. 2022). Sound emission in response to cutting injury and drought stress varies given the diverse rate of air intrusion. Drought stress involves a lower rate of air intrusion via the trachea, whereas cutting injury is characterized by a high rate of air intrusion. Consequently, drought stress leads to a slow and delayed formation of air bubbles, while cutting injury leads to a short-lived and rapid formation of air bubbles in the xylem. The occurrence of the emission of sound and its duration also varies among the types of stress. In cut (wounded) plants, sound emission persists for a shorter time compared to dry stressed plants (Khait et al. 2023).

While the understanding of the underlying mechanisms by which plants produce airborne sounds remains enigmatic, the efficient use of machine learning systems to differentiate diverse stress based on sounds emitted by plants (Khait et al. 2023) has provided a breakthrough that can have a potential role in precision farming. These interesting results provide a starting point for answering crucial ecological and evolutionary questions concerning plant acoustics.

Sound sensing in plants

Several studies have demonstrated that external acoustic signals significantly affect plant growth and development and also guide adaptation in different environmental conditions (Hassanien et al. 2014; Mishra and Bae 2019; de Melo 2023; Demey et al. 2023; Pagano and Del Prete 2024). Historically, the plant acoustics research started with speculation and debatable research claiming a positive impact of music on plant performance (Braam and Davis 1990).

Plants have been proposed to sense sound vibration at the individual organ level including leaves (Appel and Cocroft 2014), flowers (Veits et al. 2019), and roots (Gagliano et al. 2017; Rodrigo-Moreno et al. 2017). However, whether sound is sensed by a specific plant organ or perceived by individual plant cells requires further investigation. In addition, researchers have demonstrated that trichomes are involved in mechanosensing (Zhou et al. 2017; Matsumura et al. 2022) and also perceive sound emissions (Liu et al. 2017). A recent study showed how sound vibrations produced by birds, bats, and other insect herbivores affect the movement of tomato trichomes (Peng et al. 2022). However, these results exhibit the ability of plants to emit a sound at a short distance and with a loud intensity. Sound perception by plants can also be linked through vibration-triggered alterations or mechanical ion signaling in the extracellular matrix (Anderson et al. 2001; Shih et al. 2014; Son et al. 2024). However, sound perception of these mechanisms is not yet confirmed, which opens a particularly intriguing question on the potential mode of action. Recently, Nardini and coworkers (2024) also indicated that sound sensing and communication by plants is purely speculative and needs more experimental evidence.

At the molecular level, sound-induced Ca^{2+} signatures, an increase in reactive oxygen species (ROS) concentration, K^+ fluxes, and a variety of genes have been identified (Ghosh et al. 2016; Ghosh et al. 2017; Rodrigo-Moreno et al. 2017). As shown in Fig. 2, it has been hypothesized that acoustic emission triggers the Ca^{2+} channel, which stimulates the opening of channels of plasma membrane ions, such as K^+, while it also activates the expression of sound-responsive genes (Rodrigo-Moreno et al. 2017; de Melo 2023). Subsequently, K^+ is delivered to the extracellular matrix (ECM), and a burst of ROS occurs. Both Ca^{2+} and ROS may trigger the differential expression of several sound-induced gene categories (Ghosh et al. 2016; Demey et al. 2023). In *Arabidopsis* root cells, an increase of Ca^{2+} levels was observed upon acoustic stimulation (Rodrigo-Moreno et al. 2017). Similarly, a strong sound wave stimulated the Ca^{2+} redistribution within *Chrysanthemum* callus cells (Liu et al. 2001). Likewise, a Ca^{2+} involvement in strawberry callus growth upon sound stimulation was also noted (Wang et al. 2019). However, more detailed investigation is required to assess if acoustic vibrations and their stimulation are marked by only Ca^{2+} signatures. A study by Jung et al. (2020) showed that acoustic vibrations significantly triggered an epigenetic modification

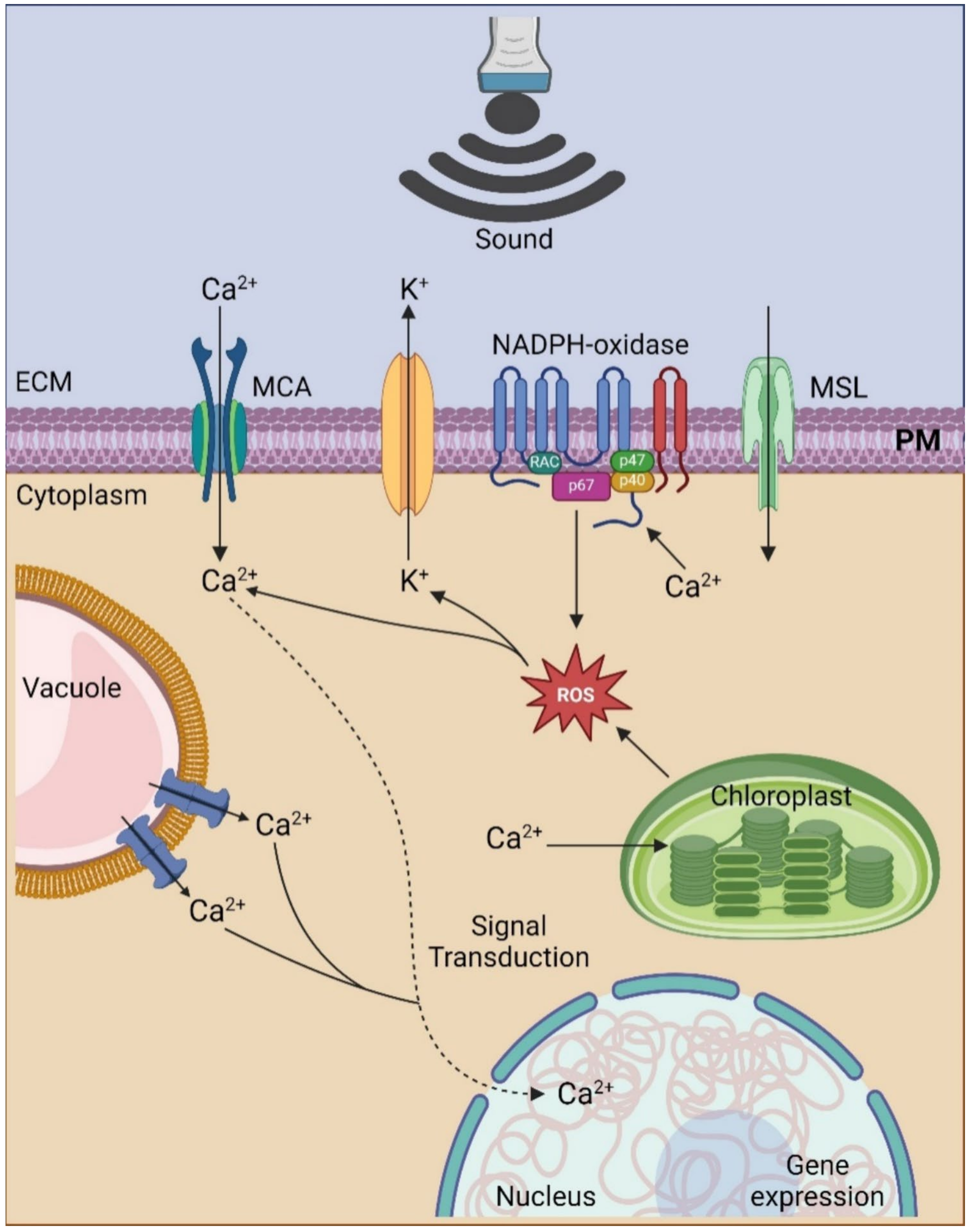

Fig. 2 A model summarizing the molecular events triggered inside a plant cell in response to sound stimulation. MSL and MCA are the two potential channels located in the plasma membrane that facilitate the sound-mediated influx and efflux of Ca^{2+}. It is hypothesized that sound stimulation causes a rapid increase in cytosolic Ca^{2+} levels. Also, there is an increased efflux of K^+, leading to a decrease in cytosolic K^+ levels as K^+ is transported from the cytosol to the ECM. Sound activates Ca^{2+} channels and produces respiratory burst oxidase homologs (RBOHs), resulting in a burst of ROS in the cytosol. ROS, which is increasingly synthesized in sound-treated cells, facilitate further activation of both Ca^{2+} and K^+ channels. The generation of $Ca.^{2+}$ transients, whether from the ECM or the vacuole, may trigger distinct signaling cascades that lead to an upregulation of gene expression. MSL, MscS-like; MCA, Mid1-complementing activity; ECM, extracellular matrix; ROS, reactive oxygen species. Images prepared with BioRender (www.BioRender.com)

to the DNA packaging protein Histone H3 (HK327me3) in *Arabidopsis* roots. Likewise, sound vibrations were observed to influence histone modification, particularly at ethylene biosynthesis in tomato fruit ripening genes (Kim et al. 2023). However, whether these sound vibrations-induced epigenetic modifications are passed on to the next generation or not still needs to be investigated. In future research, sound-induced epigenetic changes will also have to be examined across different plant species.

Phytohormones are important regulatory biochemicals which steer the plant growth and development in diverse environmental cues (Ohri et al. 2015). In *Arabidopsis*, significant changes in gene expression related to hormonal levels were observed upon exposure to sound vibrations (Ghosh et al. 2016). In *Arabidopsis thaliana* root, exposure to sound waves was also observed to upregulate the auxin biosynthesis genes, whereas the cytokinin biosynthesis genes were downregulated (Kim et al. 2021). Additionally, sound stimulation induced ethylene biosynthesis was detected in berry skin and grapes in the early stage of ripening (Yamazaki et al. 2021). Decoding the effects of sound vibration on tissue/species specific ethylene biosynthesis would help to regulate fruit ripening and shelf-life applications in agriculture. Finally, a better understanding of how the different phytohormones are involved in mediating sound-induced responses is warranted.

Conclusion and future recommendations

In a nutshell, plants emit airborne sounds upon exposure to abiotic and biotic stimuli, which depend on the severity and type of the stress as well as on the plant species. This sound emission may assist as a cue to animals and plants in the neighboring environment. To obtain novel and more comprehensive insights on sound emission by plants under stress conditions, extensive research on other plant species and other stresses is still required. For example, under nutrient deprivation, crops may produce specific sound emissions, which could be related to air intrusion in the xylem and thus the plant's water status (Bhandawat and Jayaswall 2022). Such research may facilitate optimizing plant nutrient managing practices for environmental and ecological sustainability. In future, a deeper study on plant acoustics must involve molecular mechanisms, including plant–soil feedback, plant-microbiome-animal interactions, and inter and intraspecific plant interactions for a better understanding of how plants interact in the ecosystem.

Although Khait and co-workers (2023) revealed that the plants emit airborne sounds when exposed to abiotic and biotic stresses, several outstanding questions remain unresolved and fragmented. These include:

1. How do plants emit sound? It was proposed that cavitation is important for sound emission (Khait et al. 2023). However, there is only a limited study between the observed sound frequency and the cavitation, and this requires further investigation.
2. How can insects perceive the airborne sound signals produced by stressed plants? Sound signals could be detected by insects from 3 to 5 m (Khait et al. 2023) and stressed plants are particularly susceptible to herbivore insects (Hamann et al. 2021). New emerging omics approaches should be implemented by using recorded sound emitted by plants on insects to identify the specific modifications in their expression profile.
3. Do plant-emitted airborne sounds influence plant-pollinator communication? Plants experience vibrations on their surface through surface-borne vibrations by insects that live on plant parts (Appel and Cocroft 2023). The airborne sound emitted by insects and the ability of plants to react to these sounds as well as emitting acoustic signals themselves suggest that sound may play a key role in plant–pollinator interactions. Plants respond to pollinator sounds in an ecological manner, which includes bidirectional feedback between plants and pollinators (Veits et al. 2019). This could potentially help to improve the pollination efficiency in changing environments. Hence, a detailed study on both insect pollinator and plant sounds should be performed to gain novel insights into plant–pollinator communication. Future research encompassing the rediscovering of acoustic signals made by plants may provide a model system to uncover the molecular mechanism.
4. Is there any connecting link between plant microbiome and airborne sound emitted by pathogen-infected plants?
5. A deep understanding of how plants perceived the sound signal and how it is transported to the cellular or organ level within the plant is necessary.
6. At the molecular level, knowing how the different phytohormones are involved together in sound-mediated responses is crucial.
7. How can advanced research be performed to target plant–environment communication for potential outcomes?

The capacity to produce and perceive sound signals by plants is a new area of plant research. Addressing the unanswered queries mentioned above will lead to develop an advanced plant acoustic research, as well as it will also permit its value and integration in precision agriculture (Fernandez-Jaramillo et al. 2018; Király et al. 2025).

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Declarations

Competing interests The authors declare no competing interests.

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